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Sustaining biodiversity and people in the world's anthropogenic biomes

Erle C Ellis

Humans have reshaped more than three quarters of the terrestrial biosphere into anthropogenic biomes (anthromes), embedding substantial areas of remnant and recovering novel ecosystems within the agricultural and settled landscapes that sustain human populations. The need to conserve biodiversity in anthromes is increasingly recognized as critical, as anthromes have largely replaced wildlands in Earth's most biodiverse and productive regions, and novel ecosystems now cover nearly twice the global area of wildlands. Extinction rates may still be increasing. Nevertheless, recent studies indicate that under appropriate conditions, most native taxa may be sustainable within anthromes while at the same time increasing anthrome productivity in support of human populations.

Addresses
Department of Geography & Environmental Systems, University of Maryland, Baltimore County, Baltimore, MD 21250, USA

Corresponding author: Ellis, Erle C (ece@umbc.edu)

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Introduction

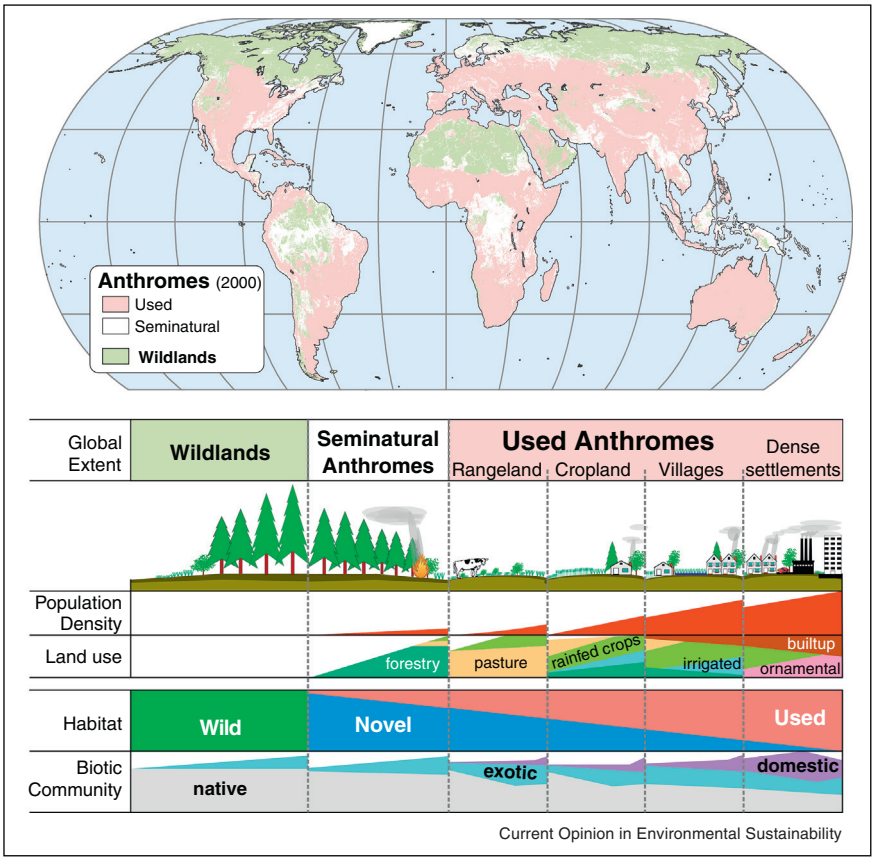
Human populations and their use of land have now transformed more than three quarters of the terrestrial biosphere into anthropogenic biomes (anthromes; [1]). Anthromes range from dense settlements, villages and croplands to rangelands and seminatural lands with only minor human populations and land use [2]. Emerging along with agriculture more than 8000 years ago, anthromes first covered more than half of the terrestrial biosphere as of 500–2000 years ago, mostly in the form of seminatural lands [3•]. Over the past century, anthrome extent and land use intensity increased rapidly together with growing human populations, leaving wildlands without human populations or land use in less than one quarter of the terrestrial biosphere [2]. This massive transformation of Earth's ecosystems for human use has occurred in parallel with enhanced rates of species extinctions, inspiring serious concerns that human use of the biosphere might not be sustainable [4,5,6••]. This review assesses recent studies on the prospects for sustaining both biodiversity and humanity in anthromes over the long-term.

Even within the most densely populated and intensively used anthromes, including urban areas and ancient village landscapes, humans rarely convert all land to agricultural and residential use because land use for crops and pastures tends to selectively concentrate in areas most productive for these uses and settlements tend to retain significant green spaces [1,3•,7–9]. As a result, anthromes generally take the form of multifunctional mosaics of used lands within which substantial remnant and less intensively managed ecosystems are often left embedded, especially where terrain is heterogeneous [1,3•,10]. It is also common for large areas of used lands to be abandoned and left to recover within anthromes, and for ecosystems never managed for production to become transformed by non-agricultural human activities ranging from informal harvests of timber, fuelwood and other natural resources, road-building, dams, habitat fragmentation, anthropogenic fire regimes, hunting, foraging, increased exposure to exotic species, and pollution [1,3•,6••,11,12]. As a result of these pervasive human influences, even the least disturbed areas of anthromes generally have biotic communities and ecosystem processes that differ substantially and potentially irreversibly from their prior historical state, broadly fitting the definition of novel ecosystems [2,10,11,13–15].

Biogeography and biodiversity of anthromes and novel ecosystems

A global map of contemporary anthromes and wildlands is presented in Figure 1, together with a conceptual diagram illustrating general patterns in human population densities and land use within and across anthromes and their relationships with the emergence of novel habitats and biotic communities. As indicated in Figure 1, human populations, land use, and anthromes tend to be concentrated in the more productive and biodiverse regions of the biosphere [16,17,18•,19]. Partly for this reason, human-induced habitat loss is considered the greatest current threat to terrestrial biodiversity [6••]. Humans have and are directly causing species extinctions, especially of megafauna, by reducing, fragmenting and transforming native habitats and by overexploiting individual species [4,6••,18•,20,21]. Yet current rates of terrestrial extinctions vary greatly by taxa, with mammals, reptiles and amphibians especially threatened [22], and the degree to which these types of extinctions are

Figure 1



Global extent of anthromes and wildlands (year 2000, on the basis of [2]) and conceptual diagram illustrating general relationships among anthrome population density, land use, habitats, and relative proportions of native, exotic and domestic species in biotic communities.

accelerating or inevitable under existing conditions, as implied by the concept of ''extinction debt'' [23], remains an area of active study [6••,18•,20–24].

Simultaneously with extinctions, humans drive major changes in biotic communities and ecosystems by intentionally and unintentionally introducing exotic species and domesticates [12,17,25••,26,27•]. Successful establishments of dominant exotic species (species invasions) have profound effects on almost every aspect of ecosystem form and function [6••,25••,26,27•,28]. However, their role in causing native species extinctions is inconsistent [26,27•,29,30]. Though local reductions are often observed in native populations, sometimes driving species towards threatened and endangered status, even highly dominant exotics are not generally known to cause regional extinctions of native species, at least in plants [29,30], though some fauna, especially those restricted to islands, appear more vulnerable [30]. The combination of high rates of invasion with lower rates of extinction has led to widespread observations of increasing biodiversity at regional scales, especially for plants, indicating that regional patterns of biodiversity may continue to increase without saturating [29,31], though risks of future extinction cannot be ruled out, even for plants [32].

Recently, trends in anthrome biodiversity have been hypothesized to follow processes of ''anthropogenic ecological succession'' [17] in which biotic communities accumulate exotics as human populations establish, grow, develop and become increasingly interconnected, as illustrated in Figure 1. Early human populations tend to be lower and often use land less intensively, by forestry or shifting cultivation in seminatural anthromes or grazing in rangelands, gradually shifting to croplands as populations increase. Land use later intensifies in more optimal environments, as anthromes support larger, denser, and better connected human populations, leaving marginal lands and remnant ecosystems to regenerate. The long-term result is a gradual but marked increase in total species richness in anthromes in parallel with growth in human populations [17], as exotic species adapted to anthropogenic habitats become established from regional and global pools of these species (biotic homogenization;

[26]), while most natives may sustain viable, albeit reduced, populations, at least transiently, in remnant and novel ecosystems [12,23,29,33,34].

Natives in anthromes

Though the biotic communities of anthromes generally differ profoundly from those in place before human establishment, there is growing evidence that viable populations of many, if not most native taxa, especially plants, may be sustainable within anthromes and novel ecosystems, at least at regional scales [6••,12,24,29–31,33–36]. Predicting native species susceptibility to extinction in human altered ecosystems is now a major subject of study, with results differing widely across taxa [6••,21,33] in part owing to the complexities of demographic and meta-population structures and their dynamics [37]. Mammals, a taxa generally considered highly threatened by direct interactions with humans, have indeed shown a greater tendency towards endangered status in the most intensively used and densely settled anthromes, but much less so in rangelands and other low intensity low population anthromes [18•]. Yet the animal taxa of Caribbean islands, which have been heavily colonized by exotics and transformed by land use, demonstrate remarkably few native extinctions across a wide range of animal taxa including birds and mammals [33].

It remains hard to evaluate the potential of specific taxa and species to be sustained within specific anthromes and novel habitats over the long term, with the exception of plants (excluding Cycads; [22]), which appear to be fairly capable in general of sustaining viable populations under these conditions [11,12,17,21,30,31,33,36,38]. Clearly, more research on the viability of native vertebrate populations under different management regimes and anthrome contexts is needed [11,21,39]. Nevertheless, despite the clear and widespread risks of local and regional extinction posed to native species by the transformation of native habitats into novel ecosystems, recorded global extinctions remain rare to date (<1200 species in the past 400 years [20]), and with the exception of especially vulnerable taxa, the majority of native species may be capable of maintaining viable populations in anthromes, at least over the near term [23,40], especially as strategies to reintroduce and manage natives are developed and implemented to ensure their long-term sustainability in novel habitats [6••,24,29,33,34].

Conservation in anthromes

The relative importance of conserving biodiversity within the working landscapes of anthromes versus in protected wildlands has been debated recently and characterized as a contrast between strategies of ''land sharing'' versus ''land sparing'' [41•], both of which aim to reconcile competing demands for biodiversity conservation and increasing agricultural production [41•]. Land sparing advocates argue that maximizing food production in existing agricultural landscapes using the most productive technologies available is optimal because it enables the more effective protection of native species in wildlands elsewhere [41•]. Land sharing is focused on balancing agricultural productivity with biodiversity conservation within working landscapes, accepting lower yielding agricultural practices when this enables native wildlife to be sustained [42•,43].

Land sharing focuses on biodiversity within anthromes while land sparing seems to focus exclusively on wildlands. Yet, as noted in many recent studies, protected areas, though tending to be larger than the novel habitats embedded within anthromes (anthromes are mapped at $\sim$85 km^2 resolution; [1]), are nevertheless usually embedded within used landscapes at larger scales, and therefore subject to many of the same conservation challenges, including species harvest, biomass removal and land use change [42•,44,45]. Further, it is increasingly recognized that human interactions with protected wildlands cannot be stopped; only guided towards more sustainable outcomes [24,44,45]. The global extent of wildlands is much lower than the novel habitats of anthromes [2] which still sustain high levels of native biodiversity [17,31,33,36]. As a result, land sharing and land sparing are increasingly seen as complementary and overlapping conservation strategies, neither of which can wisely be deemphasized. Recognizing the need to conserve biodiversity within anthromes does not in any way reduce the importance of wildland preserves. Rather, the vast global extent of anthromes highlights the rarity of areas remaining wild and underscores the challenges of conserving native species within the highly modified novel communities and ecosystems of anthromes.

Future prospects: increasing productivity and sustaining biodiversity

Human populations are expected to grow until at least midcentury while per capita demand for the products of agricultural landscapes will likely increase even faster [46]. This massive increase in potential demand for land would appear to be an unstoppable threat to biodiversity across both wildlands and anthromes. Yet current trends point towards the potential for a much more desirable future. The increasing concentration of human populations into cities is accelerating while agricultural land use in many regions is slowing and becoming increasingly concentrated in the most productive lands, offering the prospect of widespread ecosystem recovery as rural areas depopulate and marginal agricultural lands are abandoned [46,47]. If these trends can be combined with strengthened conservation governance at appropriate scales [48], it is entirely possible that in the 21st century, global trends in species extinction might be reversed at the same time as human populations thrive and reach their expected peak.

Sustaining and recovering biodiversity in anthromes will not be possible without major concerted efforts around the world. Though urbanization and land use intensification create necessary preconditions for using less land to produce more food, these processes do not in themselves protect land or species [48]. Robust and adaptive governance systems that include strong stakeholder participation must be in place to guide and enforce efficient use of land while protecting and restoring essential habitat for native species [45,48]. More importantly, such governance must be in place wherever suitable land exists both within anthromes and across remaining wildlands, as the global marketplace is now capable of instantly converting any local or regional failures in land governance into immediate opportunities for land clearing and use, such as the conversion of tropical forests into oil palm plantations in Indonesia, or the removal of hedgerows, field margin habitats and other refugia from farmlands in parts of Europe and elsewhere [42•,49,50••].

Governance systems and policies capable of protecting and restoring habitats for native species without significantly lowering land productivity have been developed and proved effective in some cases [45,48,50••,51••,52•]. In general, studies have shown that successful conservation governance requires continuous monitoring, local empowerment, and adaptation to changing social and environmental conditions at both local and global scales — including climate change and world markets [24,42•,45,53,54]. Though sustaining native species, agricultural productivity, and other land uses within anthromes is especially challenging, an array of successful strategies already exist, including ''nature friendly farming'', payments for ecosystem services, selective logging, agroforestry, restoration of buffers and corridors, and other multifunctional landscape management strategies [34,42•,50••,51••,52•,53,55,56••,57]. Much room remains for improvement and innovation in designing landscape management strategies that simultaneously enhance agricultural productivity, biodiversity conservation and other valued functions of anthromes [58]. Nevertheless, these multifunctional land management strategies represent a major, albeit challenging, planetary opportunity to sustain the ecological heritage of our planet while advancing the state of humanity in the Anthropocene [51••,59].

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