

Annual Review of Environment and Resources Land Use and Ecological Change: A 12,000-Year History

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Keywords

conservation, human-dominated ecosystems, social-ecological systems, deforestation, land system science, anthromes

Abstract

Human use of land has been transforming Earth's ecology for millennia. From hunting and foraging to burning the land to farming to industrial agriculture, increasingly intensive human use of land has reshaped global patterns of biodiversity, ecosystems, landscapes, and climate. This review examines recent evidence from archaeology, paleoecology, environmental history, and model-based reconstructions that reveal a planet largely transformed by land use over more than 10,000 years. Although land use has always sustained human societies, its ecological consequences are diverse and sometimes opposing, both degrading and enriching soils, shrinking wild habitats and shaping novel ones, causing extinctions of some species while propagating and domesticating others, and both emitting and absorbing the greenhouse gases that cause global climate change. By transforming Earth's ecology, land use has literally paved the way for the Anthropocene. Now, a better future depends on land use strategies that can effectively sustain people together with the rest of terrestrial nature on Earth's limited land.

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1. INTRODUCTION

The current global extent, intensity, and impacts of land use are all unprecedented in Earth history (1–5). Depending on how this is assessed, human use of land has directly transformed ecosystems across 75% to 95% of Earth's ice-free land area (5–10). Land use is now the leading cause of biodiversity losses around the world (11–14). Greenhouse gas emissions from land use remain a major cause of global climate change and were the main cause until overtaken by fossil fuels in the 1950s (15). Yet these are just two of the most prominent global ecological consequences of Earth's transformation through land use, which includes the conversion, fragmentation, and loss of native habitats, species introductions and invasions, and the pollution of soil and water (1, 11, 14, 16–19).

Land use is at least as old as humans are. An expanding base of archaeological and paleoecological evidence confirms that human societies have inhabited and shaped ecosystems for millennia across every continent except Antarctica by means of an increasingly diverse and transformative array of land use practices ranging from hunting and landscape burning to agriculture and urbanization that have left a permanent record across the terrestrial biosphere (5, 20–24). There is growing evidence that the land use practices of prehistoric, Indigenous, and traditional peoples, which have often been overlooked in global environmental change assessments, may have shaped and sustained ecosystems and biodiversity across most of Earth's terrestrial surface for thousands of years before the present time (5).

Land use: human cultural practices that alter terrestrial ecosystems for a societal purpose or purposes, including practices that reduce these alterations

Landscape: an area of land that is spatially heterogeneous in terms of land uses and/or ecological patterns This article reviews the global history of land use and its ecological consequences from the start of the current warm interglacial interval, 11,600 years ago, to the present day, revealing the deep cultural roots of Earth's transformation through land use. To make this possible, I introduce a land systems framework that enables long-term changes in land use practices and their ecological consequences to be understood across scientific disciplines and spatial scales from prehistory to present. I then review methods for reconstructing global land use histories and their ecological consequences, together with the most recent results of these reconstructions at global, regional, and biome scales. From this long history, further questions arise, together with lessons that could help to shape more beneficial land use pathways for people and the rest of life on Earth.

1.1. Land Use and Land Systems

Different disciplines understand land use differently. Ecologists and conservation scientists regularly characterize land use as a disturbance affecting terrestrial ecosystems (e.g., 25, 26). Anthropologists, archaeologists, geographers, and others who situate human societies within the ecosystems they use, as integral components (e.g., 27, 28), increasingly interpret long-term changes in land use, including the emergence and coevolution of domesticated species and agricultural societies, through theory on niche construction, cultural evolution, and the extended evolutionary synthesis (EES) (17, 20, 29–33; see also the sidebar titled Niche Construction, Cultural Evolution, and the Extended Evolutionary Synthesis). Through these theoretical frameworks, long-term changes in land use practices are understood as complex cultural traits coevolving together with the anthropogenic environments they produce, the genetic and epigenetic adaptations of crops, commensals, and other affected species, and the cultural, societal, and material changes of the societies engaging in these practices (17, 28, 33).

For land system scientists, the community of scholars who study contemporary changes in land use and land cover, land use is defined as the "the purposes and activities through which people interact with land and terrestrial ecosystems" (34, p. 53). Land system science integrates disciplines across the natural and social sciences, from remote sensing and ecology to economics, sociology,

NICHE CONSTRUCTION, CULTURAL EVOLUTION, AND THE EXTENDED EVOLUTIONARY SYNTHESIS

Many species, such as dam-building beavers, nest-building insects, and other ecosystem engineers, alter their environments in ways that change their adaptive fitness and that of others in their environments. Niche construction theory interprets these environmental alterations as the production of ecological inheritances, with evolutionary consequences analogous to those involving genetic inheritances. In a similar way, cultural evolution theory understands socially learned behaviors, such as mating calls and migratory pathways, as cultural inheritances. The extended evolutionary synthesis (EES) brings these novel forms of inheritances together with classic genetic and epigenetic inheritances within an integrated evolutionary theory that understands evolutionary changes as coevolutionary processes acting across this combined suite of inheritances (17). Niche construction theory has been widely used by archaeologists to explain the evolution of domesticated species and commensals through ecologically transformative human-environment interactions, like the propagation of favored species, tillage, and the use of fire to improve success in hunting and foraging (17, 20, 29–33). More recently, the EES and related theory on sociocultural niche construction (17) have been used to understand the coupling of long-term changes in cultures, societies, species, and environments, such as those relating to sedentism, agricultural intensification, and urbanization, as interacting coevolutionary processes (17, 28, 33).

Land system: a system composed of sustained interactions

sustained interactions between human societies and terrestrial ecosystems, i.e., a terrestrial socialecological system

Land use regime:

a suite of land use practices enacted by a society or social group across landscapes

Regime shift:

significant changes in land use regime(s) within a land unit political science, and geography. This is accomplished through the common theoretical framework of land systems, defined as the "complex, adaptive social-ecological systems shaped by interactions between (i) the different actors and demands that act upon land, (ii) the technologies, institutions, and cultural practices through which societies shape land use, and (iii) feedbacks between land use and environmental dynamics" (34, p. 53). With some exceptions (e.g., 2, 4), land system science has generally focused on understanding the causes and consequences of land use changes in recent decades, including tropical deforestation, land conflicts, and rapid urbanization, toward the goal of informing more sustainable governance of land systems (34, 35).

This review characterizes land use changes across the past 12,000 years together with their ecological consequences by viewing these as a history of land system changes defined by long-term evolutionary changes in land use practices. Although the focus is on the history and consequences of land use changes, not their ultimate causes or mechanisms, the integrated evolutionary perspective of the EES will help to characterize the empirical coupling of long-term changes in land use practices, societies, species, and ecosystems (17, 36).

1.2. Changes in Societies and Land Use Regimes

All behaviorally modern human societies, past and present, employ diverse toolkits of cultural practices to sustain themselves in landscapes biologically, materially, and socially (20, 37–40). We use the term land use regime to refer to this suite of cultural practices, including both the cultural practices of land use itself (which includes technologies), and the norms and institutions relating to land use, deployed by a given society or social group to sustain themselves. For this review, a land system is defined as a society or social group (a subset of a society or a superset of interacting societies), including its human populations and its land use regime, interacting with the biophysical landscapes they inhabit, including populations of nonhuman species, together with any movements of people, biota, materials, and energy into or out of these landscapes. By this definition, when people inhabit a landscape, they use it and shape its ecology and evolutionary processes through the land use practices characteristic of their society's land use regime.

To generalize across 12,000 years of land system change, we use a simplified categorization of major societal types based on land use regimes (Figure 1). These include hunter-gatherer, horticultural (agriculture without plows), agrarian (agriculture with plows), and industrial, and these also roughly correspond to ages of archaeological time (28, 36, 41, 42). Although these generalized societal types and ages help to characterize major global patterns of land use across millennia, land systems and their changes are complex, hybrid, nonlinear, path dependent, and context specific (28, 34, 42, 43), and they therefore differ in composition, timing, and sequence among regions and within regions (the only exception is the Paleolithic, which ends, by definition, 11,600 years ago at the start of the current interglacial interval). For example, in some regions, like the Fertile Crescent of the Near East, Neolithic horticultural societies emerged almost concurrently with the end of the Paleolithic, without a significant Mesolithic age of hunter-gatherers (44). In other regions, such as the Great Plains of North America, some societies shifted from horticulture to hunting dependence, adopting horse-facilitated hunting without fully abandoning cultivation (45). Hunter-gatherer societies may have long histories of evolving land use regimes that do not include agriculture and may depend on metals and hunting weapons acquired through trade (38). And when one society is colonized by another, land use regimes often shift dramatically (46-49). As these examples illustrate, hybrid land use regimes and societies, abrupt land use regime shifts. and reverse-sequence transitions are common. For this reason, the global categorization of archaeological ages, societal types, and land use regimes in Figure 1 should be interpreted with caution, especially when applying these to any specific region or timeframe.

		MER.	The Ar	E.M.		0-0-	
Hunter-g	Jatherer	Simple horticultural	Advanced horticultural	Simple agrarian	Advanced agrarian	Industrial	Emerging futures
Paleolithic Vild ~10,00	Mesolithic 00 BCE	Early Neolithic	Later Neolithic and Chalcolithic	Bronze Age	Iron Age	Industrial Age	
Sacred places Procuring						Protected areas Resto	Rewilding pration
Hunting Projectile Foraging Traps Fishing Dogs orest use	Broad Spectrum	foraging	Horses	Hunting preser		ndustrial fishing/hu Regulated fish foraging Ir	
Fuel gathering	Tin	nber harvest	Char	coal making defore	1	ndustrial deforestat forestation	ion
	dscape burning ropagation Weeding/ter	Forest	ry			Game parks	
	Tillag Man		-	Managed for Plow	orests		stainable forestry evolution
	Veç	geculture Cereals Gardens Crop Forest culture	fields Multicro Paddy rice Fruit, nut and Fallows Poly Swidden Private lands?	culture Terraces	Cor grafting Ornam	Scientific breeding Mechanization IPM nmercial fertilizers entals Chemical p	Full automation No-till est and weed contro c nitrogen Sustainable agricultu Vertical farms
		Livestock	- - - - - -	2 0 0 0 0 0	Planted forests	Agroforestry Mult	ifunctional forests
	Herd	ing Sheep Cattle Swine Goats	Pastoralism Water buffalo Horse Planting	Transhumance gs	Aquaculture Colo	onial ranching Industrial live	Wildlife farming estock
	Built		Sacred o Roya	groves Parks al gardens	Playin	g fields Yards Mu Infrastructure	
Temporary settleme Hearths	nts Permaner Cemeteries Middens Grana	Rc ries	Nonuments Mor ads raulic infrastruct	Cities	Highrises mproved roads Concrete stru Facto Public buildings	Railroads Brownfi uctures Highwa	
Mining		Wells Irrig		ge-scale irrigation Canals	Polders Sewers Reservoirs Aqueducts	Coa We	ion astal protection tland restoration am removal
Stone tools	C	eramic clay	Building stone	Metals		ndustrial mining	
Societal scales		Villages	Chiefdoms	States	Colonial mini Empires	Federated states	Planetary governance?
Small bands	Segmentary trik		Kingdo				governance:
Landscape use int	ensities	D	ense settlements				
	1			:		1	
	Wildlands						

Figure 1 (Figure appears on preceding page)

A rough guide to land use practices across societal types and archaeological ages. Major forms of land use practices are presented in relation to a stylized global sequence of society types and archaeological ages (after 17, 36). Note that societal types may share landscapes, and no specific society, region, or timeframe will follow this exact sequence or exhibit these exact characteristics. Wild uses have no permanent human habitation or resource acquisition. Procuring is the harvesting of biotic resources without managing populations or ecosystems. Producing manages populations of non-domesticated species and ecosystems to sustain harvests of biotic resources. Agriculture, Livestock, and Plantings manage populations of domesticated species and ecosystems to sustain harvests of biotic resources or maintain preferred landscape patterns (Plantings). Forest use (wood extraction), Forestry (forest management), and Forest culture (domesticated tree cultivation) are presented within Procuring, Producing, and Agriculture land uses, respectively. Built and hydraulic infrastructure are anthropogenic physical structures engineered to support human habitation, waste disposal, social interactions, trade, agriculture, industry and other social needs. Mining extracts geophysical resources for human use. Relative societal scales are indicated at bottom, along with their landscape use intensities, expressed in terms of the relative anthrome area used to sustain one person. Wildlands are without permanent human populations or intensive use, Cultured anthromes are continuously inhabited, with <20% of their area intensively used, Croplands and Rangelands have $\geq 20\%$ crop and pasture areas, respectively, and Dense settlements have population densities ≥ 100 persons km⁻². Abbreviations: GMO, genetically modified organisms; IPM, integrated pest management.

1.3. Landscapes, Land Use Intensification, Anthromes, and Ecology

Regional landscape: a globally significant landscape unit on the order of 100 km² Human societies interact with landscapes through land use practices that make use of and/or shape different parts of landscapes in different ways. For example, a Paleolithic hunter-gatherer society might forage in woodlands, hunt megafauna in shrublands, and settle in open land near water. A horticultural society might dwell in dense settlements together with livestock, surrounded by gardens, and hunt in the woodland fragments remaining between settlements. Because land use regimes generally interact with and shape heterogeneous landscapes, the ecological consequences of land use, including habitat fragmentation, are best assessed at the scale of landscapes, rather than as a function of specific land use types. In this review, long-term global changes in land use and their ecological consequences will thus be characterized at a regional landscape scale (50), with spatial units of approximately 100 km², by classifying the diverse spectrum of heterogeneous cultural landscapes into anthromes based on their patterns of land use and population, producing discrete categories analogous to biomes (5, 8; see also the sidebar titled Anthromes).

A general causal theory of land use change has yet to be widely accepted (34). However, there is broad empirical evidence across archaeology and land system science that variations in land use

ANTHROMES

Anthromes characterize the globally significant patterns of terrestrial ecology shaped by human populations and their use of land. Also known as human biomes, the concept of anthromes, a contraction of the term anthropogenic biomes, was introduced in 2008 to map human transformation of terrestrial ecology using an approach analogous to the mapping of natural vegetation biomes in relation to the global patterns of climate and terrain (7). In contrast with methods that reduce the rich global diversity of human-shaped landscapes to a single scale of human impact, from low to high, as with the mapping of human footprint (6) or human modification (9), anthromes use a rule-based system to stratify regional landscapes into a spectrum of discrete categories in relation to variations in population densities and intensive land uses (crops, pastures, and cities) (5, 8). Intensive anthromes characterize landscapes with more than 20% cover by intensive land use, cultured anthromes have lower levels of intensive land use and population, and wildlands are areas without evidence of human populations or intensive land use. Rather than homogeneous areas, anthromes represent heterogeneous landscape mosaics that emerge through sustained human-environment interactions, including less intensive land uses such as foraging, hunting, forestry, conservation, and fallow, together with the remnant habitats left embedded within the working landscapes of anthromes in varying amounts (5, 7, 8, 17).

intensity, defined as the relative amounts of food, resources, and other social needs that can be met per unit land area, tend to be directly correlated with the societal demands to meet these needs from a given landscape (17, 34, 51). In other words, higher land use intensities tend to be associated with increasing societal demands, although this relationship is not universal nor is it necessarily causal one way or the other. This relationship also leads to an association between landscape use intensification and larger-scale societies, defined in terms of larger total populations, higher population densities, more levels of hierarchical organization and/or greater wealth/power inequality, and/or higher per capita economic demands (17, 36, 41, 52). As illustrated at the bottom of **Figure 1**, general differences among societal types and their land use regimes may also be characterized in relation to societal scales and levels of landscape use intensity: the relative land use intensity of an entire landscape, part of which may not be used to meet societal needs for food or resources.

Figure 2 illustrates the potential ecological consequences of different societal land use regimes interacting with a stylized woodland landscape. Although this depiction is highly simplified and theoretical, it helps to illustrate how differences in land use regimes play out across heterogeneous landscapes. For example, in all land systems, denser human settlements and more intensive land uses, like cultivated and irrigated crops, tend to be concentrated in level terrain near water, with less intensive uses like livestock grazing and forestry in steeper terrain. Figure 2 also illustrates how land use can create heterogeneity, including habitat fragmentation, by dividing larger patches into fragments, introducing patches of crops and other plantings, and through processes of land abandonment and regrowth.

The top of **Figure 2** shows landscapes shaped by different land use regimes, in relation to indicators of relative land use intensity across each landscape (relative to the maximum possible for each society) and the relative area of intensively used land (built, cultivated, grazed). Together, these indicators constitute a measure of landscape use intensity as a whole. The classification of cultural landscapes into anthromes is also illustrated at the simplest level, with low levels of population and intensive land use shaping cultured anthromes, and larger areas of more intensive land uses (crops, pastures) producing intensive anthromes, including croplands and rangelands, with dense settlements classified in areas with dense populations and/or large urban areas. In this way, anthromes broadly categorize landscapes in terms of their relative landscape use intensity and population density, even though land use regimes produce diverse, heterogeneous, and multifunctional landscapes that also include varying amounts of nonintensive land uses, including hunting and foraging, forestry, conservation, ornamental plantings, and patches of remnant and novel habitats. It is this combination of human populations, land use regimes, and the heterogeneous landscapes that emerge from sustained human-environment interactions that together produce the ecological consequences of land use at regional landscape scales.

2. LAND SYSTEMS AND LAND USE PRACTICES

To understand long-term changes in land use and their ecological consequences, it is first necessary to understand the very different land use regimes of different types of societies and how they emerged to shape landscapes, ecosystems, and evolutionary processes around the world. A basic review of land use practices within and across societal types is presented here, assisted by the conceptual diagrams in **Figures 1** and **2**.

2.1. Hunter-Gatherers

Hunter-gatherers are the most diverse, most widely distributed, and longest-sustained human societies on this planet, with a history stretching from the Pleistocene to the present day (22, 38).

Land use intensity: the relative productivity of a used land area in meeting demands for food, resources, or other social needs

Landscape use intensification:

changes in land use within a landscape to enable more food, resources, or other social needs to be met per unit landscape area

Landscape use

intensity: the relative productivity of an entire landscape in meeting demands for food, resources, or other social needs; a combination of relative land use intensity and the relative amount of intensively used land area

Relative land use

intensity: the level of land use intensity relative to the maximum possible for a given land use regime

Intensive land uses:

land use regimes that transform ecosystems to sustain agriculture (crops and pastures) and built infrastructures, including permanent settlements

Intensively used

land: land in active intensive land use, including crops, pastures, and built up (urban) lands



(Caption appears on following page)

Figure 2 (Figure appears on preceding page)

Land systems, landscapes, anthromes, and the ecological consequences of land use. Conceptual diagram illustrating a stylized woodland landscape transformed by the land use regimes of different societal types, including spatial variations in relative land use intensity (relative to the maximum possible for each society; shown in *purple* areas) and relative amount of intensively used land area (built, cultivated, grazed; shown in *brown* areas). Spatial variations in population density, land use, and land cover are illustrated across landscapes, together with their mapping into anthromes (at the level of anthrome types) based on population densities and land use proportions, as described in **Figure 1**. Ecosystem effects are depicted for net primary production, biomass combustion in situ (lightning fires, fire escape, and fire practices, e.g., firestick farming and land clearing), ex situ (cooking, heating, smelting), and fossil fuels, organic carbon accumulation in vegetation biomass and soils, and reactive nitrogen and available soil phosphorus. Biodiversity effects (changes in biogeographic and evolutionary processes) are depicted for the relative size and isolation of woodland habitat patches, megafauna biomass (not including humans; native and domesticated), plant species richness of native, exotic, and domesticated plants, and relative landscape area without human populations or land use ("wild"), shaped by human influences but not used intensively ("novel") and intensively used ("intensive"). Figure adapted from Reference 17.

Defined as societies dependent on hunting, foraging, and fishing (22, 53), hunter-gatherer is more of a broad category than a type of land use regime (54). Some definitions encompass all hominin societies (55) and even the mega-omnivore niche in general (26). Moreover, the use of stone tools to hunt, forage, and process foods, and the control of fire to cook food and provide heat, which radically expanded foraging effectiveness and increased the breadth of the hominin niche, emerged before *Homo sapiens* (55). Nevertheless, despite clear parallels and shared ancestry among hominin hunter-gatherers of the upper Paleolithic, by the start of the current interglacial interval 11,600 years ago, only modern *H. sapiens* remained, in diverse hunter-gatherer societies established across every continent except Antarctica.

Even the least complex hunter-gatherer societies of 12,000 years ago were likely much more complex than those of any prior hominin, with a depth of cultural knowledge and practice enabling the utilization of a rich diversity of plant, animal, and fungal species through an increasing diversity of tools and technologies, including the use of projectiles (spears, atlatl, bow and arrow), traps, and collaborative hunting with dogs (56), that are believed to have contributed to earlier declines and extinctions of megafauna and landscapes reshaped through trophic cascades (17, 20, 39, 54, 55, 57–59). In many regions, the cultural capacity to utilize an ever-broadening range of species in different ways and with increasing intensities accelerated through a process that has been described as the Broad Spectrum Revolution (60, 61; see also the sidebar titled The Broad Spectrum Revolution). This process of landscape use intensification enabled hunter-gatherers to

Cultured anthromes: inhabited landscapes with <20% of their area intensively used

Intensive anthromes: inhabited landscapes with \geq 20% of their area intensively used

THE BROAD SPECTRUM REVOLUTION

The Broad Spectrum Revolution (BSR) hypothesis originated in the 1960s to characterize evidence that the number of species utilized by Near Eastern hunter-gatherers increased rapidly in the millennia preceding the emergence of agriculture (60). The term was soon applied to similar observations of rapid dietary diversifications observed prior to the emergence of agriculture in late-Pleistocene hunter-gatherer societies around the world. Initial explanations for the BSR hypothesis invoked the expanded food demands of increasing hunter-gatherer populations, in crowded, marginal, or degraded environments, as a landscape use intensification process analogous to the classic model of agricultural intensification in response to population growth. More recent explanations have used theory on niche construction and cultural evolution to explain increasing societal capacities to utilize more species, through a focus on more optimal environments and through environmental alterations to support food production, like burning, tillage, and transplanting that may have facilitated sedentism, population growth, and further increases in food demands, setting the stage for agriculture (60, 61).

Hunter-gatherer food production:

ecosystem engineering practices such as landscape burning and the propagation of favored species that enable landscape use intensification without dependence on domesticates obtain more food and resources from the same landscapes and to utilize new landscapes, allowing Broad Spectrum foragers to more broadly establish, increase, and spread their populations and cultures, leading to ever more widespread shaping of ecosystems and increasing evolutionary pressures on nonhuman species (39, 60, 61).

By the end of the Paleolithic, archaeological evidence shows that many hunter-gatherer societies were enhancing their success at hunting and foraging through a variety of cultural practices, including the burning of vegetation and the propagation of favored species (30, 40, 44, 61, 62). These practices of ecosystem engineering and novel species interactions, together with the tending, weeding, tillage, manuring, pruning, replanting, and transplanting of favored wild plant species and the protection, taming, and herding of favored wild animal prey, have been described as low-level food production (40), and more generally, as hunter-gatherer niche construction (30, 63). The precise timing, extent, and degree to which hunter-gatherer producing practices were common around the world remains a subject of active research, with much of what is known inferred from studies of contemporary hunter-gatherers, such as firestick farming by some Indigenous Australians (27, 30, 64-68). Nevertheless, hunter-gatherer food production is a form of cultural landscape use intensification that reshapes ecosystems and introduces coevolutionary relationships that help to put nonhuman species on the road to domestication (20). At the same time, the benefits of living near and using the more productive parts of landscapes, whether produced naturally or by cultural practices (61, 69), likely encouraged and facilitated the first permanent settlements near productive floodplains, freshwater and coastal environments. With permanent settlements came also the first permanent built structures, together with granaries and ceramic vessels to store harvests, middens, extensive cemeteries, harvests of timber and the mining of clay, symbolic earthworks, and other land use practices in support of larger-scale sedentary societies living in heterogeneous cultural landscapes shaped by generations of evolving cultural land use regimes (at right in Figure 2).

2.2. Horticulture and Early Agriculture

The first agricultural societies, defined by dependence on domesticated crops, likely emerged among food-producing hunter-gatherers with long histories of propagating their favored plant species in environments managed by tillage and other cultural practices that facilitated the coevolution of people and plants (30, 31, 43, 44, 70). Early agricultural societies, known as horticultural societies for their use of hand tillage, emerged in more than a dozen independent and overlapping regions through a variety of different and sometimes parallel pathways, and through the gradual spread and evolution of cultural practices and biota (29, 42, 44, 45, 51, 62, 71, 72). Some early horticultural land use regimes may have resembled those of firestick farming (65), shaping dynamic mosaics of cropped and fallow patches across landscapes that resemble the swidden, or shifting cultivation systems, still operating in some regions today (73, 74). However, there is increasing evidence that the first farmers of some regions, including the Near East, may have cultivated small gardens of annual crops near permanent settlements through intensive practices that included the manuring of soils, with swidden systems evolving later (29). In contrast with the early cereal domestications of the Near East and other Temperate Zone societies, the emergence of agriculture in tropical woodlands and elsewhere may have begun through vegeculture, the cultivation of asexually reproducing plants like taro, cassava, yam, and banana, and through polycultures of these with palms, fruit trees, vegetables, and cereals (62, 68, 71, 72, 75-77).

The first horticultural landscapes emerged around the world through diverse land use practices that ranged in intensity from woodland mosaics shaped by hunting, foraging, and shifting cultivation in multidecadal long fallow systems that allowed mature trees to regenerate, to densely populated village landscapes ringed by richly manured cereal and vegetable gardens (29, 42, 51, 68, 75). Recent molecular and archaeological evidence confirms that domesticated species emerged more broadly around the world than was previously believed, in more than a dozen distinctive centers of origin spread across the Old and New Worlds, with some domesticates then spreading rapidly across continents (62). Evidence for domesticated crops is earliest in the Near East, where domesticated wheat dates to 11,000 years ago, followed by domesticated squashes 10,000 years ago in Meso-America (Cucurbita pepo) and South America (Cucurbita moschata) together with manioc and other root crops. These are joined later by a rapidly increasing array of plant and animal domestications occurring between 8,000 and 4,000 years ago in South and East Asia, Africa, and Arabia (62, 75). In contrast with Africa, Arabia, and India, where animal domestications appear millennia before plants, the opposite is evident in the New World (62). Explanations for differences and parallels in the timing and sequence of domestications remain subject to active debates, with pathways likely varying among regions owing to multiple differences, including the relative stability versus dynamics of regional climates, the suitability and susceptibility of local species to domestication, and the dynamics of social changes favoring domestication, including sedentism, social inequality, and property rights (51, 62).

In general, over time, increasingly intensive land use regimes evolved together with largerscale societies and began to include irrigated cereals and the cultivation of wetland rice and other highly productive wetland crops, fruit and nut trees, and the construction of major earthworks and monumental stone structures as part of early urban settlements dependent on trade (78, 79). Some domestic livestock likely evolved among settled agricultural people, through a variety of pathways, including commensalism (e.g., pigs, chickens) and the management of captive herds, both in pens and on grazing lands [e.g., cattle, sheep, goats, and water buffalo (62, 80, 81)]. Investments in intensive crops, domestic livestock, and specialized elites dependent on trade may also have incentivized social arrangements including private property and inequalities that further shaped landscapes, such as walled cities, fences, and borders, although the opposite pathway has also been proposed (31, 51, 69).

2.3. Pastoral Systems

Pastoral societies, sustained by the grazing of domesticated livestock, emerged in different regions through multiple pathways that remain subject to competing claims (31, 62, 63, 80–85). Three main pathways of animal domestication have been identified: the prey pathway, in which societies manage prey species to improve their productivity, shifting from game management to herd management; the commensal pathway, in which domesticates coevolve through their attraction to a shared anthropogenic habitat; and the directed pathway, in which societies already dependent on domesticates intentionally apply selection for tameness and other traits to favored species (80, 81).

In some regions, including sub-Saharan Africa, the main pathway appears to be the domestication of prey by mobile hunter-gatherer societies, who retained nomadic lifeways (81, 82). In others, as in the Near East, overhunting by sedentary hunter-gatherers is implicated in prey adaptations leading to domestication (83). Commensalism is implicated in the domestication of dogs (80, 81). Either way, different forms of human-domesticate relations evolved into nomadic pastoralism, transhumant pastoralism (seasonal grazing), and sedentary pastoral systems, including integrated farming and extensive ranching, and gradually spread across the old world (42, 80, 84, 86). Notably, pastoralism in the Americas was restricted to the Andes until after 1500 CE (22, 49). In general, open landscapes dominated by grasses, forbs, and shrubs are optimal for livestock grazing. Pastoral land use regimes therefore either tend to clear woodlands to facilitate grazing (as illustrated in **Figure 2**) or are specialized in drylands where open vegetation predominates naturally, partly as a result of grazing by wild species. In woodland biomes, pastoral land use transforms landscapes most dramatically, through the clearing of trees and maintenance of open pasture lands, which can include the cultivation of domesticated forage crops (4). In drylands, ecosystem transformation through grazing can range from the barely perceptible effects of infrequent and temporary low-density livestock grazing, to dramatic shifts in productivity and biotic communities under intensive continuous grazing (4).

2.4. Agrarian Systems

Agrarian societies are defined by the adoption of plows and draft animals to enable larger scales of crop cultivation and surplus production in support of larger and increasingly unequal nonagricultural populations in cities (51, 78, 87). The first wooden plow, or Ard, and the use of cattle for traction, likely dates to Chalcolithic (Incipient Bronze Age) societies of the Near East more than 6,000 years ago (51, 81, 85, 88). From this time, animal traction and improved plows appear to have spread from the Near East to more densely populated agricultural regions across the Old World, including East Asia, within one or two millennia, with the exception of sub-Saharan Africa (52, 88). Ongoing innovations, including iron plowshares, emerged and spread, enabling larger and larger proportions of landscapes to be cultivated, and, when supported by irrigation, manuring, green manuring (planting of legumes and other fertility-enhancing plants), terracing of slopes, farmer-improved varieties, and even purchased inputs in some cases, landscape use intensity could be increased dramatically and sustained. These practices also increased the production of surpluses that could be extracted to sustain ever larger urban elites through systems of taxation and commerce operating at increasing spatial scales, while at the same time increasing labor demands and hardships for rural populations (2, 17, 41, 52, 87, 89). Notably, some complex large-scale agricultural societies, including those of the Americas, sustained densely populated urbanized societies rivaling any of the preindustrial Old World (87, 90, 91) without plows, animal traction, or metallurgy, through intensive horticultural land use regimes such as the Aztec Chinampa system, a form of intensive wetland cultivation (52, 88).

Agrarian land use regimes tend to be best suited to level plains and the most fertile soils and they also tend to use them to their full extent (88) (Figure 2). Depending on societal demands, steeper slopes may also be terraced to sustain production, and these and other less suitable lands may be used for livestock grazing, leaving only the most remote and unsuitable areas covered by native vegetation, where traditional hunting and fuel gathering may then intensify to satisfy the demands of dense rural populations (17). Although agrarian societies are composed mostly of subsistence farmers, agrarian landscapes tend to be increasingly restructured to sustain nonagricultural populations in cities through trade and taxation, including large-scale infrastructure projects, canals, reservoirs, irrigation projects, improved roads, concrete structures, highrises, public buildings, sewers, and ports (2, 41, 87, 89). Agrarian societies engaging in metallurgy also introduced larger-scale mining and widespread deforestation to produce charcoal to smelt metals (92). The imperial and commercial demands of colonial states, including early states in both the Old and New Worlds, also began to shape landscapes well beyond their borders through expanded mining, deforestation, and commercial plantations sustained by diverse forms of forced labor, including slavery, in increasingly globalized commodity production systems (41, 52).

2.5. Industrial Systems

Industrial land systems are defined by the use of mechanization and other commercial technologies to produce commodities demanded by large urban populations. Arguably, by introducing land use regimes aimed primarily at meeting the demands of urban, not rural, populations through increasingly globalized commercial supply chains, preindustrial colonial plantations paved the way for industrial land systems (2, 41, 52). Mechanization sustained by energy from fossil fuels, combined with commercial yield-increasing technologies, including chemical fertilizers and pest control, commercially produced seeds, and other purchased inputs, enabled industrial land use regimes to radically increase landscape use intensities while also vastly reducing rural labor demands, further increasing rural-to-urban migration (2, 17, 41).

The depopulation of rural areas and increasing scales of agriculture and settlements have tended to homogenize industrial agricultural landscapes through land consolidation, hedgerow removal, wetland drainage, and other landscape simplifications (93). However, the costly investments needed to operate high-yielding industrial land use regimes also lead to their implementation almost exclusively in the most level and productive soils, where economic returns are maximized (17, 34). As a result, less productive marginal lands with long histories of prior agricultural land use have been abandoned in many industrial regions, leading to the regeneration of forests (Figure 2) through a process known as forest transitions (34, 94; see also the sidebar titled Forest Transitions), that is also associated with rural-to-urban migrations and rapid urbanization (95). This abandonment of intensive land uses in parts of industrial regions, mostly in the Temperate Zone, is also caused by shifts in commodity production to less developed regions, including tropical woodlands, where industrial deforestation, crop production, plantations, livestock ranching, and increasingly intensive hunting pressures can cause widespread deforestation, biodiversity losses, and other dramatic ecological changes (11, 19, 34, 94, 96). Increasingly urban populations also shape landscapes through their proliferation of built infrastructures including railroads, highways, apartment buildings, factories, and other conventional gray infrastructures. At the same time, urbanized societies also create abandoned brownfields and green infrastructures of household yards, parks, and infrastructure decorated with plantings of domesticated ornamentals and turfgrass, among many

FOREST TRANSITIONS

Forest transitions are sustained shifts from net deforestation to net reforestation within a specific region (for reviews, see 34, 94). First identified in developed regions of Europe starting in the late 1800s CE, forest transitions are now increasingly observed in contemporary temperate and tropical regions around the world. Early forest transitions in Europe and elsewhere were originally explained by an economic development pathway in which urbanization and industrialization drove labor scarcity in agriculture, leading to agricultural intensification on the most suitable lands and abandonment of less productive agricultural lands, where woodlands regenerated spontaneously. More recently, economic forest transitions are also explained through a land use displacement pathway, in which woodlands recover in one region and expand in another, when agricultural demands of wealthier regions are outsourced through globalized supply chains. In recent decades, additional pathways have emerged, including state and NGO-supported tree planting programs and through land use policies and regulatory pathways supporting forest conservation and restoration. Smallholder agroforestry, land conflict and displacement, and other pathways have also been identified. Given this diversity of pathways, forest transitions associated with reductions in intensive land use and woodland recovery in any specific region may or may not result in net global woodland recovery, depending on the degree to which land use is intensified versus displaced to other regions.

others (Figures 1 and 2) (97, 98). Urbanized lifeways have also increased demands for land use in support of recreation, conservation, restoration, and a diversity of other land uses in landscapes managed for multiple functions, or multifunctional landscapes (93, 98–102).

3. RECONSTRUCTING LAND USE HISTORIES

Reconstructing global land use changes over the past 12,000 years requires the expertise of multiple disciplines, including the site-based and regional evidence from archaeology and paleoe-cology, historical and contemporary census data, and remote sensing for land use and populations. These must then be integrated through global models to produce spatially explicit historical reconstructions.

3.1. Archaeology, Paleoecology, and Environment

Archaeologists and paleoecologists use a wide array of tools and approaches to reconstruct the state and history of land use across sites and regions from the remains of plants and animals, artifacts, and other evidence (20, 22, 103, 104). Long-term changes in cultural fire regimes are reconstructed from charcoal records (24) and pollen records in sediments, and these have been extrapolated to develop spatially explicit regional and hemispheric reconstructions of vegetation cover history (23, 104). Archaeologists have long used storage vessels, built structures, tools, and other material cultures to infer the land use practices of prehistoric societies. Now, the remains of food, textiles, and other biological materials, including seeds, phytoliths, and other plant remains, the bones of animals, and residues of cooking and food storage, are being excavated, identified, analyzed, and dated to assess changes in societies, land use practices, and their evolutionary consequences across space and time (28, 62, 70).

The early evolution and spread of domesticates, both plants and animals, and the weeds and other commensals that shared the constructed niche of cultural landscapes, have been pushed back in time through a variety of novel methods (20, 44, 72, 81, 83, 105–107), including the recovery of ancient DNA from people, commensals, and domesticates (108, 109). Radiocarbon datasets (110), ancient DNA (109), and language-based studies (111) are increasingly aiding reconstructions of human population densities and the spread of specific human populations together with their land use regimes and favored and commensal species. For example, ancient DNA revealed a multistep spread of the first herders into sub-Saharan Africa (84, 112). This increasingly powerful archaeological toolkit has led to surprising recent discoveries, including the cultivation of squash and manioc in artificial islands in Western Amazonia more than 10,000 years ago (75), the domestication of sorghum more than 5,000 years ago in Eastern Sudan (113), and the cultivation of bananas on the island of New Guinea more than 7,000 years ago, together with a later spread across Oceania, to India and even to Africa, by 2,000 years ago (72).

New tools for mapping landscapes are expanding the spatial scales of archaeological reconstructions, including high-resolution satellite imagery, LiDAR, RADAR, 3D landscape reconstructions using drones and computer vision, Cold War spy imaging, and other techniques, exposing wider extents of agricultural land use, settlements, and infrastructure than previously known, even in some well-studied regions (114). For example, LiDAR imaging uncovered vast hydraulic infrastructure supporting Angkor (115) and huge expanses of mounds, plazas, and causeways surrounding Maya cities (90) and even their intensive horticultural landscapes (91), all previously hidden under dense forest canopies. Archaeologists are also expanding on their classic site, sample, and landscape-scale assessments through the use of collaborative mapping at regional scales, enabling spatially explicit regional reconstructions of long-term changes in land use (86, 116), including a recent collaboration that mapped early land use changes across 146 regions spanning the globe over the past 10,000 years (22).

3.2. Model-Based Reconstructions

The first spatially explicit global land use reconstructions spanning the past 12,000 years were published around 2010 (2, 104): HYDE 3.1 (117) and KK10 (118). Designed to represent land use alterations of land surface geophysics and biogeochemistry in Earth system models, multiple spatially explicit land use reconstructions have now been developed for shorter intervals and/or specific regions (3, 104). Although KK10 is still in use, HYDE, now in version 3.2 (4), is the only available \geq 10,000-year global reconstruction that is still under active development.

HYDE 3.2, like most other global historical land use reconstructions, is a spatially explicit backcasting model that predicts past patterns of land use at regional landscape scales using different data and methods for different time intervals. For recent decades, remote sensing and statistical data are used to generate maps of population and land use directly. These contemporary maps are then backcasted to prior times using historical records of land use and population, to the extent that these are available. Historical-data-based reconstructions are then backcasted to 10,000 BCE, first by projecting spatial patterns of human populations back to estimated populations for 10,000 BCE, and then by allocating land use to populations using regional estimates of historical land use per capita and a spatial allocation model that includes proximity to urban settlements, climate constraints, soil suitability, and distance to river floodplains (4, 117, 119, 120).

Both KK10 and HYDE, especially HYDE 3.1, have been widely criticized by archaeologists, paleoecologists, and geographers for underestimating land use by early farmers and for underrepresenting hunter-gatherer populations (2, 22, 53, 104). Although HYDE 3.2 has also been criticized for these issues (22, 104), it includes substantial improvements in representing early populations and land use, and it remains the most up to date spatially detailed representation of global patterns of land use and population that can support the mapping of cultural landscapes using anthrome classification over the past 12,000 years (5).

4. GLOBAL, REGIONAL, AND BIOME HISTORIES

Global, regional, and biome-level reconstructions of land use and populations over the past 12,000 years are illustrated using anthrome maps in Figure 3, and by changes in anthrome areas in Figures 4 and 5. As with most contemporary global assessments (6–11), anthrome mapping indicates that most of Earth's landscapes were transformed by land use by 2017 CE, with 51% of land in intensive anthromes, 30% in less intensively used cultured anthromes, and just 19% in uninhabited wildlands. Although wildlands were slightly more extensive 12,000 years ago (27.5% of global land), most of Earth's land (72.5%) was already shaped by hunter-gatherer land use regimes into the cultured anthromes that covered the vast majority of Europe, Asia, Africa, and Latin America and Caribbean (5, 22). Wildlands lingered in parts of the Near East, Eurasia, North America, and Oceania owing to their larger shares of arid and colder biomes (right side of Figure 5), but a substantial extent of what appears as uninhabited areas are likely errors resulting from biases in historical reconstructions (5, 22, 46, 48). Major uncertainties remain in all maps and estimates of early populations and land use (120), including those presented here in Figures 3-5. In particular, although archaeologists generally agree that HYDE 3.2 is a clear improvement over HYDE 3.1, this reconstruction still tends to underrepresent the extent of early human populations, and even contemporary populations, especially in areas with nomadic, seasonal, and other temporary forms of land use, and also depicts intensive agricultural land use beginning in many regions millennia later than archaeologists believe to be correct (22).

Wildlands: landscapes without evidence of human habitation or active land use









Residential woodlands Populated woodlands Remote woodlands Inhabited drylands

Rangelands



Residential
Populated
Remote

Croplands



Residential irrigated Residential rainfed Populated Remote

Villages



Rice Irrigated Rainfed Pastoral

Dense settlements



Urban Mixed settlements

(Caption appears on following page)

Global maps of anthrome change, 10,000 BCE, 1 CE, 1500 CE, 1900 CE, and 2017 CE. Anthrome maps classified in detail, based on Reference 5. Wildlands and Cultured anthromes as in **Figures 1** and **2**; Intensive anthromes have $\geq 20\%$ intensive land use area. Cultured and Intensive anthromes are further stratified by population densities, in persons km⁻², as Remote (>0 to <1), Populated (1 to <10), Residential (10 to <100), Inhabited (>0 to <100), Villages and Mixed settlements (100 to <2,500), and Urban ($\geq 2,500$). Intensive anthromes are further stratified based on their dominant intensive land use area $\geq 20\%$ in order of most intensive use (urban > rice > irrigated > cropped > pastured). Woodlands combine all forest and woodland biomes (180); Drylands comprise the remaining biomes, from savanna to tundra, excluding permanent ice. Black lines differentiate world regions. Maps in Eckert 4 projection. Abbreviations: BCE, Before the Common Era; CE, Common Era.

4.1. Regional and Biome Trends

The most general long-term trend in land use history is the decline of hunter-gatherer landscapes with the increasing spread and intensification of agriculture (22). This is illustrated in **Figures 3–5** by shifts from the less intensively used cultured anthromes of hunter-gatherers and early farmers to the intensive anthromes of larger-scale agrarian and industrial societies. For most of the past 12,000 years, the global extent of intensive anthromes has gradually increased. However, dramatic accelerations and decelerations of this global intensification are evident at different times in different regions and biomes.

The earliest regional shifts to intensive agricultural and pastoral anthromes are evident in Asia, Europe, and the Near East, where these become significant by 1,000 BCE and even earlier (**Figure 4**). In multiple regions, intensive anthromes increased and then shifted back to cultured anthromes, tracking societal dynamics like the rise and decline of the Roman Empire in Europe (4), the Han Empire in China, and the expansion of tropical city states circa 1000 CE like the Ghana Empire (121), Angkor (115), and the Classic Maya (122). Also apparent is the dramatic collapse of populations and land use across Latin America and the Caribbean caused by colonial-ism and disease during the Columbian Exchange, circa 1500 CE [The Great Dying (48, 49)]; the notable absence of this dynamic in North America is likely in error (5). Rangelands also appear in the Americas only after the colonial introduction of grazing livestock (4).

Most of Europe was transformed into intensive anthromes by 1000 CE, a level of regional landscape transformation not reached in Asia, Africa, Latin America and the Caribbean, and Oceania until the 1900s, and not at all in other regions (**Figure 4**). Among the most dramatic accelerations of land use intensification in history appear across the Americas and Oceania in the 1800s, caused by European and settler colonization, although a regional land use acceleration of similar order also appears in Europe around 700 CE. The expansion of pastoralists and rangeland anthromes across Africa is evident by 2,000 BCE and is nearly continuous to the current time, although cropland and village anthromes expand significantly in the late 1800s. Densely populated village and urban anthromes begin to cover substantial areas of Asia and Europe by 1700 and cover 37% of Asia and 23% of Europe by 2017 CE, levels more than twice the global average of 9.7% in 2017 CE.

Land use histories differ among biomes (**Figure 5**) both for regional historical reasons and because different forms of land use are better suited to different biomes. Pastoralism and rangelands tend to predominate in less productive dryland biomes, whereas more intensive agriculture, represented by croplands and villages, is concentrated in more naturally productive biomes, especially temperate and tropical woodlands, grasslands, and savannas. Most areas of the colder and drier biomes, including boreal woodlands, tundra and deserts, have never been used very intensively.

In most regions for most of history, the vast majority of land use change was produced through the transformation of cultured anthromes into intensive anthromes, not the conversion of wildlands into cultured or intensive anthromes. The longest and most intensive histories of human use appear in the temperate and tropical woodlands, and in grasslands and savanna, which

Land use intensification: changes in land use to enable more food, resources, or other social needs to be met per unit land area



Annu. Rev. Environ. Resour. 2021.46:1-33. Downloaded from www.annualreviews.org Access provided by 105.226.244.36 on 04/01/22. See copyright for approved use. Anthrome changes globally and in different world regions over the past 12,000 years. Changes in anthrome class areas as a proportion of global (*a*) and regional areas (a-i); red lines depict populations relative to contemporary maximum. Data based on Reference 5.

were almost completely cultured even in 10,000 BCE, with only small areas left as uninhabited wildlands. These biomes were also mostly transformed into intensive anthromes by the late 1800s, and by 2017 CE the vast majority of grasslands and savanna (84%), shrublands (73%), and temperate woodlands (65%) were shaped into intensive anthromes. These biomes were also the most densely populated, with village and urban anthromes covering larger areas than the global average, especially in temperate woodlands, with more than twice the global average in 2017 CE.



Figure 5

Anthrome changes across biomes over the past 12,000 years. Changes in anthrome class areas as a proportion of biome areas; red lines depict populations relative to contemporary maximum. Data based on Reference 5.

4.2. Global Intensification, Deceleration, and Transition

By the end of the 1800s, intensive anthromes were increasing rapidly almost everywhere around the world, following global increases in human populations (**Figures 3–5**). However, this general global intensification appears to level off by the mid-twentieth century, in a sharp contrast with the Great Acceleration narrative of accelerating global changes after 1950 (123). This global deceleration of intensive anthrome expansion in the latter half of the twentieth century is best explained by the widespread adoption of Green Revolution technologies. The Green Revolution "package" of improved varieties, commercial fertilizers, and chemical pesticides enabled total agricultural production to increase without increasing the area of intensively used land, driving a decoupling trend between productivity and agricultural land that continues today and is linked with rural depopulation and rural-urban migrations around the world (95, 124). In temperate woodlands, intensive anthrome area declined significantly, highlighting widespread abandonment of intensive land uses through forest transitions, with cultured woodlands recovering in what were previously croplands between 1900 and today (**Figure 3**) (94).

According to the most recent assessment of global land use history, nearly three-quarters of Earth's land was inhabited and used by human societies more than 12,000 years ago, with only approximately 17% of global land showing no evidence of prior human habitation or use over the past 12,000 years, and even these low numbers are considered to be overestimates (5, 22). Of the wildlands that covered 27.5% of Earth's land in 10,000 BCE, only a small fraction, perhaps as small as 8% of Earth's total land area or even smaller, was converted into cultured and intensive anthromes over the past 12,000 years. Clearly, the global history of human use of land is less a story of untouched wildlands recently destroyed, but more the deep history of a dynamic and used planet changing through processes of land use intensification and abandonment, and through the colonization, displacement, and appropriation of land from local peoples by larger-scale agricultural and industrial economies (5, 22).

The cultured anthromes shaped by hunter-gatherers 12,000 years ago, like those of today, vary greatly in landscape use intensity. Some represent the most minimally altered and unfragmented habitats, whereas others are profoundly reshaped by intensive food-producing practices like land-scape burning, prey management, and species translocations. Either way, the hunter-gatherer land-scapes of prehistory likely sustained a widely dispersed global population of less than 20 million, and it is doubtful that even the most productive hunter-gatherer land use regimes could sustain more than 100 million people within Earth's limited land over the long term (17). Now, land use must meet the demands of nearly 8 billion people living in the increasingly wealthy and globalized societies of today, with billions more expected in coming decades (4, 17, 95, 124).

5. GLOBAL ENVIRONMENTAL CHANGE

Over the past 12,000 years, land use, from foraging to farming to industrial cities, has reshaped ecosystems, biodiversity, and evolutionary processes more than any other driver of global environmental change, including anthropogenic global climate change (5, 11, 19). Although climate change is coming to dominate the processes of global environmental change as it continues to accelerate, interactions between land use and climate change, and the role of land use as both a driver of and a solution to climate change, are becoming even more important (12, 125). Yet the environmental consequences of land use are complex, vary greatly across time and space, and often include changes in opposing directions within the same landscapes and across regions. For example, wood-land clearing and cultivation release carbon to the atmosphere, later to be partially recaptured and sequestered in soils and vegetation wherever croplands are fallowed or abandoned, or even where

EXTINCTION FILTERING AND EXTINCTION DEBT

Species can respond very differently to land use changes, especially when these changes are slower and less extensive, allowing some to evolve adaptations whereas others slowly decline to extinction, with only the most vulnerable going extinct early on, such as large-bodied and range-limited species (19, 39). These differential and lagged responses are characterized as extinction debt when extinctions lag behind land use changes, such as when long-lived tree species lose their pollinators or seed dispersers, and as extinction filtering when the most vulnerable species are lost early, leaving communities of species better adapted to dynamic cultural landscapes and therefore less vulnerable to future changes (179). As a result of extinction debt and filtering, land use changes of the past, and their evolutionary consequences, can play a critical role in shaping current and future rates of extinction (127, 129, 130).

low-tillage practices are introduced (88, 118). Deforestation and reforestation can both increase and decrease streamflow (126). The evolutionary consequences of early land use, including burning, habitat fragmentation, population declines in prey and other species, and the adaptations of remaining species to cultural landscapes, can produce legacy effects that can lower and/or obscure future rates of extinction through extinction filtering and extinction debt, respectively, while also shaping diverse and resilient novel communities and ecosystems (19, 27, 39, 98, 99, 127–130; see also the sidebar titled Extinction Filtering and Extinction Debt). Given these complex, divergent, and often opposing ecological consequences, detailed reconstructions of long-term land use histories are essential to better understand the legacies of past land use and to enable more effective environmental governance in the future.

5.1. Biodiversity

Human use of land has shaped habitats, ecosystems and evolutionary processes across nearly threequarters of the terrestrial biosphere for at least 12,000 years (5). In some cases, hunting, habitat conversion, loss and fragmentation, species introductions, and human commensals, like rats, cats, and diseases, caused long-term population declines that contributed to species extirpations and extinctions (39). In other regions, the low-intensity land use regimes of hunter-gatherers, early farmers, and pastoralists shaped dynamic and productive mosaics of intensively used patches interspersed with habitats sustaining biodiverse novel communities in varying states of ecological succession in response to burning, tillage, middens, transplanting, and other cultural practices (17, 20, 27, 30, 66, 129, 131, 132). Areas now governed in similar ways by Indigenous and traditional peoples are some of the most biodiverse areas remaining on the planet (133–135), and landscapes under traditional low-intensity use are generally much more biodiverse than those governed by high-intensity agricultural and industrial land use regimes (131, 134-138). Although some societies practicing low-intensity land use contributed to extinctions in the past, including island endemics (139) and megafauna (57, 59), with cascading ecological consequences (57, 58), land use can also produce sustained ecological benefits through practices that expand habitats for other species (30, 140), enhance species diversity (27, 30, 86, 141–143), increase hunting sustainability (65), disperse seeds (144), and enhance soil fertility (145, 146).

Given that biodiversity was sustained for millennia around the world in cultural landscapes shaped by low-intensity land use regimes that left ample refugia for native species, land use itself cannot be the main cause of the current biodiversity crisis (5, 27, 138). In contrast, the homogeneous and ecologically simplified landscapes produced by large-scale mechanization, industrial infrastructure, and chemical pest control tend to leave no space for native species to live within or

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even to cross the landscape (5, 18, 19, 93, 101, 102). The expansion of globalized large-scale land systems also facilitates species invasions through species transported around the world and can displace and concentrate traditional hunting and fuel gathering in marginal habitats, increasing their effects on the native species remaining there.

The current biodiversity crisis cannot be explained by the conversion of untouched wildlands. Untouched wildlands were almost as rare 12,000 years ago as they are today, and wildland conversions remain as rare as they have always been. Instead, the most plausible explanation for current losses of biodiversity is the replacement of Indigenous and traditional low-intensity land use practices that sustained biodiversity for millennia with ecologically simplified and homogenous large-scale industrial landscapes (5, 34, 96, 138).

5.2. Biogeochemistry, Hydrology, Geomorphology, and Climate

Although the most potent impacts of land use tend to be experienced locally and regionally, the global environmental consequences of deforestation, defaunation, fire management, tillage, fertilizers, the mining and transport of materials, the spread of hydraulic and other built infrastructure, and other land use practices, are almost too numerous to mention (**Figures 1** and **2**) (1, 17, 19, 24, 78, 96, 97, 147). The topographic fingerprints of land use have reshaped the physical surface of Earth's land (148, 149), including the chemical and physical properties of soils (150) and the surface hydrology and atmospheric exchange of water and energy (126, 147). The global cycles of nitrogen and phosphorus have been thoroughly transformed by industrial agriculture, producing emissions of nitrous oxide, a potent greenhouse gas, while polluting freshwater and coastal ecosystems (151).

Perhaps no land use practice has altered global environments for as long as human control of fire, which first enabled hunter-gatherer societies to shape vegetation across landscapes and remains consequential today, including through contemporary practices of fire suppression (24). Use of fire to clear woodlands as well as soil tillage, livestock herding, and flood irrigation of paddy rice have all been implicated in early emissions of carbon dioxide and methane and alterations of surface heat balance that likely began warming Earth's climate as long as 5,000 years ago (118, 152). There is even evidence for a global cooling following the Great Dying in the Americas induced by land abandonment, vegetation regeneration, and carbon uptake (48). The dominant role of land use in driving global changes in climate prior to 1950 (15) only further emphasizes the degree to which land use has long coupled changes in human societies with changes in the Earth system, in both directions.

6. FUTURE RESEARCH

6.1. Reconstructing Land Use Histories

The challenges of observing and reconstructing land use changes are rapidly being overcome. New remote sensing platforms and techniques can now map multiple land use categories and their global dynamics directly (e.g., 153), a major advance over prior methods requiring the integration of census data and remote sensing to map land use from land cover. Open global historical datasets relevant to historical and prehistoric land use mapping are increasingly being developed and shared (22, 154–156). International scientific collaborations and procedures initially developed by the Earth system science community are facilitating the harmonization and systematic cross-validation of global historical land use reconstructions and future projections for the interval from 850 CE to 2100 CE, including HYDE and others (3). Paleoecological, archaeological, and historical data are also being combined systematically to reconstruct global changes in land

use over the past 12,000 years using a region-by-region approach (53, 104). Taken together, these technologies and interdisciplinary international collaborative efforts are transforming the study of global land use history.

Global collaborations are also highlighting the need to increase investments in archaeological and paleoecological field work to investigate early land use changes in understudied regions, like parts of Africa, Asia, and South America (22). Investments in new and improved techniques for field observations are also essential to resolve key uncertainties in mapping early human populations and land use practices, including population mapping using radiocarbon data (157) and the global extent and timing of landscape burning, species propagation, and other practices by food-producing hunter-gatherers and early farmers (24, 29, 46, 61, 62, 64, 66, 67, 77). New observations, especially in understudied regions, will likely only increase, not decrease, global estimates of the past extent and timing of early land use. This will be especially important to resolve ongoing debates over the extent of early land use in tropical woodlands, to assist in conserving their rich biodiversity (68, 76, 77, 158). Already, the first global compilations of archaeological knowledge on land use (22) and new compilations of field data (104) are improving the next generation of global historical land use reconstructions (HYDE 3.3), pushing widespread intensive land use deeper into the global past.

6.2. Pathways and Causes of Land Use Change

Historical reconstructions are not enough to truly understand global land use history; causal mechanisms must explain why land use changes and why pathways of change differ under different conditions. Archaeological and ecological theories, including cultural evolution, niche construction, and the EES, may help to explain long-term patterns and conditions shaping land use intensification and other regime shifts in land systems, and might also help to unify the rich diversity of middle-range theories now informing land system science (17, 28, 31–34, 43). There are good reasons why a general theory of land use change from Pleistocene to present might never be widely used or accepted across disciplines and applications (17, 34). It is nevertheless useful to ask why, when, and where contemporary and historical mechanisms of land use change might have diverged from those of prehistoric hunter-gatherer and agricultural land systems, if only because this might advance general understanding of land use changes either in the past or at the present time.

Some critical transitions in land use history are especially in need of greater study. Were the first farmers intensive cereal gardeners, or did agriculture first evolve as polyculture, vegeculture, or as long-fallow swidden systems among hunter-gatherers practicing some form of firestick farming (29–31, 33, 40, 42, 44, 62, 63, 74, 80)? Was early agriculture actually less productive than hunting and foraging-and only incentivized through the prior emergence of property rights (69)? Did domesticated grazing livestock evolve among nomadic or sedentary hunter-gatherers, or among farmers (33, 70, 80-82)? Or did these major shifts in land use regimes evolve through profoundly different pathways, differing from region to region and across time, explained by theories on niche construction and sociocultural evolution (17, 28) or by complex, multicausal, and contingent system change processes resembling those explained by contemporary theories of land system change (34)? Although such diverse and complex change trajectories might seem intractable to any single theoretical approach, characterizing the conditions producing these different pathways is of interest in itself and might also be amenable to investigation through spatially explicit social-ecological modeling approaches, potentially yielding both improved causal understandings and improved reconstructions of past land use changes and their ecological consequences (159, 160).

6.3. Learning from the Past

The most important lesson of global land use history is that so much of terrestrial nature has been shaped by human cultures for so long that the vast majority is now a cultural nature, with changes in ecosystems, biodiversity, and human societies all entangled and coevolving together (5). Conservation of Earth's last untouched wildlands, wherever these might still exist, should remain a high priority (10). However, cultural landscapes, not areas free from human influence, demand recognition as the main focus for both nature conservation and sustaining human societies over the long term (9, 99, 132, 133, 161, 162).

Sustaining more than 8 billion people together with the rest of nature on Earth's limited land is no minor challenge (124, 163). Empowering, collaborating with, and learning from Indigenous and traditional peoples, restoring their sovereignty over land, including their traditional use of fire and other land use practices, will be critical to sustaining biodiversity in cultural landscapes (24, 27, 108, 131–133, 138, 164–170). Yet even the most productive low-intensity land use regimes will not be capable of sustaining billions of people on Earth's limited land (2, 95, 124, 163). Advanced land use regimes will need to combine high productivity agriculture, dense cities, and other societal infrastructures with nature conservation, restoration, and rewilding in multifunctional landscapes designed and fairly governed to sustain people and nature together over the long term (11, 88, 93, 98, 99, 101, 102, 171–175).

Human societies have never been larger, more capable, or more globally interconnected, nor have human populations ever been more densely concentrated within cities. Today's urban lifeways are also more strongly connected to global commodity chains and social networks than to the land that sustains them (95, 124, 163). At the same time, some promising land system trends are emerging, including forest transitions (94, 163), rapid agricultural intensification and increasing urban density (95, 124, 163), increasing demands and capacities for nature conservation (11, 102, 173, 176), and efforts to integrate these into multifunctional landscape strategies (102, 161, 173–177). Nevertheless, using landscapes to meet multiple demands simultaneously is no panacea and inevitably requires trade-offs and negotiations among competing demands, stakeholders, and perspectives (100, 176), especially between intensive agriculture and nature conservation (125, 177). Without attention to these issues (176), competing demands can lead to perverse outcomes such as the loss of grasslands through tree planting programs (125, 178) and the replication of structural inequalities and social injustices in the construction and management of landscapes (172). It will take everything our diverse societies have learned over the past 12,000 years, including our deep cultural connections with land, nature, and with each other, to navigate together toward a better future.

7. CONCLUSIONS

For more than 10,000 years, the majority of Earth's terrestrial surface has been inhabited and shaped by human use of land. Earth's transformation through land use began long before agriculture and has proceeded through diverse, complex, and nonlinear pathways that differ greatly among regions. Through an increasingly diverse, intensive, and ever evolving suite of land use practices, human societies have shaped ecosystems and evolutionary processes to sustain themselves in heterogeneous multifunctional cultural landscapes. Now, the fate of all life on this planet, including ours, depends on whether human societies can shape these cultural landscapes to better sustain both people and the rest of life on Earth. Increasingly detailed and accurate reconstructions of land use history have much to offer in these efforts, by both advancing scientific understanding of the social and ecological history of Earth's limited land and highlighting the need to more fairly

and effectively share, use, conserve, and restore the cultural landscapes that must now sustain both people and terrestrial nature.

SUMMARY POINTS

- 1. Over the past 12,000 years, all human societies have engaged in varying degrees of ecologically transformative land use practices to sustain themselves, from hunting and landscape burning to agriculture and urbanization.
- 2. Land use practices are cultural and have been evolving and spreading within and across societies since prehistory.
- 3. The ecological consequences of land use practices are best understood through their shaping of heterogeneous multifunctional landscapes.
- 4. Hunter-gatherer land use includes ecologically transformative food production practices, including land clearing and species propagation, that can transform ecosystems in ways that resemble and likely paved the way to agriculture.
- 5. Land use by hunter-gatherers, farmers, and pastoralists transformed ecology across most of Earth's land surface thousands of years ago.
- 6. Low-intensity land use sustained many human societies together with the majority of their native biodiversity for thousands of years.
- 7. Contemporary environmental challenges, including the biodiversity crisis, have resulted primarily from recent increases in landscape use intensity rather than land use expansion into untouched landscapes.
- 8. Increasingly detailed and accurate reconstructions of long-term land use histories are essential to better understand the ecological legacies of past land use and to enable more effective environmental governance in the future.

FUTURE ISSUES

- 1. Additional research is needed to assess the global extent, timing, and ecological consequences of early hunter-gatherer land use practices, including landscape burning and the propagation and management of favored species, and their shaping of biodiversity and climate change.
- 2. Recognition of early and long-sustained low-intensity land use has implications for the governance of biodiversity and ecosystems today.
- 3. More research should be aimed at understanding the beneficial roles of land use practices, especially those of traditional and Indigenous peoples, in sustaining biodiverse and resilient landscapes.
- 4. Greater understanding of synergies and trade-offs between land use intensity and biodiversity is needed, beyond computations of human impacts or footprints.
- 5. Causal understandings and models of land use change might be strengthened by bringing together and comparing archaeological and land system science theories and evidence.

- The use of new archaeological techniques, including large-scale landscape observations through remote sensing, especially LiDAR, could greatly expand global assessment of land use history.
- Increasing global collaboration among archaeologists, paleoecologists, environmental historians, geographers, land system scientists, and conservation scientists could greatly advance global understanding of global land use history and its ecological consequences.
- 8. Using landscapes to meet multiple competing demands requires negotiating trade-offs, especially between intensive agriculture and nature conservation, and perverse and unjust outcomes can result when these are not taken into account.

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