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Anthropogenic transformation of the terrestrial biosphere

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Human populations and their use of land have transformed most of the terrestrial biosphere into anthropogenic biomes (anthromes), causing a variety of novel ecological patterns and processes to emerge. To assess whether human populations and their use of land have directly altered the terrestrial biosphere sufficiently to indicate that the Earth system has entered a new geological epoch, spatially explicit global estimates of human populations and their use of land were analysed across the Holocene for their potential to induce irreversible novel transformation of the terrestrial biosphere. Human alteration of the terrestrial biosphere has been significant for more than 8000 years. However, only in the past century has the majority of the terrestrial biosphere been transformed into intensively used anthromes with predominantly novel anthropogenic ecological processes. At present, even were human populations to decline substantially or use of land become far more efficient, the current global extent, duration, type and intensity of human transformation of ecosystems have already irreversibly altered the terrestrial biosphere at levels sufficient to leave an unambiguous geological record differing substantially from that of the Holocene or any prior epoch. It remains to be seen whether the anthropogenic biosphere will be sustained and continue to evolve.

Keywords: human-dominated ecosystems; land-use change; global change; agriculture; biodiversity; biogeochemistry

1. Introduction

Humans have significantly altered nearly all of Earth's systems, including its atmosphere, hydrosphere, lithosphere and biosphere [1–9]. Taken together over the past 300 years, these anthropogenic changes, especially in atmospheric chemistry and global climate, provide strong evidence that humans have altered the Earth system sufficiently to indicate the emergence of a new geological epoch: the Anthropocene [9–11].

This paper investigates just one of these many anthropogenic changes as an indicator of the Anthropocene: the direct effects of human populations and their use of land on the ecological patterns and processes of the terrestrial biosphere. Specifically, this paper explores the hypothesis that changes in the terrestrial biosphere made directly by human populations and their use of land

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represent the emergence of a suite of novel geologic processes in the Earth system comparable in scale with those used to justify the major divisions of geologic time [12].

In this investigation, climate-induced changes in the biosphere are ignored; the climate-driven patterns of the biosphere are held constant at contemporary levels across the study period, the eight millennia prior to 2000 CE. Clearly, this is a major omission, albeit one that is common in studies of Holocene land use [13,14]. Even the relatively stable climate of the Holocene has varied substantially, causing profound geographical shifts in the biosphere such as the green Sahara' period of the early Holocene [15]. However, these changes have yet to be mapped globally in adequate detail to include here [15]. Recent anthropogenic changes in global climate are also driving changes in the terrestrial biosphere [16] and these climate changes are partly the result of land-use changes that have altered greenhouse gas and aerosol concentrations in the atmosphere and Earth's albedo and surface heat balance [17]. Even in the mid-Holocene, human use of land may have significantly altered greenhouse gas concentrations and Earth's climate trajectory [14,18].

Anthropogenic changes in global climate may ultimately drive changes in the biosphere that are far greater than any of the direct effects investigated here [19]. However, massive changes in the biosphere mediated by climate change are not novel in the Earth system. For example, the biogeographic shifts caused by glacial cycles are rarely considered sufficiently novel to merit distinct epochs in the geologic record [20]. Current anthropogenic rates of climate change may exceed any experienced by most extant terrestrial species and might therefore cause a mass extinction [21], but this has yet to occur and will ultimately depend on whether anthropogenic global climate change is brought under human control [22].

Human populations and their use of land have already transformed most of the terrestrial biosphere directly [4,5,7]. In this paper, spatially explicit global estimates of human populations and their use of land during the past 8000 years are combined with approximations of the ecological changes caused by these to evaluate the global extent, duration, intensity and novelty of direct anthropogenic changes in the terrestrial biosphere across the Holocene.

(*a*) *The novelty of humans and human systems*

Any species of sufficiently large population will transform ecosystems merely by consuming the resources needed to sustain itself [23], and humans are certainly changing the biosphere in this way [2]. Yet this does not begin to explain human transformation of the terrestrial biosphere [1,2,24]. Humans differ profoundly from every other species in the way we transform ecosystems, and our differences are partly responsible for our large populations [25].

Three differences stand out. First, humans are ecosystem engineers—species like the beaver that alter their environment by mechanical or other means [23,25]. Second, we are capable of manipulating a wide array of powerful tools in this effort, including fire [26,27]. Third, we are social creatures capable of collective action and social learning in our ecosystem engineering and other activities [27–29]. Separately, none of these capacities is novel in the history of the biosphere. It is their realization within a single species that has driven the rise and evolution of human systems that are far more complex, powerful and novel in the biosphere than even the sum of their billions of individual human parts [2,24,30–32]. Even with a population of seven billion, *Homo sapiens* is not an entirely novel force of nature. But human systems are [32].

(*b*) *The emergence of human systems as a novel force for biospheric change*

Human systems have evolved over millennia, within which at least three major stages of development may be recognized. The first is the Palaeolithic human system, in which early humans, organized into tribes, began to use stone tools (*ca* 2.5 Ma) and fire (*ca* 0.7–1.5 Ma) to improve their hunting and gathering livelihoods, with populations at this stage remaining on the order of several million, beginning in Africa and ultimately spreading across most of the terrestrial biosphere by 0.1–0.015 Ma [27]. Second is the Neolithic, or agricultural human system, in which humans, beginning approximately 0.01 Ma, learned to domesticate plants and animals for food (and in the case of livestock, as a human labour substitute), while developing ever more powerful tools for ecosystem engineering and transport, and ever more sophisticated and extensive social systems, including the nation state, the marketplace and symbolic communications, with populations at this stage ultimately covering the vast majority of the terrestrial biosphere and reaching 900 million by 1800 [33]. The third stage is the industrial human system, in which humans began to use fossil fuels for energy, applied scientific methods in developing technologies that have dramatically enhanced human survival rates, including hygiene, antibiotics and synthetic nitrogen fertilizers, and formed global trading systems and social networks [34,35].

While this three-stage model vastly oversimplifies human history, it enables a rough assessment of human systems as a force transforming the terrestrial biosphere before and during the Holocene. Palaeolithic human systems never sustained large human populations [36]. Yet human systems at this stage of development became established across the vast majority of the terrestrial biosphere and still persist in some regions [29,37]. Moreover, their biospheric influence was far greater than would be presumed from their population size because their use of tools and social learning revolutionized their success in hunting and gathering [25,27,29]. Palaeolithic humans engineered ecosystems using fire and sometimes other tools to clear vegetation [25,38–41], and this, combined with their effective hunting technologies, may have helped cause the extinction of megafauna across most of the terrestrial biosphere [42], with profound ecological consequences resulting from the loss of these keystone species [43]. Nevertheless, Palaeolithic human systems did not transform ecosystems in ways entirely novel to the biosphere; enhanced fire rates and megafaunal extinctions are both common effects of climate variation that can be caused by glacial cycles [41,42]. While Palaeolithic human systems did indeed transform most of the terrestrial biosphere, this was mostly in directions the biosphere had already seen before. Agricultural human systems are another matter.

Agricultural human systems set the stage for sustained human population growth for millennia, from a few million in 10 000 BCE to billions today [33,44]. More importantly, these systems are sustained by an entirely novel biological process—the clearing of native vegetation and herbivores and their replacement by engineered ecosystems populated with domesticated plant and/or animal species whose evolution is controlled by human systems [25,45,46]. Were these agroecosystems to attain sufficient global extent, endure long enough and alter ecosystem structure and biogeochemical processes intensively enough, these alone may represent a novel transformation of the biosphere justifying a new geological epoch.

Industrial human systems, in just two centuries, have already introduced at least three clearly novel biospheric processes: the use of fossil energy to replace biomass fuel and human and animal labour, revolutionizing human capacity for ecosystem engineering, transport and other activities [11]; the industrial synthesis of reactive nitrogen to boost agroecosystem productivity [47,48]; and, most recently, genetic engineering across species [49]. This is not to mention advances in hygiene and medicine that have increased human life expectancy [50], the production of numerous synthetic compounds [51], including a wide variety used to control undesired species [52], and a long list of other anthropogenic changes that impact ecosystems [2,4]. Industrial human systems are far more strongly connected globally and tend to evolve more rapidly than prior social systems, accelerating the pace of social change, material exchange and tool development, and the tempo of human interactions with the biosphere—a change in the rate of biospheric change that may be novel in itself [53].

(*c*) *The global challenge: anthropogenic complexity meets natural variability*

It remains a challenge to assess the biospheric changes caused by direct interactions between human systems and ecosystems, even without considering climate feedbacks. First, the novelty and intensity of anthropogenic changes in ecosystems must be judged against a background of considerable natural variation in ecosystem form and process. At global scale, natural ecosystems vary in response to global patterns in climate, soil fertility (geology), fire regime and herbivore types [54,55]. These processes interact to form the classic biome patterns that have been classified, mapped and quantified globally by a variety of methods (e.g. [54,56,57]). While climate changes have altered the global patterns of the terrestrial biomes during the Holocene [15], this analysis will consider these as stable, using the potential vegetation patterns of the terrestrial biosphere *ca* 2000 as reconstructed by Ramankutty & Foley [57] as a benchmark for the natural global patterns of the terrestrial biosphere across the Holocene.

Second, human interactions with ecosystems are exceedingly complex and dynamic [31,58–61]. Humans alter terrestrial ecosystems both intentionally and unintentionally, and these alterations depend on interactions between population density, technical capacity, mode of resource use and the use opportunities afforded by native and transformed ecosystems, with all of these factors interacting and evolving across time and space within and across human systems and the biosphere [7,60–63]. As with the classic biomes, this complexity may be reduced by applying empirical methods to global data to map and classify the most globally significant ecological patterns produced by sustained direct human interactions with ecosystems [7]. This has been accomplished recently as a function of land use and human population densities, yielding anthropogenic biomes, or anthromes [7,64].

2. A simple framework for assessing human systems as agents of biospheric change

Figure 1 stratifies the wide global range of natural and anthropogenic variations in ecosystem form and process into a limited number of categories that can be mapped and measured over time. In this framework, natural variations in the biosphere are divided into three basic climate-driven biome categories, within which five levels of anthrome development are recognized. Anthrome levels are classified using the system of Ellis *et al.* [64], including wildlands without human populations or use of land, densely settled anthromes with populations greater than or equal to 100 persons km^{-2} (combining the 'village' and 'dense settlement' anthrome levels of [64]), cropland and rangeland anthromes with greater than or equal to 20 per cent agricultural use in crops or pastures, respectively, and seminatural anthromes with less than 20 per cent of their area in use for agriculture or urban settlements.

Using this framework, global patterns of natural and anthropogenic variation across the biomes and anthromes are explored, along with the causes of local variations within them. Next, anthropogenic changes in ecosystem form and process are evaluated within and across the biomes and anthromes in terms of their intensity and novelty. Finally, the extent and duration of each anthrome within each biome are estimated for 10 time periods between 6000 BCE and 2000 CE. Together, these data are used to test the hypothesis that humans have irreversibly transformed the terrestrial biosphere by introducing novel biospheric processes globally, producing a distinctive geological record.

(*a*) *Global variation across the biomes and anthromes*

Anthromes and biomes do not vary independently. Humans preferentially seek out, use and engineer ecosystems in relation to the different opportunities for use they offer in terms of their potential productivity and other ecosystem factors [7,63,65]. For example, temperate woodlands are now used preferentially for cultivated crops, and shrublands mostly for rangelands [64]. Thus, factors that predict global patterns in the biomes also help to predict global patterns in the anthromes.

Human population density is a key factor in global patterns of anthrome emergence, transitions between anthromes and variations in ecosystem form and process within anthromes [7]. Population density in a given landscape is a path-dependent function of human arrival time and the duration [29] and rate of population growth (including migration), and this in part is related to the productivity of native ecosystems [7,63,66]. In agricultural systems, humans tend to use land more intensely as population densities increase, enhancing the productivity of land both by increasing labour inputs and by adopting more labour-intensive and labour-substituting technologies, the increased productivity in turn supporting further population growth [67–71]. For example, increases in population density may push low-density populations subsisting on shifting cultivation or extensive grazing into continuous cultivation, causing seminatural anthromes to become croplands, then drive the increasing use of fertilizers and irrigation within croplands, and ultimately cause croplands to shift to densely settled anthromes with declining agricultural areas (figure 1; [7,62,64,67–70,72,73]).

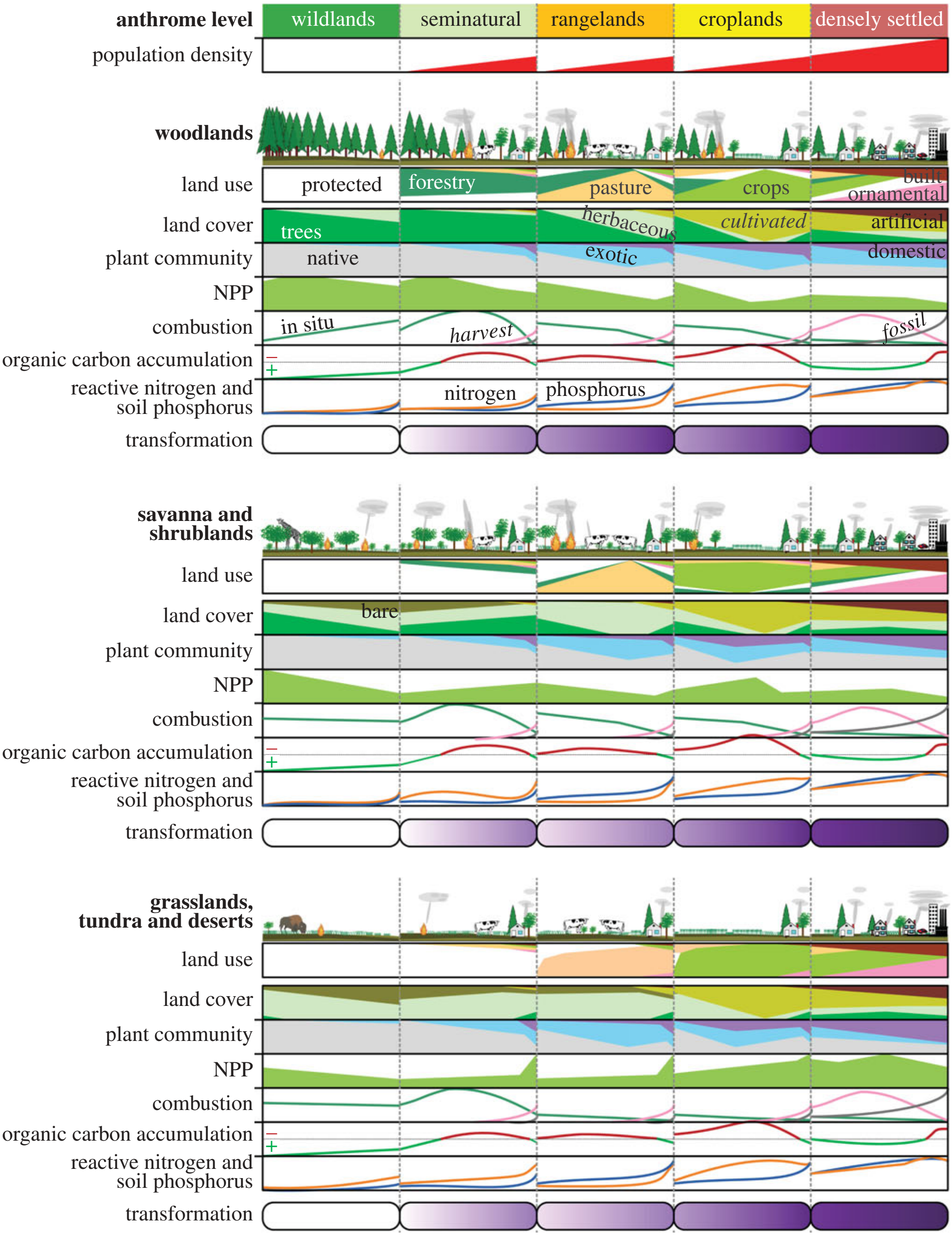

Figure 1. Conceptual framework for anthropogenic transformation of terrestrial ecosystems. Ecosystem variables are described in table 1. Trends in all variables are scaled to the typical range within each category of biome; trends within anthromes relate to variations in population density (top) and land use in each biome. Net intensity of novel anthropogenic transformation across ecosystem variables is indicated at bottom for each anthrome level in each biome. Trends are illustrated for both agricultural and industrial systems. Protected land use refers to lands free of agriculture and settlements by institutional means or by absence of demand, as in frontier regions and preserves. Ornamental land use includes yards and parks managed for aesthetic and recreational use. NPP = net primary production.

In industrial human systems, traded commodities replace local production in sustaining most human populations, making technological advances in agroecosystem engineering and trade, including mechanization, synthetic fertilizers and fossil-fuelled global transport, ever more important as global drivers of land-use change and intensification [33,62,74]. These technologies and economic systems tend to drive relationships between populations and land in the opposite direction of agricultural human systems, with less populous seminatural anthromes and wildlands being preferentially and completely converted directly to intensively cultivated croplands, and moderately populated agricultural areas tending either to lose populations, or to transition to densely settled anthromes with agriculture replaced by built infrastructure and associated yards, parks and protected lands [62–64,70,72,74].

(*b*) *Variation within the biomes and anthromes*

Ecosystem form and process vary naturally within and across landscapes in response to variations in terrain, hydrology, microclimate, dominant species, and the frequency and stage of recovery from natural disturbances including fire [54,55,75–77]. Humans take advantage of these pre-existing natural variations by extracting resources and engineering ecosystems in response to the differing ecological opportunities for use offered by different parts of landscapes [7,63,66,78,79]: for example, by clearing and farming the wooded plains first and using them more intensively, leaving the steep hillsides for grazing, hunting or shifting cultivation [59,63,72,78,79]. Humans then build on the ecological legacies of this sustained use, expanding settlements into the oldest croplands, terracing denuded hillsides for agriculture once land is scarce and abandoning agriculturally degraded lands to forestry or wildlife conservation [72,78]. Finally, human systems create novel anthropogenic patterns by interconnecting and expanding settlements and other infrastructure [80,81]. These three sources of natural and anthropogenic spatial variation combine to form complex and heterogeneous landscape mosaics characterized by diverse land uses and land covers that both conform to pre-existing natural patterns and further stratify and enhance them [7].

The mosaic structure of anthromes enables small areas of agricultural lands and settlements to transform the ecology of much larger areas, spreading human influence widely across the terrestrial biosphere [7,63,64,72]. Land use for agriculture and settlements tends to follow gentle terrain, fertile soils, surface water availability and other conditions that invite human use [50,63,82,83]. As a result, unused and less-intensively managed ecosystems, including planted forests, woodlots, parks, abandoned lands and reserves, tend to become embedded within used lands, left behind on hills and in other less-inviting environments [50,63,84]. While these embedded ecosystems may often resemble the undisturbed ecosystems of a biome, they are inevitably novel, even when never cleared or used directly, as a result of their fragmentation into smaller habitats within a matrix of used lands, anthropogenic enhancement or suppression of fire regimes, species invasions, air pollution and acid rain, hydrological alteration, and low-intensity human use for wood gathering, hunting, foraging or recreation [30,78,85–90].

Land-use patterns emerge as a complex path-dependent function of pre-existing natural variations in landscapes, human population dynamics, technologies, economic systems and their ecological results, all interacting strongly over time and space, with the duration of human occupation producing a strong legacy effect [29,91]. As a result, even where environmental and anthropogenic conditions are uniform, land-use patterns are often heterogeneous and hard to predict [50,61,91]. For example, large-scale transportation networks or other infrastructure can restructure vast plains, and large cities often include parks and even nature reserves. Nevertheless, when studied empirically, some general global patterns emerge in the fractional areas and types of land use within and across anthrome levels (top of each biome category in figure 1; [7]). These may be understood theoretically by combining natural variations within the biomes (wildlands at left in figure 1) with variations in population density (top), using a simplified model of land-use development in which: (i) the parts of biomes and landscapes most suitable for human use tend to be used and settled first, (ii) giving more time for their populations to grow and higher rates of growth, and (iii) land-use intensity increases as population densities increase, as does technical and economic development [7,62,63,72]. Figure 1 summarizes these global patterns, combining changes occurring in both agricultural and industrial systems.

3. Anthropogenic transformation of terrestrial ecosystem form and process

Humans alter ecosystems both by introducing novel processes and by altering pre-existing ones, producing a wide variety of geological and archaeological evidence, including changes in and altered spatial patterns of soil erosion, soil and sediment chemistry, sedimentation rates, isotope signatures, charcoal, artificial substances, and plant and animal remains (table 1; [4,30,35,46,78,92–94]). Ecosystem variables chosen for assessment here (figure 1 and bold text in table 1) produce geologically stable records within landscapes of novel anthropogenic processes (italic text in table 1 and figure 1) or anthropogenic changes in pre-existing processes, potentially enabling spatially explicit quantitative assessment of the scale and extent of anthropogenic transformation of the terrestrial biosphere [35,95].

Land cover is here defined from an archaeological perspective, differentiating surface areas covered by different forms of vegetation, soil management and artificial structures leaving geologically stable legacies (table 1 and figure 1; [78,92,96]). Relative changes in plant community structure indicate anthropogenic changes in biodiversity [97] caused by habitat loss and fragmentation, altered herbivory, fire regimes and other disturbances leading to local and global extinctions of native species [98], the introduction of domesticates for agriculture or ornamental use [46,78,94,99], and invasions by exotic species facilitated by ecosystem alteration, disturbance and human transport of propagules [86,90,99–102].

Changes in net primary production (NPP) are a classic general indicator of human alteration of ecosystem processes [103,104]. While the geological records of altered NPP within landscapes can be reconstructed only by proxy [105], they are used here to aid in general assessment of human transformation of ecosystems. Combustion processes often leave clear geological records and are important both ecologically and for indicating different stages of human systems, with Palaeolithic human systems often leaving records of enhanced fire rates

Table 1. Anthropogenic changes in selected terrestrial ecosystem variables and their potential geological indicators at landscape scale. Terms in bold are included in figure 1; novel anthropogenic ecological forms, processes, proximate causes and types of geological indicators are in italics.

	change variables	proximate causes	geological and archaeological indicators
Ecosystem form			
land cover	per cent land surface cover by **trees** and woody vegetation, **herbaceous** vegetation on uncultivated soils, naturally **bare** earth, ***cultivated*** soils and ***artificial*** structures (compacted, transported or artificial)	altered fire regimes (increase and suppression), land clearing, *tillage*, *forestry and ornamental plantings*, altered native and *domestic herbivore* populations, *construction of settlements and infrastructure*	plant remains (pollen, phytoliths, macrobotanical remains), *anthrosols*, altered soil structure and erosion, *artificial structures and materials*, skeletal remains (animals, humans; isotope signatures), *human artifacts*
plant community structure	relative abundance of **native**, **exotic** and ***domestic***ated species compared with undisturbed ecosystems	altered **land cover** (total habitat area and fragmentation), altered fire regimes, *enhanced introductions of exotics* (unintentional and *cultivated*), *domesticates*, altered native or *domesticated herbivore* species and populations, foraging	plant remains
Ecosystem process			
net primary production (**NPP**)	annual net carbon fixation by plants	*clearing* or *planting* forests, altered five regimes, *irrigation*, *fertilization*, biomass harvest, pest suppression, changes in native, exotic or *domestic plant and herbivore species* and population sizes	proxies: **land cover**, **plant community**, **reactive nitrogen** and **soil phosphorus**
combustion	relative annual carbon release by combustion of vegetation **in situ**, *harvested* ***biomass***, and ***fossil*** fuels	natural and anthropogenic forest and brush fires, use of fire to form *terra preta*, *harvesting of local biomass*, including *crop residues for fuel* or for *field preparation*, use of *fossil fuels*	extensive charcoal and *terra preta*, *concentrated ash* and *charcoal deposits*; *fossil fuel* $\delta^{13}C$ *signatures* in organic C fixed by local plants

organic carbon (C) **accumulation**	annual rate of organic C accumulation in soils and organic materials; **NPP** minus organic C combustion, ecosystem respiration and export	changes in **NPP**, decrease by biomass combustion and *export*, enhanced soil respiration from *tillage*, drainage (and *fertilizers, light irrigation*; these can also increase **NPP**), increased by *paddy flooding*	accumulations of organic C, δ^{13}C
reactive nitrogen (N)	reactive N concentration in soils	depletion by *biomass harvests*, increases from N-fixing legume *plantings*, manures (human and animal), ash and other wastes, *synthetic N fertilizers*, deposition from combustion of biomass and *fossil fuels*	organic N, N : C ratio, multi-isotope signatures (δ^{15}N, δ^{18}O in NO_3^{2-}) *near settlements* and *across agricultural lands*
soil phosphorus (P)	P concentrations in soil relative to undisturbed soils	loss by erosion and *biomass harvest*, increases from manures (human and animal), ash and other wastes, and *phosphorus fertilizers*	total P, organic P, labile P, P : C ratio, δ^{18}O in phosphates; *near settlements* and *across agricultural lands*
geomorphology	structural changes in land surface processes	clearing and leveling of fields, *construction of settlements*, *dams, drainage, irrigation, transport, mining*, etc.	*earthworks*, erosion features, altered soil horizons, sediment deposits
hydrology	altered water availability	*irrigation*, *drainage*, *impoundment* and *diversion* of water for *agriculture* and *settlements*	δ^{18}O, salt accumulations, *pipes*; proxies: geomorphology, **organic carbon accumulation**
biodiversity	community structure within and across taxa	altered fire regimes, altered **land cover**, *biomass harvests*, *tillage,* hunting and foraging	skeletal remains, DNA; proxies: **land cover**, **plant community**
biogeochemistry	other biogeochemical processes, including soil respiration, methanogenesis, denitrification	altered fire regimes, altered **land cover,** *irrigation*, *drainage*, *tillage, domestic livestock*, *settlements, fertilizers*	stable atmospheric trace gases (N_2O, CH_4, CO_2) and their isotopic composition, soil pH, **reactive nitrogen**, **organic carbon accumulation**, isotope ratios
residual effects	presence of *artificial substances* and concentrations other compounds and elements	*pollution*	*artificial compounds,* concentrations of metals and other elements, *radioisotopes*

and forest clearing [38], pre-industrial agricultural systems relying on harvested biomass for fuel, and industrial systems shifting to fossil fuels [41,106]. Organic carbon accumulation, like NPP, is a good indicator of ecosystem state and its alteration by humans [52], but unlike NPP, generally leaves a quantitative geologic record in soils and sediment [78,107]. Reactive nitrogen availability in ecosystems is a strong indicator of ecosystem disturbances including fire and the rise of intensive agricultural practices, such as tillage, manuring and the use of synthetic nitrogen, though its alteration is not always detectable in the geological record [52,96,107,108]. Soil phosphorus is often used in archaeology as an indicator of human settlements [109], where it tends to accumulate over time as a result of food and biomass harvest, consumption and combustion by concentrated livestock, and the manuring and, most recently, fertilization of agricultural fields with mined phosphorus fertilizers [52,96,110–113]. Other potentially useful indicators not assessed here are direct human alterations of geomorphology and hydrology (table 1 and figure 1; [3,114]), changes in taxa besides plants [93], and other biogeochemical and residual traces (table 1).

4. Intensity and novelty of ecological changes within anthromes and biomes

To assess the biospheric significance of anthropogenic changes in ecosystem form and process across anthromes and biomes, two factors must be considered. The first is the presence of entirely novel anthropogenic ecosystem forms and processes (italic text in figure 1 and table 1). The second is anthropogenic alteration of pre-existing ecosystem variables at levels of intensity that force them outside their natural range (natural ranges are illustrated for wildlands shown at left in figure 1). By assessing these two factors across the different levels of anthrome development in each biome, the relative area of each anthrome level within each biome may provide a simple indicator of the extent of geologically significant anthropogenic transformation of the terrestrial biosphere.

Densely settled anthromes incorporate the widest variety of novel ecosystem forms and processes and are the most intensively transformed, leaving unambiguous geological evidence well documented in the archaeological literature for every biome, including tropical rainforests [30,59,115]. Cropland anthromes tend to be less completely transformed than densely settled anthromes, but their widespread soil tillage, domesticated species and other processes also leave unambiguous geological evidence of profound and novel ecosystem transformation [46,59,78,92,116,117].

Rangeland anthromes tend to be less altered than croplands, though their alteration tends to increase with population. Domesticated grazing livestock are typically adapted to grasslands and savannas, so their ecological alteration of these biomes tends to be less novel, except when stocking rates are very high [118,119]. In woodlands, however, forests must generally be cleared to sustain substantial populations of domestic livestock, so the development of rangelands in these biomes tends to produce intense and novel alteration of ecosystems, pushing forest cover, NPP and organic carbon accumulation into decline, and dramatically increasing the abundance of exotic species along with domesticated forages [118,120,121]. In savannas, shrublands and grasslands, rangeland development may produce only minor alteration of land cover and NPP, depending on the extent and intensity of land clearing and grazing [118,120]. Yet, even in savannas and grasslands, exotic species tend to become established at high rates in grazed areas, and, when especially intense, can include encroachment by woody and other species unpalatable to domesticated herbivores [121]. Other ecological effects common across rangelands include increased fire rates at low human population densities and fire suppression at higher populations [41]. Overall, however, development of rangelands within woodlands causes far more intense and novel alteration of ecosystems than in grasslands, savannas and shrublands [85,118–120,122].

Seminatural anthromes are the least heavily used and therefore least transformed anthromes, with novel anthropogenic processes occurring primarily when population densities are highest, which tends to occur mostly in industrial systems. At the lower population densities common in agricultural systems, seminatural anthromes tend to represent shifting agriculture in woodlands and nomadic and low-intensity pastoral systems in drier biomes [33,64]. The most significant anthropogenic changes in these systems tend to be increased fire frequencies, with fire suppression at higher population densities in industrial systems [41], and the shifting of plant communities towards exotics and small numbers of domesticates [85,102]. While these transformations are significant and may be locally intense and leave geological records, they tend to be the least intense and novel of all anthrome levels in every biome [95].

In summary, densely settled and cropland anthromes, together with rangelands developed in woodlands, are the most completely transformed by human systems, with pre-existing ecological patterns shifted outside their natural range and novel processes such as cultivation and domestication producing unambiguous geological evidence. Seminatural anthromes and rangelands in savannas, shrublands and grasslands are also significantly transformed, but at lower levels of intensity and novelty that leave more ambiguous geological evidence.

5. Assessing global patterns of anthrome change

Given that different levels of anthrome development indicate different levels of anthropogenic transformation within each biome, anthropogenic transformation of the terrestrial biosphere over time may be assessed by mapping and measuring the extent of each anthrome level within each biome over time. To accomplish this, spatially explicit global estimates at 5 arc minute spatial resolution (geographical grid cells of approx. 85 km^2 at the equator) were obtained for potential vegetation biomes ([57]; aggregating woodlands by region, shrublands, and tundra with deserts and barren lands), and intersected with anthrome maps at 10 time periods across the Holocene using a geographic information system (figures 2 and 3). Anthromes were classified and mapped using two different historical land-use and population datasets, the History Database of the Global Environment (HYDE) [13] and that due to Kaplan & Krumhardt in 2010 (KK10) [14], in an effort to incorporate and understand uncertainties in historical reconstructions ([123]; spatial data are downloadable at: http://ecotope.org/anthromes/data/). Both HYDE and KK10 use fairly conservative population models constrained by widely accepted historical reconstructions [14,123]; some models predict substantially higher prehistoric populations and land use [124].

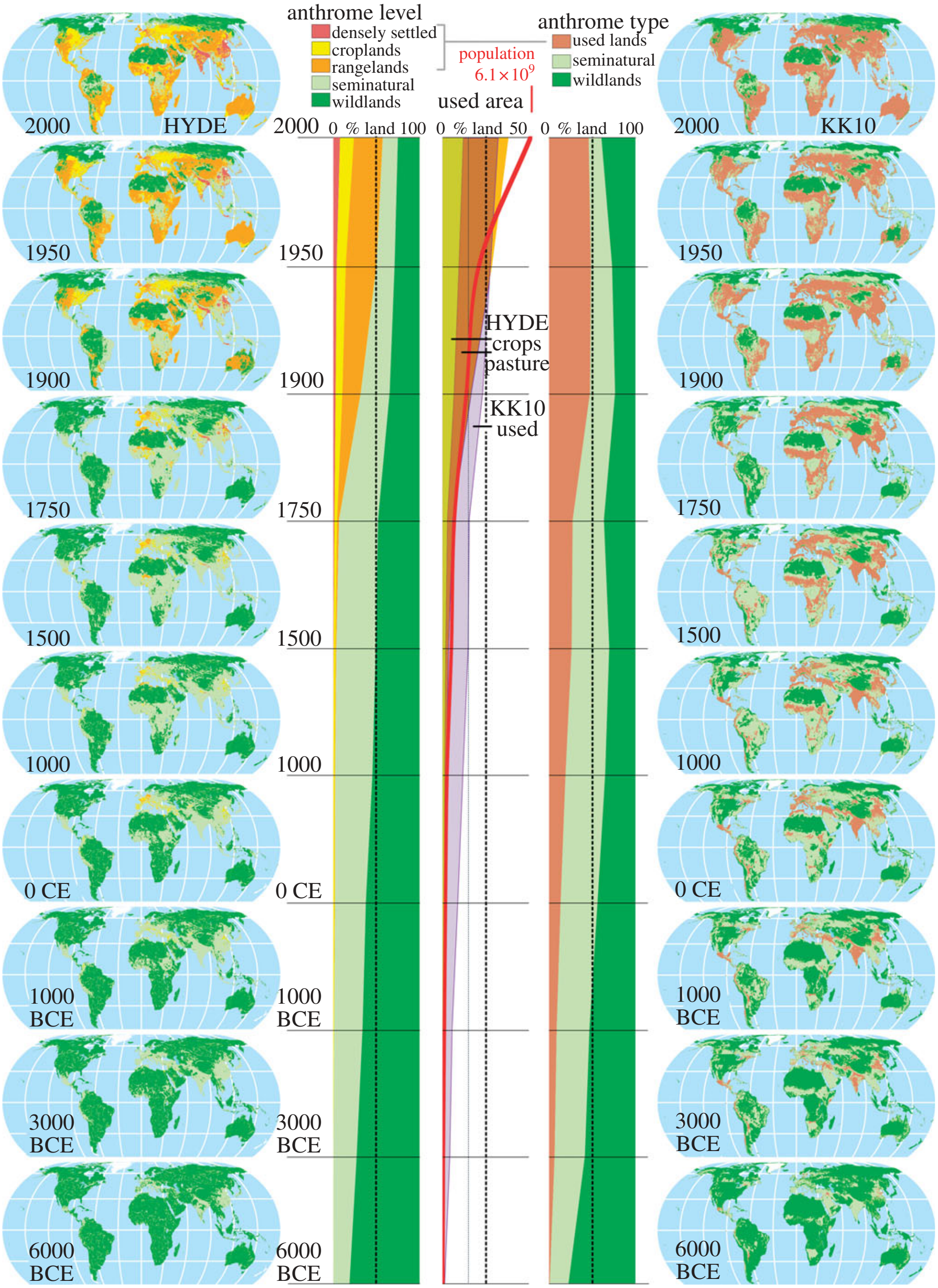

Figure 2. Anthropogenic transformation of the terrestrial biosphere, 6000 BCE to 2000. Global anthrome level maps and area changes at left are derived from HYDE land-use and population data [13,125]; anthrome type maps and area changes at right are from KK10 land-use data [14]. Centre chart shows global land areas under crops and pastures from HYDE, and used areas (crops + pastures) from KK10, overlaid with global trends in human population.

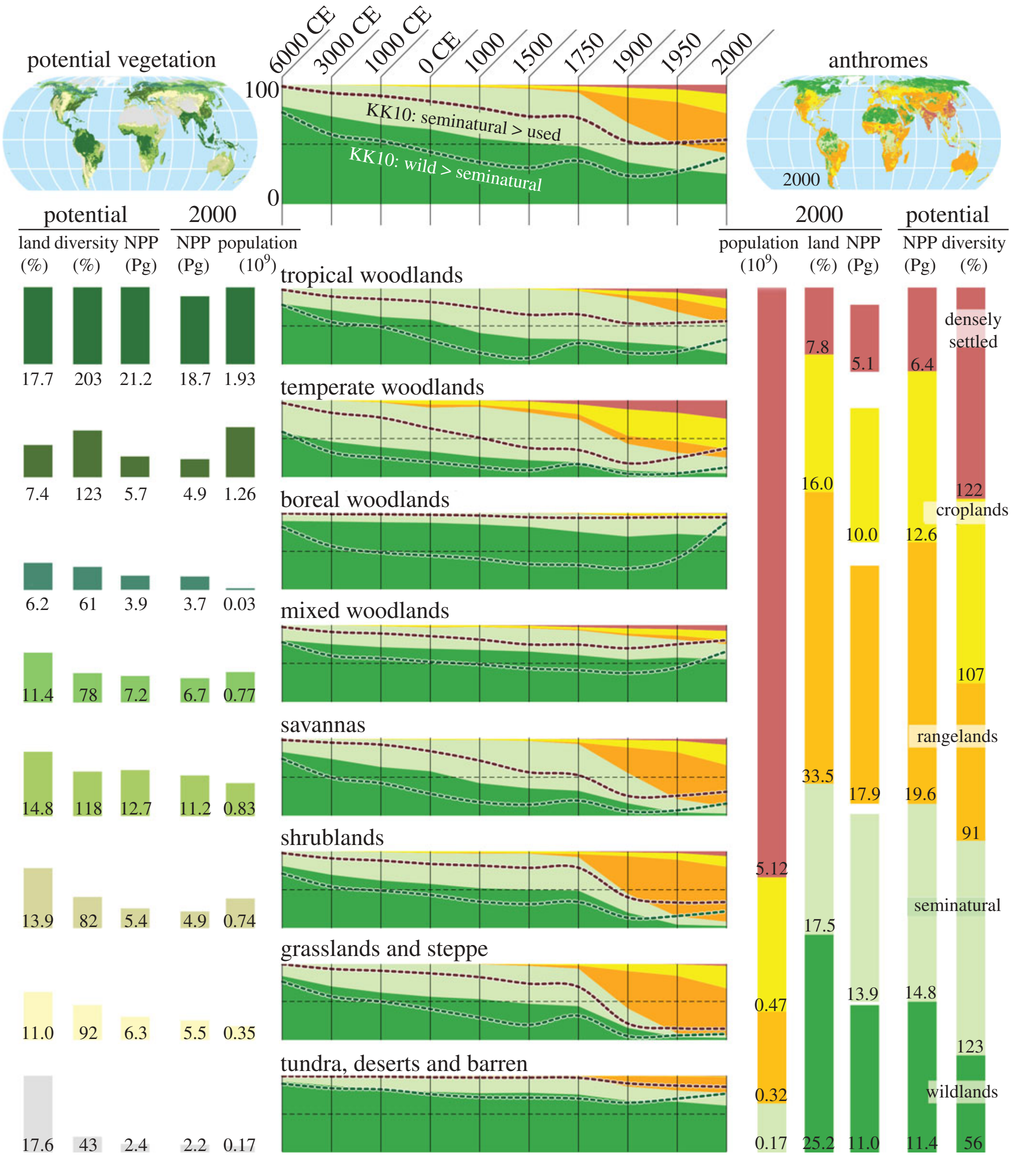

Figure 3. Anthropogenic transformation of the biomes, 6000 BCE to 2000. Potential vegetation biomes are based on Ramankutty & Foley [57]. Anthromes are classified using HYDE and KK10 datasets as in figure 2. Global estimates for biomes and anthromes compare land (per cent of global ice-free land area), plant diversity (vascular plant species richness in regional landscapes as a percentage of the global median based on [127]), potential NPP and actual NPP in 2000 [104].

The HYDE land-use model allocates land to mapped historical populations by assuming stable land use *per capita* over time based on contemporary levels [13,125]. As a result, HYDE produces conservative estimates of early land use, because land use *per capita* is generally much higher under earlier agricultural conditions, declining by an order of magnitude or more as population densities increase and land use intensifies [13,67,68,73,125,126]. KK10 predicts early land use from an empirical model of prehistoric population and land-clearing relationships across Europe prior to 1700, adjusted for global variations in NPP [14,122], merging thereafter with the census-based model of Ramankutty & Foley [57]. As a result, KK10 may more accurately portray early land-use patterns, except those involving pastures, which differ substantially between Europe and other world regions [33]. KK10 data for crops and pastures are, therefore, portrayed in figures 2 and 3 using aggregated 'used areas' (crops + pastures) and a 'used lands' anthrome type (densely settled + croplands + rangelands anthrome levels); HYDE data incorporate regional histories of cultivation and livestock grazing [13]. Spatial data for NPP (potential and actual in 2000; [104]) and potential plant species richness in regional landscapes (estimated within 7800 km^2 equal-area hexagons; [127]) were also obtained to assess anthropogenic alteration of NPP and plant biodiversity.

Both land-use models agree that, as of 2000 CE, most of the terrestrial biosphere was already transformed into anthromes, leaving only about 25 per cent (HYDE) to 40 per cent (KK10) in wildlands (figure 2). Both also agree that 8000 years ago the opposite was true, with about 80 per cent of the terrestrial biosphere in wildlands and 20 per cent in seminatural anthromes. In between, the models tend to disagree, with the more conservative HYDE dataset indicating that by 1750 CE only about 7 per cent of the terrestrial biosphere was transformed into intensively used anthromes ('used lands' anthromes type), and KK10 indicating that this level of biospheric transformation was reached by 3000 BCE (figure 2). In both models, the global extent of seminatural anthromes peaks at about 45 per cent of global ice-free land area, but in 1500 CE for HYDE and 1000 CE for KK10, with seminatural anthromes surpassing wildlands at the same time according to KK10, but never reaching this level in HYDE.

Most importantly, both land-use models basically agree in their estimation of what is probably the simplest indicator of biospheric transformation, the time period when more than half of the terrestrial biosphere was transformed into intensively used anthromes, with KK10 putting this at 1900 and HYDE at 1950. This agreement is not entirely surprising, as population and land-use data for the past century are better constrained by observations than those before [123].

6. Anthropogenic transformation of the terrestrial biosphere over time

Anthropogenic transformation of terrestrial biomes across the Holocene is illustrated in figure 3, with the global extent and ecological importance of each biome indicated at left in terms of land area, plant diversity and potential NPP, and actual NPP and population in 2000 CE. For example, figure 3 indicates that, by all criteria, tropical woodlands are the most important biome, with greater extent, NPP, diversity and human populations than all others. Temperate woodlands support comparatively large populations relative to their global extent, and the drier and colder biomes have significant global extents but contribute far less to global NPP or biodiversity, and also have much lower human populations. Global patterns in the same variables across anthrome levels are illustrated at right in figure 3.

Holocene trends in anthrome development differ dramatically among biomes, with temperate woodlands showing the most intensive and sustained development of all biomes (figure 3). Savannas, shrublands and grasslands show dramatic recent increases in rangelands and also to some degree croplands, while the coldest biomes (boreal woodlands and tundra) show little change over time. Different land-use models yield different trends in anthrome development, with KK10 showing greater and much earlier intensive transformation of the temperate and tropical woodlands and savannas than HYDE, but with similar trends in other biomes, except boreal woodlands, which have far larger extents of seminatural anthromes across time in KK10. Model disagreements, however, do not make much difference to the overall pattern: temperate woodlands have long been transformed at relatively high levels, savannas, shrublands and grasslands have come under intensive use rapidly in recent centuries, driving most recent global change in anthrome development, and tropical woodlands have been transformed more gradually, mostly by conversion to seminatural anthromes until recently.

By the least conservative measure of biospheric transformation, the conversion of all biomes to any level of anthrome, the terrestrial biosphere was 75 per cent transformed in 2000 and 50 per cent transformed in 1750 according to HYDE, while the KK10 model indicates this level of transformation was reached between 1000 BCE and 0 CE. Another simple indicator of biospheric transformation is the percentage of global land covered by crops, irrespective of their distribution among landscapes or biomes, with a level of 15–20 per cent being recently regarded as an unsustainable threshold [8]. While this level has never been reached, and is currently at about 12 per cent in both models (figure 2), HYDE data show it increasing dramatically in recent centuries, while KK10 indicates that contemporary levels of cultivation were reached more than 500 years ago and may have actually peaked early in the twentieth century. Clearly, the history of biospheric transformation depends on which model is used, with the more conservative land-use model (HYDE) indicating that intensive transformation of the biosphere is mostly recent, and the more empirical prehistoric land-use model (KK10) indicating that contemporary levels of intensively used anthromes may have been sustained for centuries.

If we consider only the most conservative indicator of biospheric transformation, the development of densely settled and cropland anthromes across biomes, and the development of rangelands only in woodland biomes, and use the most conservative land-use model to measure this (HYDE), the result is 29 per cent anthropogenic transformation of the terrestrial biosphere as of 2000, 19 per cent in 1950, 12 per cent in 1900 and only 5 per cent by 1750. Approximating the same indicator for KK10 by applying HYDE ratios of croplands to rangelands yields a fairly steady 22 per cent transformation starting in 1500, dropping to 17 per cent in 1000 CE, 13 per cent in 0 CE, 9 per cent in 1000 BCE and down to 1 per cent 8000 years ago. If we accept a 20 per cent global land area threshold as sufficient indication of irreversible biospheric change [8] and apply it to the most intensively transformed anthromes, then this threshold was crossed last century or even earlier.

7. Have human systems irreversibly transformed the terrestrial biosphere?

Taking the most conservative view, nearly one-third of the terrestrial biosphere has now been transformed into anthromes in which pre-existing ecosystem forms and processes have been shifted outside their native range and novel anthropogenic ecological processes predominate. The ecological forms and processes within these anthromes have no precedent in the history of the biosphere and have certainly left ample and unambiguous geological evidence of their presence spread widely across Earth's terrestrial surface. Their global extent and NPP exceed that of wildlands, and they occupy the most biodiverse regions of the planet (figure 3). Another third or more of the terrestrial biosphere is now transformed into rangelands and seminatural anthromes with lower levels of ecosystem change and novelty. These less transformed ecosystems do not contribute nearly as much to NPP and other global biospheric processes, but they certainly add to the global geological evidence of novel anthropogenic transformation of the terrestrial biosphere.

One of the most general and irreversible anthropogenic changes observed across the terrestrial biosphere is altered patterns of biodiversity [34]. Even in anthromes with low levels of population and land use, plant community structure and ecosystem processes related to these tend to be highly altered by invasions of exotic species [86,90,128,129]. Species invasions are increasingly recognized as one of the most significant anthropogenic global changes in the biosphere [86,90] and have even been proposed as singular grounds for the designation of a new geological epoch, the 'Homogocene' [130]. If anthropogenic global changes in community structure are considered adequate grounds for the Anthropocene, its emergence might be pushed back to the Palaeolithic, when anthropogenic megafaunal extinctions and use of fire certainly transformed communities and ecosystems significantly across large regions, albeit in ways that might prove hard to distinguish from the effects of the glacial cycles [42,43].

Taken together, the evidence seems more than adequate to support the hypothesis that the present state of the terrestrial biosphere is predominantly anthropogenic, with ecological forms and processes unprecedented in the Holocene or before, heralding the emergence of the Anthropocene. Many of these novel forms and processes have been sustained for millennia across significant areas of the terrestrial biosphere, especially in temperate woodlands. Even where human systems and populations have collapsed, their geologic records remain for centuries or longer [59,78,115]. It therefore seems almost certain that, were human populations to disappear instantly from this planet, the global geological record of anthropogenic transformation of the terrestrial biosphere would persist.

It is uncertain how long the anthropogenic biosphere we have created will persist. There is ample archaeological and historical evidence of widespread declines in human populations and human system collapse to earlier levels of technological and social capability [35,131]. Such a collapse would diminish or halt many novel anthropogenic biospheric processes. Yet, the same evidence also demonstrates that, even in the face of catastrophic decline, *Homo sapiens* has not become extinct locally or globally, nor have human systems permanently lost fire, domesticated species, or most other powerful tools for ecosystem engineering. Even were human populations or societies to collapse globally, the historical record argues for their eventual recovery and the restoration of the anthropogenic biosphere in some form.

8. Confirming the Anthropocene transition

The evidence presented here generally supports the hypothesis that human systems have, as of the past century at least, created a novel anthropogenic terrestrial biosphere that has permanently altered the Earth system at levels of equal consequence to that of past biospheric changes that have justified major divisions of geological time. Yet there remain a number of serious challenges to effective confirmation of this hypothesis.

This study's criteria for delimiting the threshold between the wild biosphere of the Holocene and the anthropogenic biosphere of the Anthropocene may be questioned. To consider the biosphere transformed, this study required intense novel anthropogenic changes to occur across at least 20 per cent of Earth's ice-free land surface; a higher threshold than the 15 per cent global crop area used recently by Rockstrom *et al.* [8]. Two different global datasets were used to test this threshold and produced similar results in the century for which this test was positive, though they diverged substantially before that time. Still, a different observer might choose different indicators or require a higher threshold before accepting or rejecting the hypothesis.

Perhaps most interesting is the question of whether indisputable quantitative measurements of anthropogenic transformation could be made across the terrestrial biosphere to assess the scale and timing of an Anthropocene transition. In this study, multiple indicators of novel ecosystem forms and processes, relating to different levels of anthropogenic transformation of terrestrial ecosystems, were combined into a rough general indicator of significant anthropogenic transformation of the biomes. This generality has the advantage of simplifying global assessment. Nevertheless, a spatially explicit quantitative global assessment of anthropogenic transformation of ecosystems across the Holocene, ideally based on archaeological and geological field measurements within a global sampling and data aggregation system, would ultimately be needed to confirm the results presented here [35,95].

9. Ecology in the Anthropocene

It seems clear that the terrestrial biosphere is now predominantly anthropogenic, fundamentally distinct from the wild biosphere of the Holocene and before. From a philosophical point of view, nature is now human nature; there is no more wild nature to be found, just ecosystems in different states of human interaction, differing in wildness and humanness [132]. As evolution and other ecological processes now occur primarily within human systems, biology and ecology must incorporate human systems into their mainstream research and educational paradigms. The experience of archaeologists and global change scientists will be useful in this effort, as natural scientists already comfortable with an anthropocentric view [78,118,133,134].

Perhaps the most important repercussions of embracing our anthropogenic biosphere will come from changes in social, political and economic points of view, and the social learning processes that drive the collective actions of our human systems [53,118]. Environmentalist traditions have long called for a halt to human interference in ecology and the Earth system [132]. In the Anthropocene, the anthropogenic biosphere is permanent, the legacy of our ancestors, and our actions as human systems a force of nature, making the call to avoid human interference with the biosphere irrelevant [132,135]. The implication is clear; the current and future state of the terrestrial biosphere is up to us, and will be determined by human systems of one form or another, whether it is the momentum of our past or new pathways we are able to achieve in the future.

In considering the future of anthropogenic transformation of the biosphere, a key question is whether the biosphere we have now created is desirable, or merely a degraded byproduct produced by rapid human population growth and obsolete human systems that use resources destructively. The answer is not as clear as it might seem. There is no doubt that many terrestrial ecosystems have been degraded to levels where they produce no desirable outcomes for humans or other organisms—yet there is also little doubt that the anthropogenic biosphere we have created now provides most human populations with the highest standard of living humans have ever attained [136]. It would seem that, on balance, human systems have transformed most of the biosphere for our own benefit, sustaining growing human populations and increased standard of living over time.

Still, it seems evident that we are approaching the point where the global extent of anthromes cannot increase much further in most biomes (figure 3). This does not necessarily herald an end to anthrome development or the imminent collapse of the human systems that depend on them, though this is a possibility deserving serious consideration. As the terrestrial limits of the biosphere draw near, the internal patterns of anthrome development appear to be evolving towards increasingly intense land use in the anthromes we have already created. Human populations are rapidly moving to urban areas, where the quality of life is highest in industrial human systems [81], reducing populations elsewhere. Moreover, there is growing evidence that agricultural systems are intensifying in the most suitable lands for production [137], sparing less agriculturally productive parts of landscapes [138], and leading to increasing forest cover in many nations (the 'forest transition'; [139,140]). Human systems may be moving in a sustainable direction, with anthromes evolving with them.

In forecasting the future of the anthropogenic biosphere, we must still contend with rapid anthropogenic global climate change and the potential mass extinction of species as a result of this and in response to the increasing anthropogenic transformation of tropical woodlands. Tropical woodlands are fast moving towards the same fate as temperate woodlands—heavily used and densely populated, with little wildland remaining [141]. This may be desirable for populations in these regions but will probably produce the greatest direct anthropogenic change in the biosphere ever experienced in the Holocene; tropical woodlands are by a large margin the most diverse and productive of the biomes. Most importantly, if human systems fail to alter their current and predicted climate forcing, we may either accept the resulting mass extinctions, or even create a more novel biosphere than climate forcing or anthrome transformation themselves could bring, if efforts at facilitated migration to mitigate extinctions succeed in translocating species more rapidly and comprehensively than pre-existing natural and human processes combined [142].

10. Conclusions

All species have complex interactive effects on ecosystems. Humans, with their unrivalled capacity for ecosystem engineering, have outsized effects and add even greater complexity and novelty by acting both as individual agents of change and collectively as human systems with adaptive social learning networks. A single human being can intentionally transform a pristine forest to pasture using fire and livestock or unintentionally by introducing an invasive species. Human systems can sustain cities in the desert and convert factories to woodlands. Yet human transformation of terrestrial ecology is always incomplete: some native species flourish even in the mostly densely populated cities.

This paper has tested the hypothesis that humans have altered the terrestrial biosphere sufficiently to indicate that the Earth system has entered a new geological epoch. Results demonstrate, with some reservations, that this hypothesis is probably correct; that, by the latter half of the twentieth century, the terrestrial biosphere made the transition from being shaped primarily by natural biophysical processes to an anthropogenic biosphere in the Anthropocene, shaped primarily by human systems. This transformation remains incomplete, as significant wildlands persist and much of the anthropogenic biosphere consists of novel ecosystems altered significantly but not completely. It remains to be seen whether the anthropogenic biosphere will be sustained at current levels, expand to cover a greater extent, most likely within the tropical woodlands, and continue to evolve new and more intensive and novel anthropogenic ecological forms and processes.

Humans have altered this planet permanently at levels equivalent to that of many past geological events that have justified major divisions of geological time. As we accept responsibility for the anthropogenic biosphere we have created and begin to practice the planetary stewardship we have earned in the Anthropocene, we can only hope that human systems will continue to evolve in their capacity to create and sustain the biosphere we want and need.

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References

1 Turner II, B. L., Clark, W. C., Kates, R. W., Richards, J. F., Mathews, J. T. & Meyer, W. B. 1990 *The Earth as transformed by human action: global and regional changes in the biosphere over the past 300 years*. Cambridge, UK: Cambridge University Press; and New York, NY: Clark University.

2 Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. 1997 Human domination of earth's ecosystems. *Science* **277**, 494–499. (doi:10.1126/science.277.5325.494)

3 Vörösmarty, C. J. & Sahagian, D. 2000 Anthropogenic disturbance of the terrestrial water cycle. *BioScience* **50**, 753–765. (doi:10.1641/0006-3568(2000)050[0753:ADOTTW]2.0.CO;2)

4 Steffen, W. *et al.* 2004 *Global change and the earth system: a planet under pressure*, 1st edn. Berlin, Germany: Springer.

5 Foley, J. A. *et al.* 2005 Global consequences of land use. *Science* **309**, 570–574. (doi:10.1126/science.1111772)

6 Wilkinson, B. H. & McElroy, B. J. 2007 The impact of humans on continental erosion and sedimentation. *Geol. Soc. Am. Bull.* **119**, 140–156. (doi:10.1130/B25899.1)

7 Ellis, E. C. & Ramankutty, N. 2008 Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* **6**, 439–447. (doi:10.1890/070062)

8 Rockstrom, J. *et al.* 2009 Planetary boundaries: exploring the safe operating space for humanity. *Ecol. Soc.* **14**, 32. See http://www.ecologyandsociety.org/vol14/iss2/art32/.

9 Zalasiewicz, J. *et al.* 2008 Are we now living in the Anthropocene? *GSA Today* **18**, 4–8. (doi:10.1130/GSAT01802A.1)

10 Crutzen, P. J. 2002 Geology of mankind. *Nature* **415**, 23–23. (doi:10.1038/415023a)

11 Steffen, W., Crutzen, P. J. & McNeill, J. R. 2007 The Anthropocene: are humans now overwhelming the great forces of nature. *AMBIO: J. Hum. Environ.* **36**, 614–621. (doi:10.1579/0044-7447(2007)36[614:TAAHNO]2.0.CO;2)

12 Gradstein, F. & Ogg, J. 2004 Geologic time scale 2004—why, how, and where next! *Lethaia* **37**, 175–181. (doi:10.1080/00241160410006483)

13 Klein Goldewijk, K., Beusen, A., van Drecht, G. & de Vos, M. In press. The HYDE 3.1 spatially explicit database of human induced global land use change over the past 12 000 years. *Global Ecol. Biogeogr.* (doi:10.1111/j.1466-8238.2010.00587.x)

14 Kaplan, J. O., Krumhardt, K. M., Ellis, E. C., Ruddiman, W. F., Lemmen, C. & Klein Goldewijk, K. In press. Holocene carbon emissions as a result of anthropogenic land cover change. *Holocene.* (doi:10.1177/0959683610386983)

15 Wanner, H. *et al.* 2008 Mid- to late-Holocene climate change: an overview. *Quat. Sci. Rev.* **27**, 1791–1828. (doi:10.1016/j.quascirev.2008.06.013)

16 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)

17 Dale, V. H. 1997 The relationship between land-use change and climate change. *Ecol. Appl.* **7**, 753–769. (doi:10.1890/1051-0761(1997)007[0753:TRBLUC]2.0.CO;2)

18 Ruddiman, W. F. 2007 The early anthropogenic hypothesis: challenges and responses. *Rev. Geophys.* **45**, RG4001. (doi:10.1029/2006RG000207)

19 Thomas, C. D. *et al.* 2004 Extinction risk from climate change. *Nature* **427**, 145–148. (doi:10.1038/nature02121)

20 Webb, T. & Bartlein, P. J. 2003 Global changes during the last 3 million years: climatic controls and biotic responses. *Annu. Rev. Ecol. Syst.* **23**, 141–173. (doi:10.1146/annurev.es.23.110192.001041)

21 Jackson, S. T. & Overpeck, J. T. 2000 Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26**, 194–220. (doi:10.1666/0094-8373(2000)26[194:ROPPAC]2.0.CO;2)

22 Novacek, M. J. & Cleland, E. E. 2001 The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc. Natl Acad. Sci. USA* **98**, 5466–5470. (doi:10.1073/pnas.091093698)

23 Jones, C. G., Lawton, J. H. & Shachak, M. 1994 Organisms as ecosystem engineers. *Oikos* **69**, 373–386. (doi:10.2307/3545850)

24 Sherratt, T. N. & Wilkinson D. M. 2009 When did we start to change things? In *Big questions in ecology and evolution* (eds T. N. Sherratt & D. M. Wilkinson), p. 312. Oxford, UK: Oxford University Press.

25 Smith, B. D. 2007 The ultimate ecosystem engineers. *Science* **315**, 1797–1798. (doi:10.1126/science.1137740)

26 McBrearty, S. & Brooks, A. S. 2000 The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563. (doi:10.1006/jhev.2000.0435)

27 Ambrose, S. H. 2001 Palaeolithic technology and human evolution. *Science* **291**, 1748–1753. (doi:10.1126/science.1059487)

28 Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123–135. (doi:10.1002/evan.10110)

29 Hamilton, M. J., Burger, O., DeLong, J. P., Walker, R. S., Moses, M. E. & Brown, J. H. 2009 Population stability, cooperation, and the invasibility of the human species. *Proc. Natl Acad. Sci. USA* **106**, 12 255–12 260. (doi:10.1073/pnas.0905708106)

30 Kirch, P. V. 2005 Archaeology and global change: the Holocene record. *Annu. Rev. Environ. Resour.* **30**, 409. (doi:10.1146/annurev.energy.29.102403.140700)

31 Turner II, B. L., Lambin, E. F. & Reenberg, A. 2007 The emergence of land change science for global environmental change and sustainability. *Proc. Natl Acad. Sci. USA* **104**, 20 666–20 671. (doi:10.1073/pnas.0704119104)

32 Ellis, E. C. & Haff, P. K. 2009 Earth science in the Anthropocene: new epoch, new paradigm, new responsibilities. *EOS Trans.* **90**, 473. (doi:10.1029/2009EO490006)

33 Grigg, D. B. 1974 *The agricultural systems of the world: an evolutionary approach.* Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511665882)

34 Chapin III, F. S. *et al.* 2000 Consequences of changing biodiversity. *Nature* **405**, 234–242. (doi:10.1038/35012241)

35 Costanza, R., Graumlich, L., Steffen, W., Crumley, C., Dearing, J., Hibbard, K., Leemans, R., Redman, C. & Schimel, D. 2007 Sustainability or collapse: what can we learn from integrating the history of humans and the rest of nature? *AMBIO: J. Hum. Environ.* **36**, 522–527. (doi:10.1579/0044-7447(2007)36[522:SOCWCW]2.0.CO;2)

36 McEvedy, C. & Jones, R. 1978 *Atlas of world population history.* London, UK: Puffin Books.

37 Headland, T. N. *et al.* 1989 Hunter–gatherers and their neighbors from prehistory to the present (and comments and replies). *Curr. Anthropol.* **30**, 43–66. (doi:10.1086/203710)

38 Clark, J. D. & Harris, J. W. K. 1985 Fire and its roles in early hominid lifeways. *Afr. Archaeol. Rev.* **3**, 3–27. (doi:10.1007/BF01117453)

39 Bliege Bird, R., Bird, D. W., Codding, B. F., Parker, C. H. & Jones, J. H. 2008 The 'fire stick farming' hypothesis: Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proc. Natl Acad. Sci. USA* **105**, 14 796–14 801. (doi:10.1073/pnas.0804757105)

40 Williams, M. 2008 A new look at global forest histories of land clearing. *Annu. Rev. Environ. Resour.* **33**, 345. (doi:10.1146/annurev.environ.33.040307.093859)

41 Bowman, D. M. J. S. *et al.* 2009 Fire in the Earth system. *Science* **324**, 481–484. (doi:10.1126/science.1163886)

42 Koch, P. L. & Barnosky, A. D. 2006 Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* **37**, 215–250. (doi:10.1146/annurev.ecolsys.34.011802.132415)

43 Johnson, C. N. 2009 Ecological consequences of Late Quaternary extinctions of megafauna. *Proc. R. Soc. B* **276**, 2509–2519. (doi:10.1098/rspb.2008.1921)

44 Weisdorf, J. L. 2005 From foraging to farming: explaining the Neolithic revolution. *J. Econ. Surv.* **19**, 561–586. (doi:10.1111/j.0950-0804.2005.00259.x)

45 Diamond, J. 2002 Evolution, consequences and future of plant and animal domestication. *Nature* **418**, 700–707. (doi:10.1038/nature01019)

46 Purugganan, M. D. & Fuller, D. Q. 2009 The nature of selection during plant domestication. *Nature* **457**, 843–848. (doi:10.1038/nature07895)

47 Smil, V. 1991 Population growth and nitrogen: an exploration of a critical existential link. *Popul. Dev. Rev.* **17**, 569–601. (doi:10.2307/1973598)

48 Galloway, J. N. & Cowling, E. B. 2002 Reactive nitrogen and the world: 200 years of change. *AMBIO: J. Hum. Environ.* **31**, 64–71. (doi:10.1579/0044-7447-31.2.64)

49 Dale, P. J., Clarke, B. & Fontes, E. M. G. 2002 Potential for the environmental impact of transgenic crops. *Nat. Biotech.* **20**, 567–574. (doi:10.1038/nbt0602-567)

50 Fogel, R. W. & Costa, D. L. 1997 A theory of technophysio evolution, with some implications for forecasting population, health care costs, and pension costs. *Demography* **34**, 49–66. (doi:10.2307/2061659)

51 Alloway, B. J. & Ayres, D. C. 1997 *Chemical principles of environmental pollution*, 2nd edn. New York, NY: Chapman and Hall.

52 Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. 1997 Agricultural intensification and ecosystem properties. *Science* **277**, 504–509. (doi:10.1126/science.277.5325.504)

53 Steffen, W. 2009 Looking back to the future. *AMBIO: J. Hum. Environ.* **37**, 507–513. (doi:10.1579/0044-7447-37.sp14.507)

54 Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. & Solomon, A. M. 1992 A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134. (doi:10.2307/2845499)

55 Sankaran, M. *et al.* 2005 Determinants of woody cover in African savannas. *Nature* **438**, 846–849. (doi:10.1038/nature04070)

56 Haxeltine, A. & Prentice, I. C. 1996 BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Glob. Biogeochem. Cycles* **10**, 693–710. (doi:10.1029/96GB02344)

57 Ramankutty, N. & Foley, J. A. 1999 Estimating historical changes in global land cover: croplands from 1700 to 1992. *Glob. Biogeochem. Cycles* **13**, 997–1027. (doi:10.1029/1999GB900046)

58 Folke, C., Holling, C. S. & Perrings, C. 1996 Biological diversity, ecosystems, and the human scale. *Ecol. Appl.* **6**, 1018–1024. (doi:10.2307/2269584)

59 Redman, C. L. 1999 *Human impact on ancient environments*. Tucson, AZ: University of Arizona Press.

60 Rindfuss, R. R., Walsh, S. J., Turner II, B. L., Fox, J. & Mishra, V. 2004 Developing a science of land change: challenges and methodological issues. *Proc. Natl Acad. Sci. USA* **101**, 13 976–13 981. (doi:10.1073/pnas.0401545101)

61 Liu, J. *et al.* 2007 Complexity of coupled human and natural systems. *Science* **317**, 1513–1516. (doi:10.1126/science.1144004)

62 Lambin, E. F. *et al.* 2001 The causes of land-use and land-cover change: moving beyond the myths. *Glob. Environ. Change Hum. Policy Dimens.* **11**, 261–269. (doi:10.1016/S0959-3780(01)00007-3)

63 Huston, M. A. 2005 The three phases of land-use change: implications for biodiversity. *Ecol. Appl.* **15**, 1864–1878. (doi:10.1890/03-5281)

64 Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. 2010 Anthropogenic transformation of the biomes, 1700 to 2000. *Glob. Ecol. Biogeogr.* **19**, 589–606. (doi:10.1111/j.1466-8238.2010.00540.x)

65 Huston, M. 1993 Biological diversity, soils, and economics. *Science* **262**, 1676–1680. (doi:10.1126/science.262.5140.1676)

66 Smil, V. 1991 *General energetics: energy in the biosphere and civilization*, 1st edn. New York, NY: John Wiley & Sons.

67 Boserup, E. 1965 *The conditions of agricultural growth: the economics of agrarian change under population pressure*. London, UK: Allen & Unwin.

68 Boserup, E. 1981 *Population and technological change: a study of long term trends*. Chicago, IL: University of Chicago Press.

69 Cowgill, G. L. 1975 On causes and consequences of ancient and modern population changes. *Am. Anthropol.* **77**, 505–525. (doi:10.1525/aa.1975.77.3.02a00030)

70 Meyer, W. B. & Turner, B. L. 1992 Human population growth and global land-use cover change. *Annu. Rev. Ecol. Syst.* **23**, 39–61. (doi:10.1146/annurev.es.23.110192.000351)

71 Netting, R. M. 1993 *Smallholders, householders: farm families and the ecology of intensive sustainable agriculture*. Stanford, CA: Stanford University Press.

72 DeFries, R. S., Foley, J. A. & Asner, G. P. 2004 Land-use choices: balancing human needs and ecosystem function. *Front. Ecol. Environ.* **2**, 249–257. (doi:10.1890/1540-9295(2004)002[0249:LCBHNA]2.0.CO;2)

73 Ruddiman, W. F. & Ellis, E. C. 2009 Effect of per-capita land use changes on Holocene forest clearance and CO_2 emissions. *Quat. Sci. Rev.* **28**, 3011–3015. (doi:10.1016/j.quascirev.2009.05.022)

74 Binswanger, H. P. & McIntire, J. 1987 Behavioral and material determinants of production relations in land-abundant tropical agriculture. *Econ. Dev. Cult. Change* **36**, 73–99. (doi:10.1086/451637)

75 Jenny, H. 1958 Role of the plant factor in the pedogenic functions. *Ecology* **39**, 5–16. (doi:10.2307/1929960)

76 Whittaker, R. H. 1972 Evolution and measurement of species diversity. *Taxon* **21**, 213–251. (doi:10.2307/1218190)

77 Sitch, S. *et al.* 2003 Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Change Biol.* **9**, 161–185. (doi:10.1046/j.1365-2486.2003.00569.x)

78 Butzer, K. 1982 *Archaeology as human ecology: method and theory for a contextual approach*. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511558245)

79 Wrbka, T., Erb, K.-H., Schulz, N. B. N. B., Peterseil, J., Hahn, C. & Haberl, H. 2004 Linking pattern and process in cultural landscapes. An empirical study based on spatially explicit indicators. *Land Use Policy* **21**, 289–306. (doi:10.1016/j.landusepol.2003.10.012)

80 Forman, R. T. T. & Alexander, L. E. 2003 Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* **29**, 207–231. (doi:10.1146/annurev.ecolsys.29.1.207)

81 Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X. & Briggs, J. M. 2008 Global change and the ecology of cities. *Science* **319**, 756–760. (doi:10.1126/science.1150195)

82 Ellis, E. C., Wang, H., Xiao, H. S., Peng, K., Liu, X. P., Li, S. C., Ouyang, H., Cheng, X. & Yang, L. Z. 2006 Measuring long-term ecological changes in densely populated landscapes using current and historical high resolution imagery. *Remote Sensing Environ.* **100**, 457–473. (doi:10.1016/j.rse.2005.11.002)

83 Ellis, E. C. *et al.* 2009 Estimating long-term changes in China's village landscapes. *Ecosystems* **12**, 279–297. (doi:10.1007/s10021-008-9222-4)

84 Daily, G. C., Ehrlich, P. R. & Sanchez-Azofeifa, G. A. 2001 Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.* **11**, 1–13. (doi:10.1890/1051-0761(2001)011[0001:CBUOHD]2.0.CO;2)

85 Hobbs, R. J. & Huenneke L. F. 1992 Disturbance, diversity, and invasion—implications for conservation. *Conserv. Biol.* **6**, 324–337. (doi:10.1046/j.1523-1739.1992.06030324.x)

86 Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A. 2000 Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710. (doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)

87 Fahrig, L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)

88 Hobbs, R. J. *et al.* 2006 Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.* **15**, 1–7. (doi:10.1111/j.1466-822X.2006.00212.x)

89 Hegetschweiler, K., van Loon, N., Ryser, A., Rusterholz, H.-P. & Baur, B. 2009 Effects of fireplace use on forest vegetation and amount of woody debris in suburban forests in northwestern Switzerland. *Environ. Manage.* **43**, 299–310. (doi:10.1007/s00267-008-9194-3)

90 Bradley, B. A., Blumenthal, D. M., Wilcove, D. S. & Ziska, L. H. 2010 Predicting plant invasions in an era of global change. *Trends Ecol. Evol.* **25**, 310–318. (doi:10.1016/j.tree.2009.12.003)

91 Verburg, P. H., van de Steeg, J., Veldkamp, A. & Willemen, L. 2009 From land cover change to land function dynamics: a major challenge to improve land characterization. *J. Environ. Manage.* **90**, 1327–1335. (doi:10.1016/j.jenvman.2008.08.005)

92 Berglund, B. E. (ed.) 1991 *The cultural landscape during 6000 years in southern Sweden: the Ystad project.* Copenhagen, Denmark: Munksgaard.

93 Goudie, A. 2005 *The human impact on the natural environment: past, present, and future*, 6th edn. New York, NY: Wiley-Blackwell.

94 Dearing, J., Battarbee, R., Dikau, R., Larocque, I. & Oldfield, F. 2006 Human–environment interactions: learning from the past. *Reg. Environ. Change* **6**, 1–16. (doi:10.1007/s10113-005-0011-8)

95 Dearing, J. 2006 Climate–human–environment interactions: resolving our past. *Clim. Past* **2**, 187–203. (doi:10.5194/cp-2-187-2006)

96 Sandor, J. A. & Eash, N. S. 1991 Significance of ancient agricultural soils for long-term agronomic studies and sustainable agriculture research. *Agron. J.* **83**, 29–37. (doi:10.2134/agronj1991.00021962008300010011x)

97 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C. S. 2004 Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* **35**, 557–581. (doi:10.1146/annurev.ecolsys.35.021103.105711)

98 Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. 1995 The future of biodiversity. *Science* **269**, 347–350. (doi:10.1126/science.269.5222.347)

99 Jones, G., Charles, M., Bogaard, A., Hodgson, J. & Palmer, C. 2005 The functional ecology of present-day arable weed floras and its applicability for the identification of past crop husbandry. *Vegetation History Archaeobot.* **14**, 493–504. (doi:10.1007/s00334-005-0081-z)

100 Vitousek, P. M., Dantonio, C. M., Loope, L. L., Rejmanek, M. & Westbrooks, R. 1997 Introduced species: a significant component of human-caused global change. *NZ J. Ecol.* **21**, 1–16.

101 Lonsdale, W. M. 1999 Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536. (doi:10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2)

102 Sax, D. F. & Gaines, S. D. 2003 Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* **18**, 561–566. (doi:10.1016/S0169-5347(03)00224-6)

103 Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H. & Matson, P. A. 1986 Human appropriation of the products of photosynthesis. *BioScience* **36**, 368–373. (doi:10.2307/1310258)

104 Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C., Gingrich, S., Lucht, W. & Fischer-Kowalski, M. 2007 Quantifying and mapping the human appropriation of net primary production in Earth's terrestrial ecosystems. *Proc. Natl Acad. Sci. USA* **104**, 12 942–12 947. (doi:10.1073/pnas.0704243104)

105 Bowling, D. R., Pataki, D. E. & Randerson, J. T. 2008 Carbon isotopes in terrestrial ecosystem pools and CO_2 fluxes. *New Phytol.* **178**, 24–40. (doi:10.1111/j.1469-8137.2007.02342.x)

106 Marlon, J. R., Bartlein, P. J., Carcaillet, C., Gavin, D. G., Harrison, S. P., Higuera, P. E., Joos, F., Power, M. J. & Prentice, I. C. 2008 Climate and human influences on global biomass burning over the past two millennia. *Nat. Geosci.* **1**, 697–702. (doi:10.1038/ngeo313)

107 McLauchlan, K. 2006 The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems* **9**, 1364–1382. (doi:10.1007/s10021-005-0135-1)

108 Bogaard, A., Heaton, T. H. E., Poulton, P. & Merbach, I. 2007 The impact of manuring on nitrogen isotope ratios in cereals: archaeological implications for reconstruction of diet and crop management practices. *J. Archaeol. Sci.* 34, 335–343. (doi:10.1016/j.jas.2006.04.009)

109 Eidt, R. C. 1977 Detection and examination of anthrosols by phosphate analysis. *Science* **197**, 1327–1333. (doi:10.1126/science.197.4311.1327)

110 Thorp, J. 1940 Soil changes resulting from long use of land in China. *Proc. Soil Sci. Soc. Am.* **4**, 393–398. (doi:10.2136/sssaj1940.036159950004000C0118x)

111 Zhang, M. K. 2004 Phosphorus accumulation in soils along an urban–rural land use gradient in Hangzhou, southeast China. *Commun. Soil Sci. Plant Anal.* **35**, 819–833. (doi:10.1081/CSS-120030360)

112 Holliday, V. T. & Gartner, W. G. 2007 Methods of soil P analysis in archaeology. *J. Archaeol. Sci.* **34**, 301–333. (doi:10.1016/j.jas.2006.05.004)

113 Vitousek, P. M., Porder, S., Houlton, B. Z. & Chadwick, O. A. 2010 Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* **20**, 5–15. (doi:10.1890/08-0127.1)

114 Wilkinson, B. H. 2005 Humans as geologic agents: a deep-time perspective. *Geology* **33**, 161–164. (doi:10.1130/G21108.1)

115 Heckenberger, M. & Neves, E. G. 2009 Amazonian archaeology. *Annu. Rev. Anthropol.* **38**, 251–266. (doi:10.1146/annurev-anthro-091908-164310)

116 Dupouey, J. L., Dambrine, E., Laffite, J. D. & Moares, C. 2002 Irreversible impact of past land use on forest soils and biodiversity. *Ecology* **83**, 2978–2984. (doi:10.1890/0012-9658(2002)083[2978:IIOPLU]2.0.CO;2)

117 Foster, D. R., Motzkin, G. & Slater, B. 1998 Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* **1**, 96–119. (doi:10.1007/s100219900008)

118 Butzer, K. W. 1996 Ecology in the long view: settlement histories, agrosystemic strategies, and ecological performance. *J. Field Archaeol.* **23**, 141–150. (doi:10.2307/530500)

119 Walker, B. H. 1993 Rangeland ecology: understanding and managing change. *AMBIO* **22**, 80–87. See http://www.jstor.org/stable/4314051.

120 Buschbacher, R. J. 1986 Tropical deforestation and pasture development. *BioScience* **36**, 22–28. (doi:10.2307/1309794)

121 DiTomaso, J. M. 2000 Invasive weeds in rangelands: species, impacts, and management. *Weed Sci.* **48**, 255–265. (doi:10.1614/0043-1745(2000)048[0255:IWIRSI]2.0.CO;2)

122 Kaplan, J. O., Krumhardt, K. M. & Zimmermann, N. 2009 The prehistoric and preindustrial deforestation of Europe. *Quat. Sci. Rev.* **28**, 3016–3034. (doi:10.1016/j.quascirev.2009.09.028)

123 Klein Goldewijk, K. & Ramankutty, N. 2004 Land cover change over the last three centuries due to human activities: the availability of new global data sets. *GeoJournal* **61**, 335–344. (doi:10.1007/s10708-004-5050-z)

124 Wirtz, K. W. & Lemmen, C. 2003 A global dynamic model for the neolithic transition. *Clim. Change* **59**, 333–367. (doi:10.1023/A:1024858532005)

125 Klein Goldewijk, K., Beusen, A. & Janssen, P. 2010 Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. *Holocene* **20**, 565–573. (doi:10.1177/0959683609356587)

126 Turner II, B. L., Hanham, R. Q. & Portararo, A. V. 1977 Population pressure and agricultural intensity. *Ann. Assoc. Am. Geogr.* **67**, 384–396. (doi:10.1111/j.1467-8306.1977.tb01149.x)

127 Kreft, H. & Jetz, W. 2007 Global patterns and determinants of vascular plant diversity. *Proc. Natl Acad. Sci. USA* **104**, 5925–5930. (doi:10.1073/pnas.0608361104)

128 McKinney, M. L. & Lockwood, J. L. 1999 Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14**, 450–453. (doi:10.1016/S0169-5347(99)01679-1)

129 Stohlgren, T. J., Barnett, D. T. & Kartesz, J. T. 2003 The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.* **1**, 11–14. (doi:10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2)

130 Rosenzweig, M. 2001 The four questions: what does the introduction of exotic species do to diversity? *Evol. Ecol. Res.* **3**, 361–367.

131 Costanza, R., Graumlich, L. & Steffen, W. 2007 *Sustainability or collapse? An integrated history and future of people on Earth.* Cambridge, MA: MIT Press; Berlin, Germany: Dahlem University Press.

132 Cronon, W. 1996 The trouble with wilderness: or, getting back to the wrong nature. *Environ. History* **1**, 7–28. (doi:10.2307/3985059)

133 Briggs, J. M., Spielmann, K. A., Schaafsma, H., Kintigh, K. W., Kruse, M., Morehouse, K. & Schollmeyer, K. 2006 Why ecology needs archaeologists and archaeology needs ecologists. *Front. Ecol. Environ.* **4**, 180–188. (doi:10.1890/1540-9295(2006)004[0180:WENAAA]2.0.CO;2)

134 Leemans, R. *et al.* 2009 Developing a common strategy for integrative global environmental change research and outreach: the Earth System Science Partnership (ESSP). *Curr. Opin. Environ. Sustainability* **1**, 4–13. (doi:10.1016/j.cosust.2009.07.013)

135 Botkin, D. B. 1990 *Discordant harmonies: a new ecology for the twenty-first century.* New York, NY: Oxford University Press.

136 Raudsepp-Hearne, C., Peterson, G. D., Tengo, M., Bennett, E. M., Holland, T., Benessaiah, K., MacDonald, G. K. & Pfeifer, L. 2010 Untangling the environmentalist's paradox: why is human well-being increasing as ecosystem services degrade? *BioScience* **60**, 576–589. (doi:10.1525/bio.2010.60.8.4)

137 Siebert, S., Portmann, F. T. & Döll, P. 2010 Global patterns of cropland use intensity. *Remote Sensing* **2**, 1625–1643. (doi:10.3390/rs2071625)

138 Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. 2005 Farming and the fate of wild nature. *Science* **307**, 550–555. (doi:10.1126/science.1106049)

139 Rudel, T. K., Coomes, O. T., Moran, E., Achard, F., Angelsen, A., Xu, J. C. & Lambin, E. 2005 Forest transitions: towards a global understanding of land use change. *Glob. Environ. Change Hum. Policy Dimens.* **15**, 23–31. (doi:10.1016/j.gloenvcha.2004.11.001)

140 Rudel, T. K. *et al.* 2009 Agricultural intensification and changes in cultivated areas, 1970–2005. *Proc. Natl Acad. Sci. USA* **106**, 20 675–20 680. (doi:10.1073/pnas.0812540106)

141 Geist, H. J. & Lambin, E. F. 2008 Proximate causes and underlying driving forces of tropical deforestation. *BioScience* **52**, 143–150. (doi:10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2)

142 Heller, N. E. & Zavaleta, E. S. 2009 Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* **142**, 14–32. (doi:10.1016/j.biocon.2008.10.006)