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Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions

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The exhibition of increasingly intensive and complex niche construction behaviors through time is a key feature of human evolution, culminating in the advanced capacity for ecosystem engineering exhibited by *Homo sapiens*. A crucial outcome of such behaviors has been the dramatic reshaping of the global biosphere, a transformation whose early origins are increasingly apparent from cumulative archaeological and paleoecological datasets. Such data suggest that, by the Late Pleistocene, humans had begun to engage in activities that have led to alterations in the distributions of a vast array of species across most, if not all, taxonomic groups. Changes to biodiversity have included extinctions, extirpations, and shifts in species composition, diversity, and community structure. We outline key examples of these changes, highlighting findings from the study of new datasets, like ancient DNA (aDNA), stable isotopes, and microfossils, as well as the application of new statistical and computational methods to datasets that have accumulated significantly in recent decades. We focus on four major phases that witnessed broad anthropogenic alterations to biodiversity—the Late Pleistocene global human expansion, the Neolithic spread of agriculture, the era of island colonization, and the emergence of early urbanized societies and commercial networks. Archaeological evidence documents millennia of anthropogenic transformations that have created novel ecosystems around the world. This record has implications for ecological and evolutionary research, conservation strategies, and the maintenance of ecosystem services, pointing to a significant need for broader cross-disciplinary engagement between archaeology and the biological and environmental sciences.

biodiversity | extinctions | invasive species | novel ecosystems | Anthropocene

The reshaping of global biodiversity is one of the most significant impacts humans have had on Earth's ecosystems. As our planet experiences its sixth "mass extinction event" (1), the effect of anthropogenic landscape modification, habitat fragmentation, overexploitation, and species invasions could not be more apparent (2, 3). These transformations are linked largely to the industrial economies, burgeoning populations, and dense transport networks of contemporary human societies. Accordingly, the human-mediated alteration of species distributions has been characterized as a modern phenomenon with limited, and largely insignificant, historical antecedents. This conventional understanding fails to account for several decades of archaeological, paleoecological, and genetic research that reveal a long and widespread history of human

transformation of global biodiversity (4–6). The evolutionary trajectory of *Homo sapiens* has seen growing capacities for advanced cognition and demographic and geographic expansion, along with an exponential increase in the scope and impact of human niche constructing activities (7) that have culminated in fundamental changes to planetary ecosystems.

Drawing upon findings from a range of new methods and datasets, including new cross-disciplinary research programs, we explore this uniquely human trajectory and reveal a pattern of significant long-term, anthropogenic shaping of species distributions on all of the earth's major occupied continents and islands. We show that, even before the Age of Discovery, cumulative human activities over millennia resulted in dramatic changes to the abundance and

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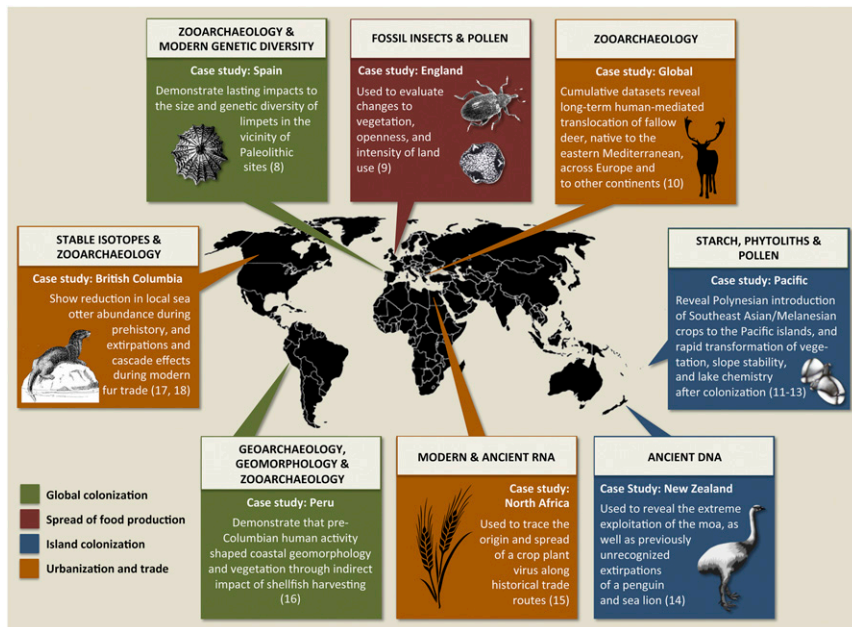


Fig. 1. Case studies in the application of archaeological science methods to understand past human-mediated biological translocations and transformations relating to the following: global colonization, origins and spread of food production, island colonization, and trade and urbanization (8–18).

geographic range of a diverse array of organisms across taxonomic groups. Few, if any, regions can be characterized as pristine. Extinction has been the starkest of these anthropogenic impacts, but widespread changes to species abundance, composition, community structure, richness, and genetic diversity as a result of human niche construction are also increasingly demonstrable and of equally lasting impact.

We highlight the role of new classes of data, such as ancient DNA (aDNA), stable isotopes, and microfossils, as well as new approaches, including powerful morphometric, chronometric, computational, and statistical methods, for understanding changes to species distributions at various scales (Fig. 1). The increasingly systematic application of traditional environmental archaeology methods in the last few decades is also yielding new insights. While acknowledging that human engagement in niche construction has very early origins, we focus on examples from four key phases of more recent and wide-reaching anthropogenic change: the Late Pleistocene near-global dispersal of *H. sapiens*; the emergence and spread of agriculture beginning in the Early Holocene; the colonization of the world's islands; and the premodern expansion of urbanization and trade beginning in the Bronze Age. Although not exhaustive, our review highlights key trends, including the significant prehistoric and historic reorganization of species distributions at local, regional, and intercontinental scales; a broadly accelerating but uneven rate of alien species introductions across multiple geographical regions; and the involvement of a wide range of species, including plant and animal domesticates, as well as a diverse array of wild, commensal, invasive, and pathogenic species. We emphasize the role of these cumulative changes in contributing to the creation of novel ecosystems over the long term. We conclude by considering the implications of an archaeologically informed perspective on contemporary biodiversity for how we understand, study, and conserve the earth's biomes, as well as how we comprehend the evolutionary pressures exerted by human ecosystem engineering.

Four Key Phases of Anthropogenic Transformation

Global Colonization. Fossil evidence demonstrates that *H. sapiens* was present ~195,000 y ago (195 ka) in East Africa (19) and that, by 12 ka, our species had dispersed to the far corners of Eurasia, Australia, and the Americas (20). Mounting evidence indicates that these Late Pleistocene dispersals, and the increase in global human populations with

which they are associated, were linked in complex ways with a variety of species extinctions, extirpations, translocations, and new modes of niche modification. Evaluating Pleistocene anthropogenic impacts remains challenging, but novel methods and approaches are providing solutions to long-standing problems posed by limited preservation and chronological resolution.

New data link the geographic and demographic expansion of *H. sapiens* to fire regime change and transformations to plant community composition. For example, pollen and microcharcoal records indicate that the early colonists of New Guinea deliberately burned and disturbed tropical rainforests to promote the growth of useful plants, especially gap colonizers like yams (*Dioscorea* spp.), which have been identified from microscopic starch residues extracted from some of the region's earliest stone tools (21). (For species other than *H. sapiens*, this manuscript employs common species names, although the scientific name for each species discussed is also provided at first mention. For humans, the scientific name is further specified when it is important to distinguish from other hominid species.) Vegetation burning also enhanced hunting opportunities by drawing game and other faunal resources to new plant growth. A human contribution to the shaping of early fire regimes has been demonstrated for Africa and, after human arrival, in Borneo, Australia, and the Americas (22–25).

The human-mediated translocation of species now dates back to the Late Pleistocene. For example, the northern common cuscus (*Phalanger orientalis*), endemic to New Guinea, was transported to eastern Indonesia, the Solomon Islands, and the Bismarck Archipelago beginning ~20–23 ka, becoming a key subsistence species (26, 27). Other taxa were also moved; together with a species of bandicoot (*Echymipera kalubu*) and the Admiralty cuscus (*Spilocuscus kraemeri*), the *Canarium indicum* tree was introduced to Manus by ~13 ka, followed a few millennia later by the rat *Rattus praetor* (26). Translocation patterns mirror patterns of maritime obsidian exchange in Melanesia in the Late Pleistocene and Early Holocene (26).

Evidence of human overexploitation has been suggested for some Late Pleistocene faunal sequences. Diverse archaeological assemblages, from Africa, Europe, and South Asia, for example, document the Late Pleistocene appearance of small, quick, and difficult-to-catch game, such as fish, birds, rabbits, rodents and monkeys, that may signal anthropogenic impacts to resource availability (28, 29). Other studies document

decreases in the size of certain species, such as limpets and tortoises, that may also reflect resource overexploitation (e.g., refs. 8 and 30). Some of these changes may result from the expansion of bone, stone, shell, fiber, and other tool repertoires in the Late Pleistocene, enabling new forms of intensive exploitation (e.g., refs. 31 and 32).

One of the most significant impacts of the Late Pleistocene expansion of our species may have been on megafauna (Fig. S1). The human role in the Late Quaternary extinction episode, which saw at least 101 of 150 genera of Earth's megafauna (animals larger than 44 kg) go extinct between 50 and 10 ka (33), has long been contentious (e.g., refs. 34–36). Recent analyses support at least a partial anthropogenic impetus in numerous regions, and a dominant human role in others (37, 38). Of particular importance are new global analyses drawing on higher resolution data and computational modeling approaches. These studies indicate an important role for humans and an inverse relationship between severity of extinction and duration of hominin–megafauna coevolution, with uniformly high extinction rates in areas where *H. sapiens* was the first hominin to arrive (39, 40) (Fig. S1).

New regional analyses support these findings. For example, recent high-resolution paleoecological and stable isotope data from Australia, where no hominins existed before ~55 ka, show that megafaunal collapse occurred during a period of climatic stability and most closely correlates with human arrival (41). Improved chronologies for various Australian and Tasmanian sites (e.g., refs. 42 and 43) support anthropogenic rather than climatic explanations for megafaunal extinctions. Chronometric resolution remains poor for South America, although recent studies support a human role in megafaunal extinction in Patagonia (44), whereas data from aDNA studies suggest that climatic extinction drivers were more influential in northern regions (e.g., ref. 45). Implicating humans in Late Pleistocene megafaunal extinctions suggests an anthropogenic role in subsequent and major biosphere transformations that followed their demise (33, 46, 47). Megafauna were keystone species whose disappearance had dramatic effects on ecosystem structure, fire regimes, seed dispersal, land surface albedo, and nutrient availability (41, 46, 48) (Fig. 2A).

Emergence and Spread of Agriculture and Pastoralism. The beginning of the Holocene (<11.7 ka) witnessed fundamental shifts in climatic and geological regimes globally, as well as in human societies. The Early to Middle Holocene in many regions worldwide saw the beginning of agricultural economies, placing new evolutionary pressures on plants, animals, and microbes, and resulting in major demographic expansions for humans (55). This Neolithic period opened the way for a radical transformation in the human capacity for niche construction, increasingly demonstrated through the accumulation of zooarchaeological

and archaeobotanical data, as well as the application of biomolecular techniques.

One of the major outcomes of the Neolithic was the inexorable spread of agriculture from ~14–20 centers of early domestication (56) to encompass large swaths of the Old and New Worlds. This expansion had unprecedented and enduring impacts on species distributions. Key among these transformations was the promotion and expansion of a range of human-favored taxa, including newly created species (and subspecies) of domesticated crops and animals. Cumulative archaeological data show that crops and animals saw significant prehistoric and historic range expansion (Fig. 3). The scale of agriculture and land use in some regions was significant; for example, expansion of land area used for livestock and rice (*Oryza sativa*) paddy agriculture was sufficient to increase atmospheric methane emissions between 4,000 and 1,000 y B.P. (57) whereas deforestation and tillage are suggested to have contributed to increasing CO₂ over the past 8,000 y (58).

Modern and aDNA studies are shedding light on patterns of genetic adaptation and hybridization that shaped crop dispersal (e.g., ref. 59) whereas plant microfossil and genetic studies are beginning to clarify the spread of tropical species (e.g., refs. 60 and 61). The geographic expansion of agricultural crops was a complex process that carried along other species and transformed local ecosystems in diverse ways (Fig. 3 A–C). Crops often moved as part of ecological packages that included nondomesticated or weed species. In the European Neolithic, for example, some crop weeds derived ultimately from the Near East whereas others were European plants promoted by anthropogenic disturbance and the novel ecologies of cultivated plots (e.g., ref. 62). Such weeds came to be important components of regional wild vegetation, in some cases becoming more common in regions where they were introduced than in their zones of origin. This naturalization occurred to such a degree that, for many of the most widespread weeds, it is unclear where in the world they originated (63).

Domesticated animals also dispersed across the world's landmasses. New high resolution aDNA, protein, isotope, and geometric-morphometric techniques join standard archaeobiological methods to reveal the expansion of different livestock species across the globe (Fig. 3 D and E). Sheep (*Ovis aries*), goat (*Capra hircus*), and cattle (*Bos taurus*) were domesticated in the Near East ~10.5 ka and arrived in Europe, Africa, and South Asia within a few millennia (57, 64). Chickens (*Gallus gallus*) were domesticated in East Asia (although the specific timing and location remains contentious), reached Britain by the second half of the last millennium before the common era (B.C.E.), and now outnumber people by more than three to one (65). Wild boar (*Sus spp.*) populations in East Asia and Anatolia were domesticated independently, and, like all major animal domesticates, pigs (*Sus scrofa*) are now

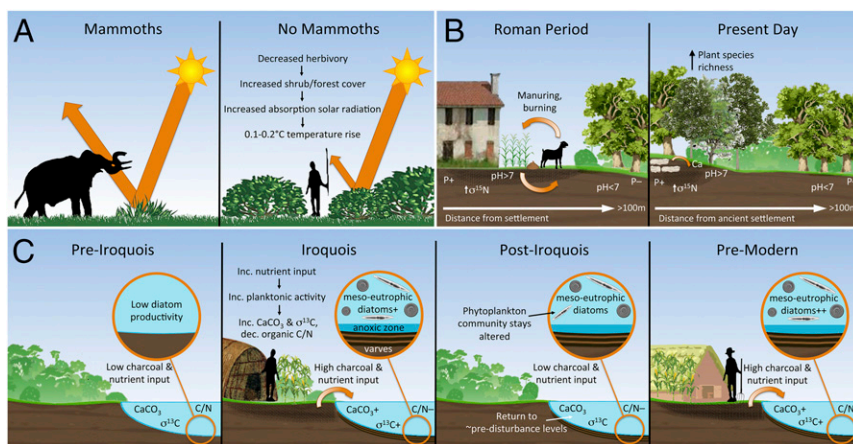


Fig. 2. Cascade effects of changes to species, showing long-term transformation of landscapes. (A) Impact of eliminating large herbivores (49). (B) Long-term effects of ancient agriculture on soil geochemistry and plant biodiversity in forests (50–52). (C) Limnological responses to cultural disturbance of lake watershed (53, 54).

associated with humans well outside their natural Old World distribution (66). Dogs (*Canis familiaris*), the only animal domesticated before the emergence of agricultural societies, are now the most abundant and ubiquitous carnivore, with an estimated 700 million to 1 billion dogs worldwide (67). The biomass of wild vertebrates is now vanishingly small compared with that of domestic animals (68).

Neolithic dispersals also featured pathogens. Ancient DNA, stable isotope, and other studies are clarifying the spread of pathogens favored by shifts in diet, lifestyle, mobility, and human–animal relationships with the onset of agriculture. Ancient DNA from *Yersinia pestis* and *Mycobacterium tuberculosis* has been identified from Neolithic human skeletons (e.g., refs. 69 and 70) and linked to large-scale population movements (69, 71). Plant and animal pathogens also spread in the Neolithic. The northwest European elm decline (3700–3600 B.C.E.) may have been caused in part by the spread of a pathogen, such as the fungal disease *Ophiostoma*, carried by the elm bark beetle (*Scolytus scolytus*), which saw habitat expansion with clearance for agriculture (72).

The spread of human populations and the species they favored altered the distributions of existing species, sometimes in synergy with Holocene climatic changes. Numerous regional studies demonstrate the link between Neolithic agriculture and the creation of more open landscapes, facilitated through various means from fire to the cutting and coppicing of trees (73, 74). For example, the early Neolithic corresponded with shifts away from deciduous tree cover in various regions of central and northern Europe (e.g., ref. 74). The spread of farmers into central Africa caused an encroachment on rainforest by some expanded savannah species (75). Early rice cultivation in the coastal wetlands of eastern China was linked to clearance of alder-dominated wetland scrub (76).

Early to Middle Holocene forest clearance correlates with a variety of broader species and habitat impacts. The transformation of forests and tall grassland into pastures that began 7–8 ka in central and northern Eurasia is linked to radically increased herbivore load due to the grazing of introduced species (77, 78). Together with forest burning, this activity significantly accentuated climate-induced vegetation change, with resultant changes in albedo in Tibet suggested to have impacted the monsoon system (78). Forest removal and agricultural activities increased erosion and impacted lake biota, including lacustrine microfloras and microfaunas (e.g., diatoms, macrophytes, and foraminifera) (Fig. 2C). Paleolimnological studies in lowland Europe, for example, suggest human-mediated increases in mesotrophic–eutrophic planktonic diatoms, including *Asterionella formosa* and *Fragilaria crotonensis*, by 5,000 y B.P. (79).

Island Colonization. The colonization of islands was a feature of *H. sapiens* expansion from the Late Pleistocene onwards but accelerated significantly in the Holocene as maritime technological advances enabled humans to reach increasingly remote oceanic islands (80). Evidence from global island-focused research programs suggests that ancient humans had major impacts on island ecosystems that often lacked the resilience of continental biomes (81, 82). Island ecologies are often characterized by high endemism, naive and/or disharmonic fauna, and low functional redundancy (83). Thus, the overall impact on islands of human-transported species, anthropogenic fire, deforestation, and predation was often the radical restructuring of island ecosystems.

Species translocations to islands were so common in the past that archaeologists often speak of “transported landscapes” (84). These new landscapes included a broad range of domesticated animals, commensals, crops, weeds, microbes, and other species carried by humans. For example, Neolithic colonizers who arrived on Cyprus brought domestic cereals, pulses, sheep, goat, cattle, pigs, domestic dogs, and cats (*Felis catus*), as well as mainland game animals such as fallow deer (*Dama dama*), fox (*Vulpes vulpes*), and wild boar beginning 10.6 ka (64, 85). Polynesian people, expanding across the Pacific after ~3,500 y B.P. (84), introduced a broad range of domesticated species, including the crops taro (*Colocasia esculenta*), yam (*Dioscorea* spp.), and banana (*Musa* spp.), and such animals as the domestic pig, chicken, dog, and Pacific rat (*Rattus exulans*). In the Caribbean, Archaic and Ceramic period peoples introduced a variety of species, including wild avocado (*Persea americana*), manioc/cassava (*Manihot esculenta*), maize (*Zea mays*), tobacco (*Nicotiana rustica*), and various trees, as well as dogs, opossums (*Didelphis* sp.), guinea pigs (*Cavia porcellus*), and shrews (*Nesophontes edithae*) (86).

Such introductions played a role in making islands more habitable for humans. Before human habitation, Cyprus had a low density of food animals (85), and the islands of the Pacific often lacked edible plants and possessed limited nonmarine fauna (87). In island Southeast Asia, humans transported a range of domesticates, as well as various species of deer, primate, civet, cuscus, wallaby, bird, shrew, rat, and lizard to generate habitats more favorable to human sustenance (27). Anthropogenic landscapes were created through species introductions, as well as habitat modification, including fire and other means, which reshaped the composition and abundance of native species. On the Pacific island of Tonga, Polynesians introduced at least 40 plant species, mostly trees, shrubs, and herbaceous cultigens (88). They burned and cleared indigenous rainforests, altering the abundance and distribution of species to favor useful native plants such as *Canarium harveyi*, *Casuarina equisetifolia*, *Erythrina variegata*, and *Pandanus tectorius* (88). Not all translocated plants were introduced for subsistence; paper mulberry (*Broussonetia*

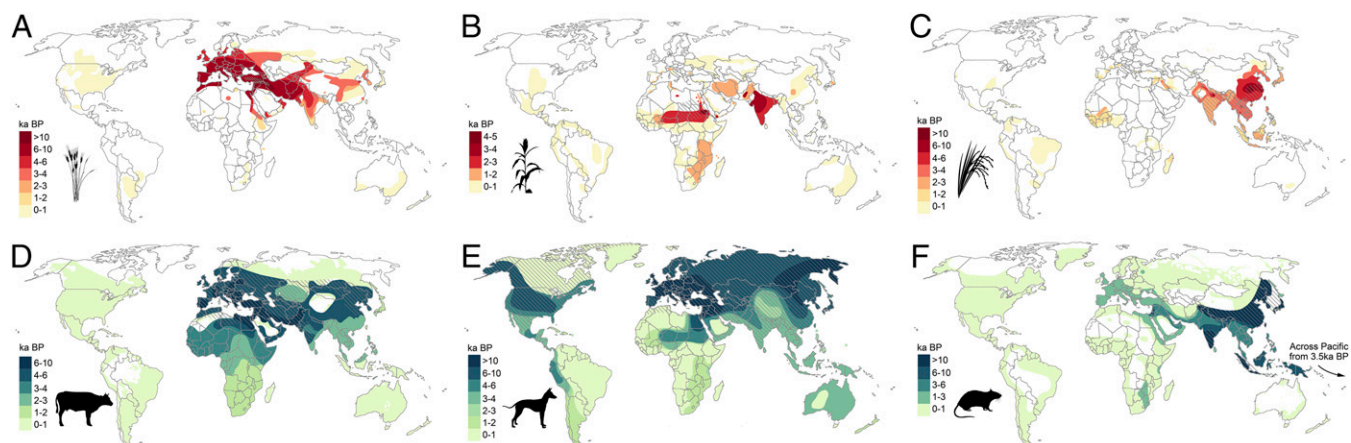


Fig. 3. Global spread of selected food crops (red) and domesticated and commensal animals (blue) through time. (A) Wheat (*Triticum* spp.). (B) Sorghum (*Sorghum bicolor*). (C) Rice (*Oryza sativa*, *Oryza glaberrima*). (D) Cattle (*Bos taurus*, *Bos indicus*). (E) Dog (*Canis familiaris*). (F) Rat (*Rattus rattus*, *Rattus tanezumi*, *Rattus norvegicus*, *Rattus exulans*). The major spread of rats to global islands beginning by 3 ka is not apparent at the scale shown. (Note that maps use different temporal scales, appropriate to individual species and their temporality of spread; hatching indicates natural distribution.)

papyrifera), for example, is a fiber crop introduced across the Pacific in prehistory for making barkcloth (89).

Numerous species were unintentionally introduced to islands, including commensal and parasitic species adapted to the human niche. Although a variety of plants were deliberately carried to the subtropical islands of Polynesia in the pre-European era, at least 17 were unintentionally introduced weed species (90). Pacific rats and black rats (*Rattus rattus*) were widely introduced to global islands as accidental stowaways on boats beginning in the Middle Holocene (Fig. 3C), as were house mice (*Mus musculus*), various commensal shrews and lizards, and numerous insects and land snails, with the movements of many now clarified through genetic and aDNA studies. Genetic data demonstrate that *Helicobacter pylori*, a human pathogen, moved with prehistoric populations expanding through Melanesia and into the Pacific (91).

Extinctions and extirpations were a common consequence of island colonization in prehistory. Thousands of bird populations in the Pacific went extinct after Polynesian colonization (92). One recent study of nonpasserine birds on 41 Pacific islands shows that two-thirds went extinct between initial prehistoric colonization and European contact (93). Bird species extinctions impact important ecosystem processes like decomposition, pollination, and seed dispersal, leading to trophic cascades (94). Human impacts have been primarily responsible for the extinction of four genera of giant sloths in the Caribbean, as well as nine taxa of snakes, lizards, bats, birds, and rodents on Antigua between 2350 and 550 B.C.E. (82, 95). Floral extinctions have not been as well-studied, but a range of island plant species went extinct on islands in prehistoric times. Pollen and wood charcoal analyses demonstrate at least 18 plant extinctions on Rapanui (Easter Island), for example, and show dense palm forest disappearing within 200 y of human settlement (96).

New chronometric data are revealing the rapidity with which prehistoric extinctions sometimes unfolded (80). New Zealand saw numerous vertebrate extinctions after Polynesian arrival (e.g., refs. 80 and 92), including the elimination of various species of moa (*Dinornis*) within two centuries of human colonization (97). Recent studies of sea lion and penguin aDNA show that several New Zealand species once thought to have survived early human impacts were extirpated soon after human arrival and replaced within a few centuries by nonindigenous lineages from the subantarctic region (98).

Extinction and extirpation rates underestimate human impacts because not all species under pressure went extinct. Although Hawaiian geese (*Branta sandvicensis*), unlike other species, survived the prehistoric colonization of Hawaii by humans, aDNA research points to a drastic reduction in their genetic diversity after human arrival (99). Zooarchaeological data from the Caribbean point to the overharvesting and decline of a variety of island marine species beginning ~2,000 y ago, with biomass, mean trophic level, and average size all radically altered (86). Research on California's Channel Islands points to similar impacts on a broad range of marine animals as a result of overexploitation by prehistoric hunter-gatherers (81, 82), patterns increasingly recognized on islands around the world.

Urbanization and the Elaboration of Trade Networks. By the Middle to Late Holocene, agriculture and the production of food surpluses paved the way for the emergence of larger human populations, increasingly dense, urbanized settlements, and more complex and intensive networks of trade, travel, and dispersal in many parts of the world. Cultural niche construction became intense and elaborate, with dramatic implications for species diversity and distributions.

Multidisciplinary datasets reveal that agricultural intensification, in response to factors like growing populations and emerging markets, was a major driver of ecological change across the Old World from the Bronze Age onwards (100). In the Near East, Bronze Age datasets reveal pervasive turnover from deciduous to evergreen oak and replacement of indigenous forest with cultivated orchard crops like olive (*Olea europaea*), grape (*Vitis vinifera*), and fig (*Ficus carica*) (e.g., refs. 101 and 102). Cereal crops and vegetation indicative of grazing and other anthropogenic disturbance (e.g., *Rumex*, *Plantago*, and *Artemisia*) increased.

Archaeological study of wood charcoal points to a decline in tree taxa richness from the Middle Bronze Age to the Late Iron Age (103). By 1000 B.C.E., one archaeologically tested model suggests that 80–85% of areas suited to agriculture in much of the Near East were cultivated (104).

Similar trends can be seen for all early urban societies that have been studied. Increased deforestation, linked to agricultural intensification and urbanization in the Iron Age, is evident in diverse sedimentary and paleoecological records in China (e.g., refs. 105 and 106). European and Near Eastern landscapes in the Roman period also saw significant transformation, with expansion of cultivation into previously marginal areas, growth of the cash crop industry, and a new emphasis on high yield agro-pastoralism (100). Sedimentary sequences across the eastern Mediterranean record the highest Holocene rates of soil erosion and sedimentation during the Classical era (102). Population growth and political expansion in lowland Mayan civilization have been linked to forest removal and erosion (107, 108).

Deforestation and the expansion of species favoring anthropogenic disturbance were not continual processes, and many sequences reveal temporary reversals in these long-term trends. For example, the arrival of plague in Europe at several points from the Late Neolithic onwards, as now confirmed by recovery of *Yersinia pestis* aDNA from human skeletons (69, 109), seems to have been linked to episodes of forest regrowth due to abandonment of agricultural fields (104, 110). By the Iron Age and sometimes earlier, however, changing species compositions were often irreversible. Recent multidisciplinary research in "ancient" forests in France demonstrated a strong correlation between Roman sites and present-day forest plant diversity, with areas altered by Roman agriculture and settlement favoring nitrogen-demanding and ruderal species (e.g., refs. 50 and 51) (Fig. 2C). Grassland diversity in present-day Estonia maps closely to Late Iron Age human population density (111).

Defaunation is another enduring legacy of ancient human activities. The emergence of socially stratified urban societies in the Near East and Egypt, for instance, was linked to the extirpation of a number of wild animal species. Onager (*Equus hemionus*), Persian gazelle (*Gazella subgutturosa*), hartebeest (*Alcelaphus buselaphus*), Arabian oryx (*Oryx leucomyx*), and ostrich (*Struthio camelus*) were all extirpated from the southern Levant, largely through ungulate mass kills, by the second millennium B.C.E. (112). Ancient urbanization contributed to a major reduction in large-bodied mammal species in Egypt, from 37 in the Late Pleistocene/Early Holocene to only 8 today (113). Roman era hunting and acquisition of wild animals for arena and other events led to species reductions and extirpations across Europe and North Africa (114). Stable isotope analysis of archaeological fish remains from northern and western Europe demonstrates that overexploitation of local fish reserves prompted increasing globalization of the fishing industry as early as the 13th to 14th century of the common era (C.E.) (115).

Despite such trends, and contrary to popularized narratives of overexploitation-fueled environmental and cultural collapse (e.g., ref. 116), recent studies also demonstrate that agricultural and other practices of early civilizations helped maintain ecosystem services. Intensification through human practices shifted carrying capacity upwards (5). Parts of the Amazon, a region long viewed as pristine tropical forest, are now known to have supported densely settled, highly productive, and powerful regional polities for millennia before European arrival (117). These societies created areas of fertile anthropogenically modified soil that enabled cultivation and the growth of populations in regions viewed today as marginal (118). Although caution is needed regarding claims of basin-wide anthropogenic alterations (119), it is clear that, in some regions, forests were converted into patchy, managed landscapes that included large-scale transformations to forest plants, animals, and wetlands (117). The Maya also created highly managed landscapes and forest gardens that enabled significant population growth and political complexity (107, 108, 120, 121). Studies in Africa demonstrate an anthropogenic role in forest creation (122), with prehistoric parallels suggested for several regions globally, including the Fertile Crescent, where oak parkland with wild cereals is argued to be ancient but largely anthropogenic (123).

The increasingly intensive long-distance translocation of species from the Bronze Age onwards was part of this wider picture of habitation transformation that was sometimes destructive and other times promoted the provision of ever-increasing human populations. Widespread translocation of invasive species like the black rat and house mouse with improved maritime and terrestrial transport systems, as revealed by zooarchaeological and molecular genetic studies (124), led to negative ecosystem and disease impacts (e.g., refs. 80 and 96). Plant pathogens and pests also spread. In Britain, for example, a range of nonnative but now established synanthropic beetle grain pests (e.g., *Sitophilus granarius*, *Oryzaephilus surinamensis*, *Laemophloeus ferrugineus*) first appeared in Roman times, probably carried over with grain imports (125).

On the other hand, through time, the extraordinary diversification of food economies based on widespread circulation of new plant and animal domesticates contributed to more diverse diets, many of which were impoverished by the prehistoric shift from foraging to food production (126). A recent estimate from Britain, where some of the most systematic archaeobotanical studies have been carried out, indicates that at least 50 new plant foods (mostly fruits, herbs, and vegetables) were introduced in the Roman period alone, with many entering into cultivation (127). Genetic and aDNA studies have revealed that various domesticates were transported between the Pacific Islands and South America, including coconut (*Cocos nucifera*) and chicken (128, 129). In short order, these taxa became key food species in their new homelands, enriching human diets and transforming ecologies. Coconut palm, for example, widely dispersed by prehistoric humans, has important impacts on the floristic, structural, and soil characteristics of forests (130). Genetic and archaeological studies demonstrate that the medieval Indian Ocean saw the circulation and adoption of a broad array of new plant and animal domesticates, many of which improved nutrient availability and agricultural resilience (e.g., ref. 131). Nondomesticated species also continued to spread in this period, with zooarchaeological and genetic (including aDNA) studies of species, ranging from snails and geckos to birds and deer, indicating anthropogenic alterations to range distributions as a result of increasing globalization (132, 133).

Broad Patterns of Ancient Anthropogenic Change

A review of global archaeological, paleoecological, and historical datasets, distilled here into key trends and examples, suggests a number of general patterns concerning the long-term human shaping of biodiversity. First, human niche construction activities have had a major impact on the abundance, composition, distribution, and genetic diversity—as well as extinction rates and translocation pathways—of species globally. Late Pleistocene human impacts are the most difficult to assess, but, placed in the context of longer-term trends, they seem highly likely, especially given that even conservative estimates of anthropogenic contribution to megafaunal extinctions, extirpations, and depletions imply significant ecosystem impacts (38, 47).

Second, there is a strong link between present-day patterns of biodiversity and historical processes (Fig. 2). The combined effects of human activity over the millennia include the creation of extensively altered, highly cosmopolitan species assemblages on all landmasses. “Pristine” landscapes simply do not exist and, in most cases, have not existed for millennia. Most landscapes are palimpsests shaped by repeated episodes of human activity over multiple millennia (5, 36, 100).

Third, there is widespread evidence for increasing rates of human-mediated species translocation, extinction, and ecosystem and biodiversity reshaping through time. This acceleration is not constant but is characterized by pulses and pauses that reflect cultural, ecological, and climatic transformations at local, regional, and global scales. These changes have increasingly concentrated biomass into particular sets of human-favored plants and animals (134).

Fourth, archaeological and paleoecological data are critical to identifying and understanding the deep history and pervasiveness of such human impacts (6, 36, 135). Ecologists and other researchers are often insufficiently aware of archaeological and other historical datasets. The continued default position among many researchers is that a landscape

or seascape that does not have obvious, contemporary human alterations has experienced little human manipulation (136). In fact, as exemplified by the revelation of dense prehistoric human settlements in parts of the Amazon, the more appropriate default expectation is one of anthropogenic transformation, regardless of how pristine a modern landscape may superficially seem.

Finally, negative consequences of human activity, such as extinction, reduced biodiversity, and habitat destruction, tend to receive more attention from researchers than examples of resilience and sustainability (100), probably because these transformations are more dramatic and visible in the archaeological record (137). The anthropogenic reshaping of species distributions, however, has been central to the creation of landscapes capable of supporting increasingly dense human populations through time. Domesticated ecosystems enhance human food supplies, reduce exposure to predators and natural dangers, and promote commerce (138). The creation of novel ecosystems (139) has enabled the provision of ecological goods and services, not just in the modern era but throughout the Holocene and in the Late Pleistocene as well (5, 100, 140).

These broad historical patterns have implications not only for how we understand the past, but also for how we address the present and the future. This realization calls for archaeologists and other historical scientists to weigh in on key ecological and political debates. One of these controversies concerns the date for the start of the Anthropocene, the current, human-dominated phase of Earth’s geological sequence (141). Even the partial and coarse-grained historical datasets currently available suggest that widespread reshaping of global biodiversity probably began in the Late Pleistocene or Early Holocene, with attendant geomorphological, atmospheric, oceanic, and biogeochemical changes (6, 141, 142). The assertion that preindustrial societies had only local and transitory environmental impacts is mistaken and reflects lack of familiarity with a growing body of archaeological data.

Another important consideration is the role of human niche construction as a major evolutionary force on the planet. Processes of human niche creation have reshaped, and continue to influence, the evolutionary trajectories of a broad array of species. Except for studies of domestication and antibiotic/pesticide resistance, however, investigation into processes of gene-culture coevolution has otherwise minimally explored the role of human culture in driving evolution in nonhuman species. However, human activities have exerted novel selection pressures that have had important evolutionary consequences not just for humans but also for the rest of the natural world (143).

Recognizing the long-term human shaping of global biodiversity is also key to understanding contemporary human-ecology interactions and to predictive modeling of future transformations. Present day landscape processes cannot be fully understood without recognizing past processes that have shaped terrestrial and aquatic ecosystems around the world for millennia. Determining the consequences of past ecological change will also inform predictions of how modern communities may respond to ongoing anthropogenic or climatic factors (113, 144). Archaeological data can additionally help prioritize conservation efforts by enabling assessment of how enduring specific types of changes to biodiversity are over the long term (145).

If an archaeological perspective is key to conservation efforts, it also challenges elements of their foundation. If change is the only constant in human-ecology relationships, it remains unclear what “natural” targets ecological restoration should aim for (139). The wholesale appropriation of land and resources for environmental ends—“green grabbing”—at the expense of the needs and livelihoods of local and indigenous groups (often seen as destructive of pristine ecologies) is also further problematized (146). Appreciation of historical data shifts conservation ecology away from concern with a return to original ecological conditions, suggesting the need for pragmatic solutions that acknowledge the integral role humans have long played in shaping natural systems (36, 139). The impact of human agency on ecosystems is neither completely avoidable nor entirely undesirable. People have inhabited a growing range of environments at ever increasing densities only through the continual anthropogenic transformation of ecosystems. Rather than an impossible return to pristine conditions, what is needed is

the historically informed management of emerging novel ecosystems to ensure the maintenance of ecological goods and services (139). Such efforts need to account for the needs of all stakeholders and balance local livelihoods against first world agendas.

Historical datasets not only caution against unrealistic goals, but also provide clues for shaping more resilient domesticated landscapes. Although anthropogenic processes have certainly had catastrophic ecological impacts through time, they have also played a significant role in generating sustainable ecosystems (138). Humans may have contributed to the Late Pleistocene megafaunal extinctions that disrupted biogeochemical cycling in the Amazon (48), for instance, but they also created extraordinary *terra preta* soils that supported productive agriculture and large human populations on nutrient-poor Amazon soils by 2,000 y B.P. (118). The fertile *terra preta* anthrosols created by indigenous Amazonians have been the focus of attempts to understand, and replicate, their unique chemistry and microbial communities to promote sustainable agriculture and long-term CO₂ sequestration (147). A variety of ancient anthropogenic ecosystems in the Mediterranean, Americas, Africa, and elsewhere are attracting attention for similar reasons (e.g., refs. 140 and 148).

Archaeologists have an obligation to share their increasing knowledge of the major anthropogenic role in shaping global species distributions, as well as other ecosystem properties. Present-day changes to the

diversity, composition, and distribution of species are part of long-term processes that need to be factored into programs of research, planning, conservation, and management. The urgent challenges of mediating and managing present-day anthropogenic forces demand a fully informed approach that recognizes that today's societies possess exceptional but not unique capacities for reshaping global ecosystems. Highlighting a long-term human role in shaping biodiversity does not absolve present-day populations of taking responsibility for Earth's environments. Instead, it reaffirms the human capacity for ecological transformation that is denied by those interest groups that challenge scientific evidence for anthropogenic global warming, and suggests that we should own up to our role in transforming ecosystems and embrace responsible policies benefiting a species that has engaged in millennia of ecological modification.

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