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RESEARCH PAPER

Anthropogenic transformation of the biomes, 1700 to 2000

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ABSTRACT

Aim To map and characterize anthropogenic transformation of the terrestrial biosphere before and during the Industrial Revolution, from 1700 to 2000.

Location Global.

Methods Anthropogenic biomes (anthromes) were mapped for 1700, 1800, 1900 and 2000 using a rule-based anthrome classification model applied to gridded global data for human population density and land use. Anthropogenic transformation of terrestrial biomes was then characterized by map comparisons at century intervals.

Results In 1700, nearly half of the terrestrial biosphere was wild, without human settlements or substantial land use. Most of the remainder was in a seminatural state (45%) having only minor use for agriculture and settlements. By 2000, the opposite was true, with the majority of the biosphere in agricultural and settled anthromes, less than 20% seminatural and only a quarter left wild. Anthropogenic transformation of the biosphere during the Industrial Revolution resulted about equally from land-use expansion into wildlands and intensification of land use within seminatural anthromes. Transformation pathways differed strongly between biomes and regions, with some remaining mostly wild but with the majority almost completely transformed into rangelands, croplands and villages. In the process of transforming almost 39% of earth's total ice-free surface into agricultural land and settlements, an additional 37% of global land without such use has become embedded within agricultural and settled anthromes.

Main conclusions Between 1700 and 2000, the terrestrial biosphere made the critical transition from mostly wild to mostly anthropogenic, passing the 50% mark early in the 20th century. At present, and ever more in the future, the form and process of terrestrial ecosystems in most biomes will be predominantly anthropogenic, the product of land use and other direct human interactions with ecosystems. Ecological research and conservation efforts in all but a few biomes would benefit from a primary focus on the novel remnant, recovering and managed ecosystems embedded within used lands.

Keywords

Agriculture, anthromes, anthropogenic landscapes, conservation, environmental history, global change, land-use change, novel ecosystems, terrestrial ecosystems.

INTRODUCTION

For millennia, humans have reshaped the form and process of ecosystems across the terrestrial biosphere, both intentionally and unintentionally (Turner II *et al.*, 1990; Redman, 1999; Kirch, 2005; Dearing *et al.*, 2006;). Starting with fairly transient practices like hunting and gathering and building towards the increasingly permanent use of land for agriculture and settlements, the widespread and sustained presence of human populations has transformed ecosystems locally, regionally and

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globally. Human activities have facilitated species extinctions, invasions, introductions and domestications, increased soil erosion, altered fire frequency and hydrology, and incited profound changes in primary productivity and other key biogeochemical and ecosystems processes (Turner II *et al.*, 1990; Vitousek *et al.*, 1997; Defries *et al.*, 2004; Foley *et al.*, 2005; Dearing *et al.*, 2006; Hobbs *et al.*, 2006; Ellis & Ramankutty, 2008; Hansen & Galetti, 2009).

Global estimates of direct transformation of ecosystems by humans vary among studies, but there is growing consensus that humans have now transformed ecosystem pattern and process across most of the terrestrial biosphere (Sanderson *et al.*, 2002; Kareiva *et al.*, 2007; Ellis & Ramankutty, 2008). As a result, global patterns of the form and function of terrestrial ecosystems are no longer accurately depicted by the now classic approach to mapping and modelling biomes as a function of climatic and physiographic variables (Shelford, 1932; Holdridge, 1947; Küchler, 1949; Dansereau, 1957; Whittaker, 1970; Prentice *et al.*, 1992).

While there is no doubt that global patterns of ecosystem form and process will continue to be influenced and constrained by climate and other geophysical and biotic factors, wherever human populations and activities are present, the realized form and dynamics of terrestrial ecosystems, including the presence of trees and their successional state, are determined largely by the type, intensity and duration of human interactions with ecosystems (Hobbs *et al.*, 2006; Ellis & Ramankutty, 2008). To characterize and understand these interactions and the global ecological patterns produced by them, Ellis & Ramankutty (2008) introduced the concept of anthropogenic biomes, or anthromes, and developed a global classification and map of these as a new framework for global ecology and earth science (Alessa & Chapin, 2008). Here we build on this framework by assessing and mapping the anthropogenic transformation of climate-based 'potential natural vegetation' biomes (also termed 'classic biomes' or 'potential vegetation') into anthromes beginning in 1700, an entirely pre-industrial time period, and proceeding through the Industrial Revolution to 2000, with the goal of understanding the history and current state of anthropogenic transformation of the terrestrial biosphere.

Ellis & Ramankutty (2008) classified anthromes empirically using a cluster analysis algorithm that identified globally significant patterns in land use and human population density; key variables characterizing the type and intensity of direct human interactions with ecosystems (Ellis & Ramankutty, 2008). However, this *a posteriori* approach fits anthrome classes and their statistical signatures to the unique statistical patterns within a specific dataset, thereby producing optimal, but different, classifications when input datasets differ by time period or estimation method. To investigate changes in anthromes across time periods, we therefore developed an *a priori* anthrome classification procedure to facilitate consistent identification of anthrome classes similar to those of Ellis & Ramankutty (2008) across time periods based on the same land-use and human population variables.

Previous studies have analysed changes in the extent and composition of the classic biomes caused by land-use changes over the past 300 years (e.g. Ramankutty & Foley, 1999; Klein Goldewijk, 2001; Hurtt *et al.*, 2006). In this study, we investigate the transformation of classic biomes into anthromes with the goal of understanding the context and history of the novel anthropogenic ecosystems created by humans over the long term (Hobbs *et al.*, 2006). Towards this end, we investigate both the intentional use of land for agriculture and settlements and the major unintended consequence of this use: the embedding of remnant, recovering and other non-agricultural and non-urban lands within the complex anthropogenic landscape mosaics created by human use of land (Ellis & Ramankutty, 2008).

MATERIALS AND METHODS

Global patterns of anthropogenic transformation of terrestrial biomes were assessed at 5′ resolution by comparing potential natural vegetation maps with anthrome maps at century intervals from 1700 to 2000 using overlay analysis and other analytical geographic information system (GIS) software tools. Anthrome classification and mapping was achieved using a newly developed rule-based anthrome classification model applied to existing global data for human population density and agricultural and urban land use. All spatial data, including inputs and results, are available for download at http://ecotope.org/anthromes/v2.

Potential natural vegetation – the classic biomes

Ramankutty & Foley's (1999) 'potential natural vegetation' dataset served as the primary biome system used in this study, as its native 5′ resolution and derivation from both remote sensing and ground-based maps makes it an especially reliable base dataset. Pixels missing from the original dataset, constrained by a relatively restricted land mask (mostly missing some island and coastal areas), were filled using a nearest neighbour algorithm. Separate broadleaf and needleleaf classes were combined, as were 'desert' and 'polar desert' to produce a simplified 12-class 'potential vegetation' biome dataset from the 15 original classes. For an alternative 'classic' view of the biosphere, we also conducted analyses using the 'Olson biomes' of Olson *et al.* (2001), the most commonly used current biome dataset, as described in Appendix S1 in Supporting Information.

Anthromes

Data sources

Data inputs for anthrome classification were obtained for years 1700, 1800, 1900 and 2000 from existing and newly produced global 5′ datasets, to match those of Ellis & Ramankutty (2008). Global data for human population density and percentage cover by urban, crop and pasture lands at 5′ resolution were obtained using the HYDE data model (Klein Goldewijk & van Drecht, 2006), a widely used standard in global investigations of land-use change and its effects (Feddema *et al*., 2005; Hurtt *et al*., 2006). Data used here were obtained using an updated version of the HYDE 3.1 data model, based on Klein Goldewijk & van Drecht (2006) in three configurations: an initial data model very similar to the original published HYDE 3.1 dataset (http://www.pbl.nl/hyde), a revised 'best' data model (the standard used in this analysis) and lower and upper bounds datasets designed to highlight uncertainties in the HYDE dataset. HYDE population data for the year 2000 were obtained by spatial aggregation of Landscan population data (Oak Ridge National Laboratory, 2006), and 2000 croplands and pastures combine remotely sensed land cover with and agricultural census data. HYDE historical population and land-use estimates were produced from historical population and land-use data obtained at several administrative levels (the largest units are country level) by using these to constrain spatial allocation models that distribute historical population densities and agricultural land areas based on their proximity to urban settlements, climate constraints, soil suitability, distance to rivers and terrain (Klein Goldewijk & van Drecht, 2006). Data for the percentage of irrigated land were produced by combining the global map of irrigation areas for 2000 (Siebert *et al*., 2007) with a set of historical irrigation statistics and adjusting these to match crop area data in the 'best' data model (see Appendix S2).

Global 5′ data for rice cover in 2000 were obtained from Monfreda *et al*. (2008). Regions with substantial rice cover (> 20%) in previous centuries were then mapped from this by assuming that, in 1700, rice areas within the densely settled regions of the world (> 100 persons km^{-2} or urban cover ≥ 20%) would have been similar to 2000, but for the conversion of some rice lands into settlements and other non-agricultural uses. While this approach does not allow the calculation of historical rice areas, it did allow 'rice villages' to be identified in historical periods using the areas of substantial rice cover mapped for each century. Rice villages were determined by combining substantial rice-cover cells with the densely settled cells located within 1 geographic degree of these in 2000 to create a 'maximum rice' layer, and then removing the densely settled cells present in each century.

Classification system

To classify anthromes consistently across time periods, a new *a priori* anthrome classification algorithm was developed to emulate the basic form of the *a posteriori* anthrome classification of Ellis and Ramankutty ('Anthromes 1'; 2008), using a relatively simple and transparent *a priori* classification model built on standardized thresholds for classifying the same variables ('Anthromes 2'; Table 1; see Appendix S3). First, the initial stage of the Anthromes 1 classification was replicated by stratifying 5′

Table 1 Description of anthrome classes.

Level	Class	Description
Dense settlements		Urban and other dense settlements
11	Urban	Dense built environments with very high populations
12	Mixed settlements	Suburbs, towns and rural settlements with high but fragmented populations
Villages		Dense agricultural settlements
21	Rice villages	Villages dominated by paddy rice
22	Irrigated villages	Villages dominated by irrigated crops
23	Rainfed villages	Villages dominated by rainfed agriculture
24	Pastoral villages	Villages dominated by rangeland
Croplands		Lands used mainly for annual crops
31	Residential irrigated croplands	Irrigated cropland with substantial human populations
32	Residential rainfed croplands	Rainfed croplands with substantial human populations
33	Populated rainfed cropland	Croplands with significant human populations, a mix of irrigated and rainfed crops
35	Remote croplands	Croplands without significant populations
Rangeland		Lands used mainly for livestock grazing and pasture
41	Residential rangelands	Rangelands with substantial human populations
42	Populated rangelands	Rangelands with significant human populations
43	Remote rangelands	Rangelands without significant human populations
Seminatural lands		Inhabited lands with minor use for permanent agriculture and settlements
51	Residential woodlands	Forest regions with minor land use and substantial populations
52	Populated woodlands	Forest regions with minor land use and significant populations
53	Remote woodlands	Forest regions with minor land use without significant populations
54	Inhabited treeless and barren lands	Regions without natural tree cover having only minor land use and a range of populations
Wildlands		Lands without human populations or substantial land use
61	Wild woodlands	Forests and savanna
62	Wild treeless and barren lands	Regions without natural tree cover (grasslands, shrublands, tundra, desert and barren lands)

For details of classification see Appendix S3.

cells into six population density classes differing by orders of magnitude (urban, > 2500 persons km^{-2}; dense, > 100 persons km^{-2}; residential, 10–100 persons km^{-2}; populated, 1–10 persons km^{-2}; remote; < 1 person km^{-2}; wild, 0 persons km^{-2}). Then, anthromes were classified by applying a sequence of classification thresholds to global gridded data for land area covered by urban settlements, rice, irrigated and rainfed crops and pastures as detailed in Appendix S3 and described below.

The Anthromes 2 classification used the same five basic anthrome classification levels as Anthromes 1 (see Appendix S3; anthrome 'groups' in Ellis & Ramankutty, 2008) while simplifying the system to improve the consistency and interpretability of anthrome classes. The 'forested' level of Anthromes 1 was broadened to a 'seminatural' level incorporating both woodlands and 'inhabited treeless and barren lands', retaining the general meaning of this level as lands with relatively low levels of agriculture and urban land use (Table 1; see Appendix S3). The most distinctive aspects of Anthromes 1 classes were retained while simplifying anthrome class identification and interpretation by collapsing village classes from 6 to 4, croplands classes from 5 to 4, and wildlands classes from 3 to 2. Classification was further simplified by standardizing to a single 'dominant' land-cover threshold of 20% and using this to classify anthromes in declining order of their land-use intensity and population density, starting with the most intensively used (urban > rice > irrigated > cropped > pastured) and densely populated (urban > dense > residential > populated > remote) anthromes and finishing with wildlands at the end (see Appendix S3). The identity of village anthromes was clarified by limiting these only to regions with histories of intensive subsistence agriculture (areas outside of North America, Australia and New Zealand; see Appendix S3). To simplify interpretation, anthrome levels were aggregated into three basic categories: 'Used anthromes' (a combination of the dense settlements, village, cropland and rangeland anthrome levels), 'seminatural anthromes', and wildlands. Though the spatial configuration of earth's remaining wildlands is partly the result of human activity, their ecology is still considered distinct from that of anthromes and they are therefore referred to as 'wildlands' and not as 'wildlands anthromes'.

Classification sensitivity

To develop the Anthromes 2 classification procedure used here, a variety of algorithms were explored towards the goal of replicating the Anthromes 1 classes as closely as possible using a simple procedure, both from the original Anthromes 1 input dataset and from the year 2000 data of our historical dataset. Similarities between maps with different class definitions and numbers of classes were tested using Cramer's V statistic (Rees, 2008), a dimensionless symmetric indicator of association corrected for chance that is similar to Kappa, with 1 representing identical maps and 0 representing no relationship between maps, calculated from land-area-weighted cross-tabulations of mapped grid cells (see Appendix S4). Values of Cramer's V above 0.4 and 0.6 indicate 'relatively strong' and 'strong' similarities between datasets, respectively (Rea & Parker, 1997).

The strong similarity of Anthromes 1 and 2 classification was demonstrated by high values of Cramer's V when the Anthromes 2 model was applied to the Anthromes 1 input dataset (0.67; see Appendix S4 and Table 1). Similarity remained relatively strong, even when the two different classification models were applied to their two different native datasets (Cramer's $V = 0.53$), especially when considering Anthromes 2 maps for 2000 in comparison with 1900 (Cramer's $V = 0.46$) and the comparison of potential vegetation biomes (Ramankutty & Foley, 1999) with Olson biomes (Olson *et al.*, 2001; Cramer's $V = 0.49$). The sensitivity of Anthromes 2 classification to choice of model threshold, variations in input datasets, and the spatial resolution of analysis was also tested relative to changes between time periods, and in comparison with the Anthromes 1 map and potential vegetation maps as detailed in Appendix S4. With only one exception, the largest differences between maps were observed across time periods (Cramer's V of 0.46 for 2000 compared with 1900, declining to 0.33 in 1700; Appendix S4 and Table 1), with changes in anthrome level areas of 82% to 135% relative to 2000 (Appendix S4 and Table 2). Coarsening the spatial resolution of analysis (0.5° grid and 7700 km^2 equal-area hexagons) had the next largest effect (Cramer's V as low as 0.48) especially at the dense settlements level, producing the only instance of a larger effect than temporal change. Halving and doubling the anthrome classification thresholds for land and population classes also produced significant differences, but these were much lower than those between time periods and spatial resolutions (Cramer's V as low as 0.59; anthrome level changes between 19% and 89%), while the use of input datasets with different model assumptions and with higher and lower population and land use had the smallest effects, with Cramer's Vs greater than 0.94 and anthrome level changes between 4% and 51% of the standard year 2000 values.

Areas of anthromes, 'used lands' and 'unused lands'

Anthrome areas represent total land areas within anthrome cells, and therefore include both lands in use for agriculture and settlements and those without such use. Areas of different land-use classes may therefore be calculated within each anthrome class, for example the area of pasture or crops land use within rangelands anthromes, crops and urban lands within croplands anthromes, or crops and urban lands within urban anthromes. To facilitate global investigation of lands with and without use for agriculture and settlements, we further define the category of 'used lands' as the sum of all crop, pasture and urban land-use areas within each cell. Areas of 'unused lands' were then calculated from land areas remaining in cells after 'used land' areas were subtracted. 'Unused lands' are thus defined as 'lands not in use for agriculture or urban settlements' and therefore still containing land managed for uses other than crops, pasture and urban settlements (e.g. forestry, mining, parks and non-urban housing), together with terrestrial ecosystems either recovering from some use, or never used directly by humans. Unless otherwise noted, 'unused lands' include both unused lands embedded within anthromes and wildland areas outside anthromes.

RESULTS

Global and regional changes in biomes and anthromes, 1700–2000

Changes in global areas

Anthromes are mapped by century in Fig. 1 and characterized as a percentage of ice-free land by biome and region in Fig. 2 (see Appendix S5 for more comprehensive statistics; original datasets and online maps are available at: http://ecotope.org/anthromes/v2). Figure 3 illustrates the percentage of global population and used and unused lands found within each anthrome. In 1700, about 95% of earth's ice-free land was in wildlands and seminatural anthromes (Fig. 2a). By 2000, 55% of earth's ice-free land had been transformed into rangelands, croplands, villages and densely settled anthromes, leaving less than 45% of the terrestrial biosphere wild and seminatural (Fig. 2a). Further, anthropogenic changes between 1700 and 1800 were far smaller than those of the following centuries, and the rate of change increased over time. As a result, the 20th century stands out not only as the most dynamic period of anthropogenic ecosystem transformation of the past 300 years, but also as the period during which the terrestrial biosphere transitioned from a primarily wild and seminatural state to a primarily used state (Fig. 2a).

Changes in biomes

Anthropogenic transformation of most biomes followed similar trends, with some key exceptions (Fig. 2b). The colder and drier biomes, including boreal and mixed woodlands, tundra, and deserts, showed very little change in wild area over time. The same was observed in the analogous Olson biomes (see Appendix S1), except for the 'deserts and xeric shrublands' biome, probably because it merges shrublands with deserts. Temperate deciduous woodlands were already used fairly heavily in 1700 (28% in used anthromes), but most other woodlands, savannas and grasslands were predominantly in use at lower, seminatural levels. Over the next 300 years, most of these biomes were converted from wild and seminatural lands to croplands, rangelands and other more intensively used anthromes (Fig. 2b).

Differences in biome composition help explain some regional differences in biome transformation patterns (Fig. 2c), including the long-term maintenance of wildlands in the Near East, Africa and Eurasia, which have large deserts and/or boreal areas. But other regional differences are distinct from this, including the high pre-industrial levels of wildlands in North America, Australia and New Zealand, and in Latin America and the Caribbean, and their very dramatic conversion to used anthromes by 2000. These regions contrast with Africa, Asia and Oceania, which were primarily seminatural in 1700 and were then transformed into more heavily used cropland and village anthromes. Europe, which was mostly used in 1700, stayed that way.

Changes in human population

As human populations and their use of land expanded from 1700 to 2000, their distribution among anthromes also changed (Fig. 3a). In 1700, nearly half of earth's human population lived in seminatural lands – thinly dispersed in relatively extensively used landscapes, with the remainder dwelling about equally in croplands and villages (Fig. 3a). By 2000, this had changed completely, with only 4% still living in seminatural anthromes and more than half dwelling in villages (51%). Half of earth's population now lives in cities (UNFPA, 2007), of which about 60% reside in urban anthromes (29% of global population) with the other 40% of urban populations dwelling in the smaller cities and towns embedded within villages and other anthromes.

Changes in land distribution within and among anthromes

Changes in the distribution of ice-free land among anthromes followed similar trends as population, with a dramatic shift away from seminatural anthromes and wildlands towards the used anthromes (Fig. 3a, b). Still, dense settlements and villages, the most populous anthrome levels, even today account for less than 8% of global ice-free land. Change trends in unused lands (Fig. 3c) continued to resemble those of total land (Fig. 3b) even while their total area declined by 34% globally, from nearly 95% of earth's ice-free land in 1700 to just 61% in 2000. Over this period, the portion of unused lands that were embedded within the seminatural and used anthromes, and therefore outside of wildlands, remained fairly stable, hovering near half of the global total from 1700 to 1800 and increasing to about 60% in 1900 and staying there (Fig. 3c) However, the global proportion of unused lands embedded within the used anthromes increased tenfold from 1700 to 2000, from 3% to 30% of the global total, with unused lands embedded in the seminatural anthromes simultaneously declining from 45% to 29% of global land remaining unused.

From 1700–2000, lands used for agriculture and urban settlements increased from 5% to 39% of total ice-free land area, while retaining a fairly constant proportion of dense settlements, villages and croplands (Fig. 3d). However, the extent of rangelands increased rapidly in every century, eventually replacing seminatural as the dominant anthrome level between 1900 and 2000 (Fig. 3b, d). As a result, the foremost global land-use change of the Industrial Revolution in terms of total area was the expansion of pastures from 3% of ice-free land in 1700 to 26% in 2000 (Fig. 3e). During this period, pastures shifted from being predominantly a minor land use embedded within the seminatural anthromes to becoming essentially an anthrome unto itself, with nearly three quarters of all pastures located within rangelands anthromes by 2000 (Fig. 3e). Similarly, crop areas rose spectacularly during the Industrial Revolution, from about 2% in 1700 to about 12% of global land area by 2000, and like pasture lands, crops also became less a component of seminatural anthromes than the defining component of cropland and village anthromes over this period (Fig. 3f). Irrigated areas also increased very rapidly, yet were always concentrated

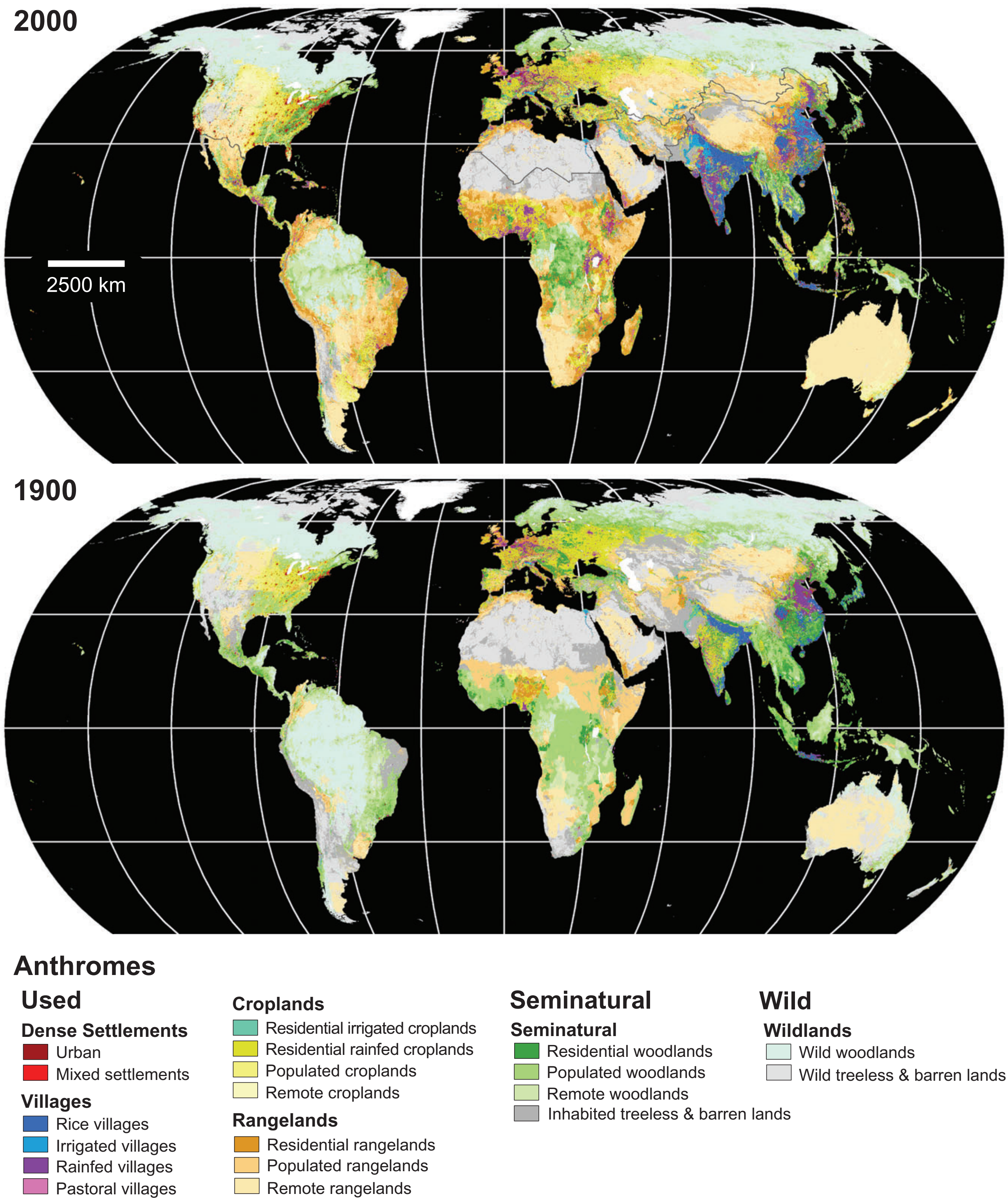

Figure 1 Anthropogenic biomes, 1700–2000 (anthromes; class descriptions in Table 1). Region boundaries (2000) are distinguished by black lines; same regions as Ellis & Ramankutty (2008). Eckert IV projection.

within the most intensively used of the agricultural anthromes – the villages and croplands – with their increase causing 'rice villages', 'irrigated villages' and 'residential irrigated croplands' to expand over time (Fig. 3g). Finally, the most intensively transformed lands on earth, urban lands, also expanded in the most dramatic fashion of all, changing by a factor of 40 from almost insignificant in 1700 (0.01% of all land) to 0.4% of all land in 2000 (0.53×10^6 km^2), shifting from a minor component of

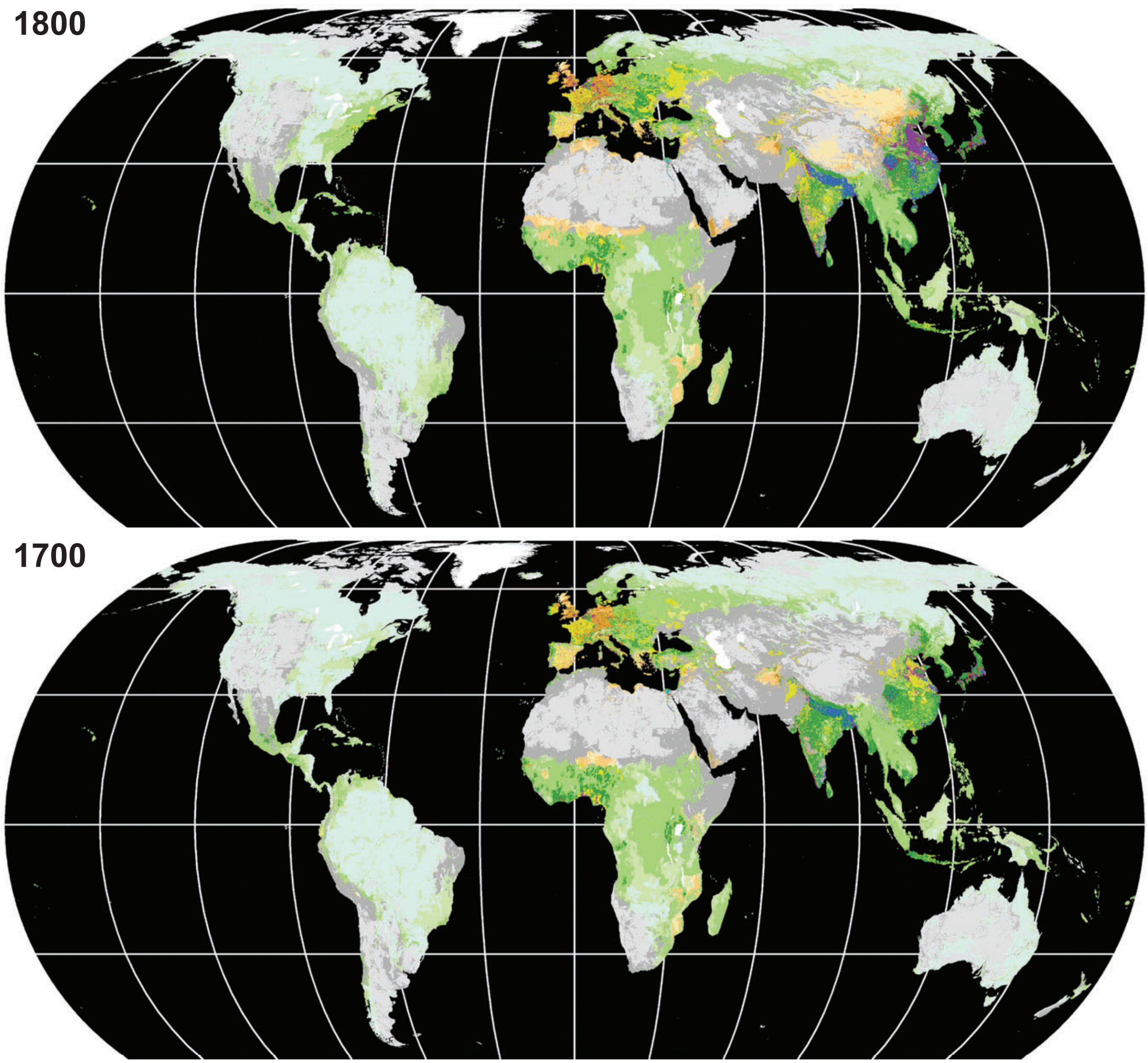

Figure 1 *Continued*

villages and croplands to becoming the defining land use of urban anthromes by 2000 (Fig. 3h).

Pathways and dynamics of biome transformation

The classic view of the biosphere, as composed of natural vegetation biomes, is illustrated in Fig. 4(a) together with maps portraying the global extent to which these were transformed into anthromes by 1700 (Fig. 4c) and 2000 (Fig. 4b). From these figures it is clear that even in 1700, slightly more than half of the terrestrial biosphere was already inhabited and used significantly (Fig. 4c), albeit mostly at relatively low seminatural levels and mostly in Europe, sub-Saharan Africa, South and East Asia and Central America. By 2000, the overwhelming majority of the terrestrial biosphere had been transformed into anthromes (Figs 2a, 4b & 5a), the result of converting about half of both the wildlands (Figs 4d & 5a) and the seminatural anthromes (Figs 4e & 5a) of 1700 into used anthromes. The historical wildlands of 1700 became rangelands in most parts of the world and croplands in North America and South Australia (Fig. 4d). The seminatural lands of 1700 became a mix of rangelands and croplands in most of the world, and villages in Asia (Fig. 4e).

The dynamics of anthropogenic transformation differed profoundly among biomes (Fig. 5b). Boreal and mixed woodlands, tundra and deserts changed little over the past 300 years, with less than 20% of their wildlands transformed and most change occurring in areas already transformed to seminatural anthromes by 1700. Contrasting with this, grasslands, savannas and shrublands showed the greatest changes over time, with all of these experiencing > 80% conversion to used anthromes from

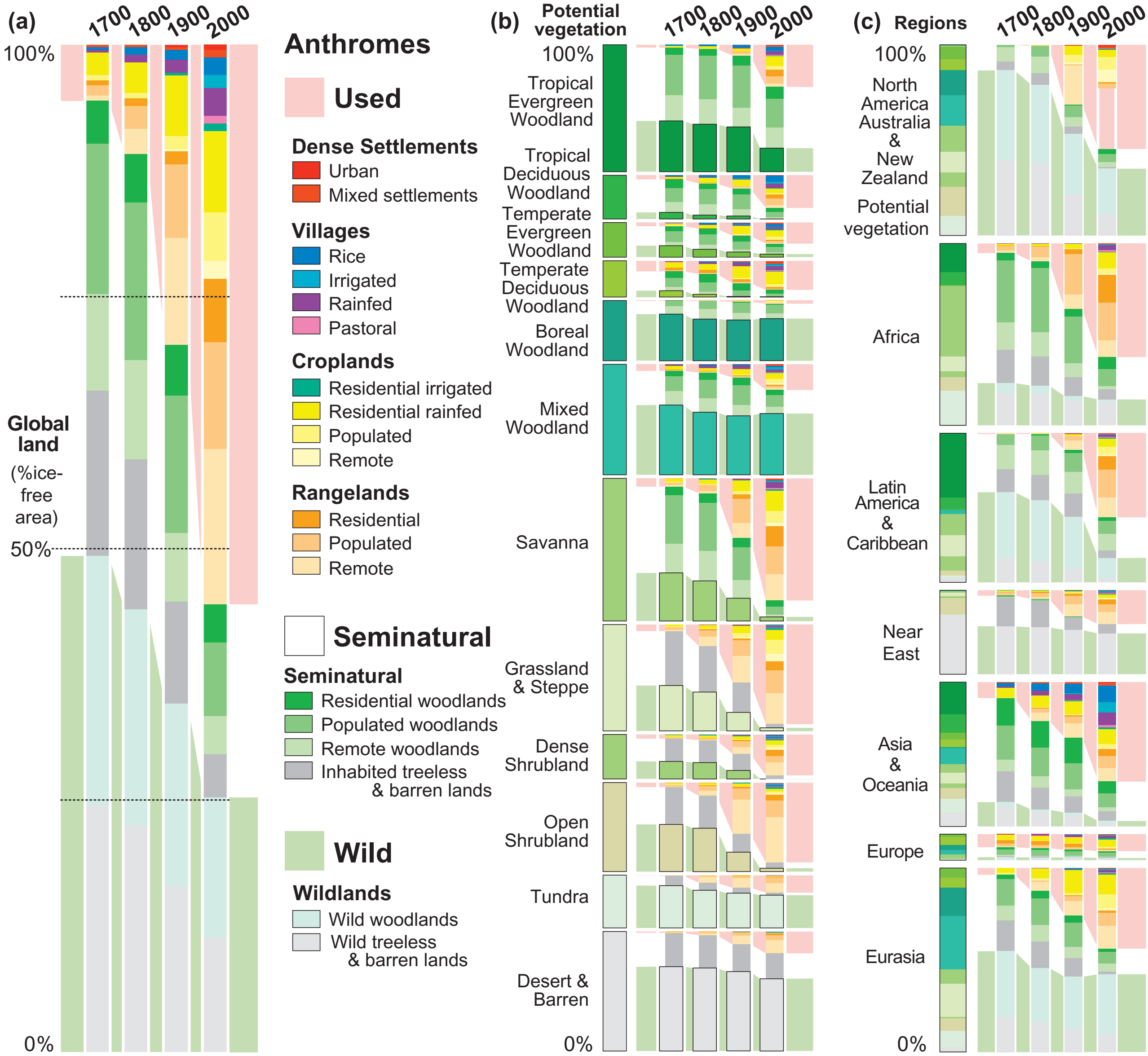

Figure 2 Global changes in anthromes, 1700–2000, expressed as a percentage of global ice-free land area (a), as a percentage of land area within potential natural vegetation biomes (b; Ramankutty & Foley, 1999) and as a percentage of global region area (c; regions outlined in Fig. 1). Columns in (a), (b) and (c) sum to 100% global ice-free land area. Trends in the combined areas of 'used' anthromes are highlighted by red shading and wildlands by green shading; seminatural anthromes left blank. Anthrome changes within Olson biome classes (Olson *et al.*, 2001) are in Appendix S1.

1700 to 2000. Most of this was the result of converting both wildlands and seminatural anthromes to rangelands, though the conversion to croplands was substantial in grasslands (28%), savanna (23%) and dense shrublands (19%).

Woodlands showed more moderate change. Over the course of the Industrial Revolution, about one-third of earth's tropical evergreen woodlands were converted into used anthromes (from wildlands and seminatural anthromes), and about 22% of their wildlands were converted to seminatural and rangeland anthromes. More than half of the area of the other woodlands biomes were transformed into used anthromes between 1700 and 2000. Tropical deciduous woodlands were transformed predominantly into rangelands (28%) and villages (24%), while the temperate woodlands were transformed into croplands (23–28%), villages (14–18%) and dense settlements (4–7%), with most change occurring in areas previously covered by seminatural anthromes.

Current state of the anthropogenic biosphere

The history and intensity of land transformation varies tremendously across the surface of the earth, with some biomes and

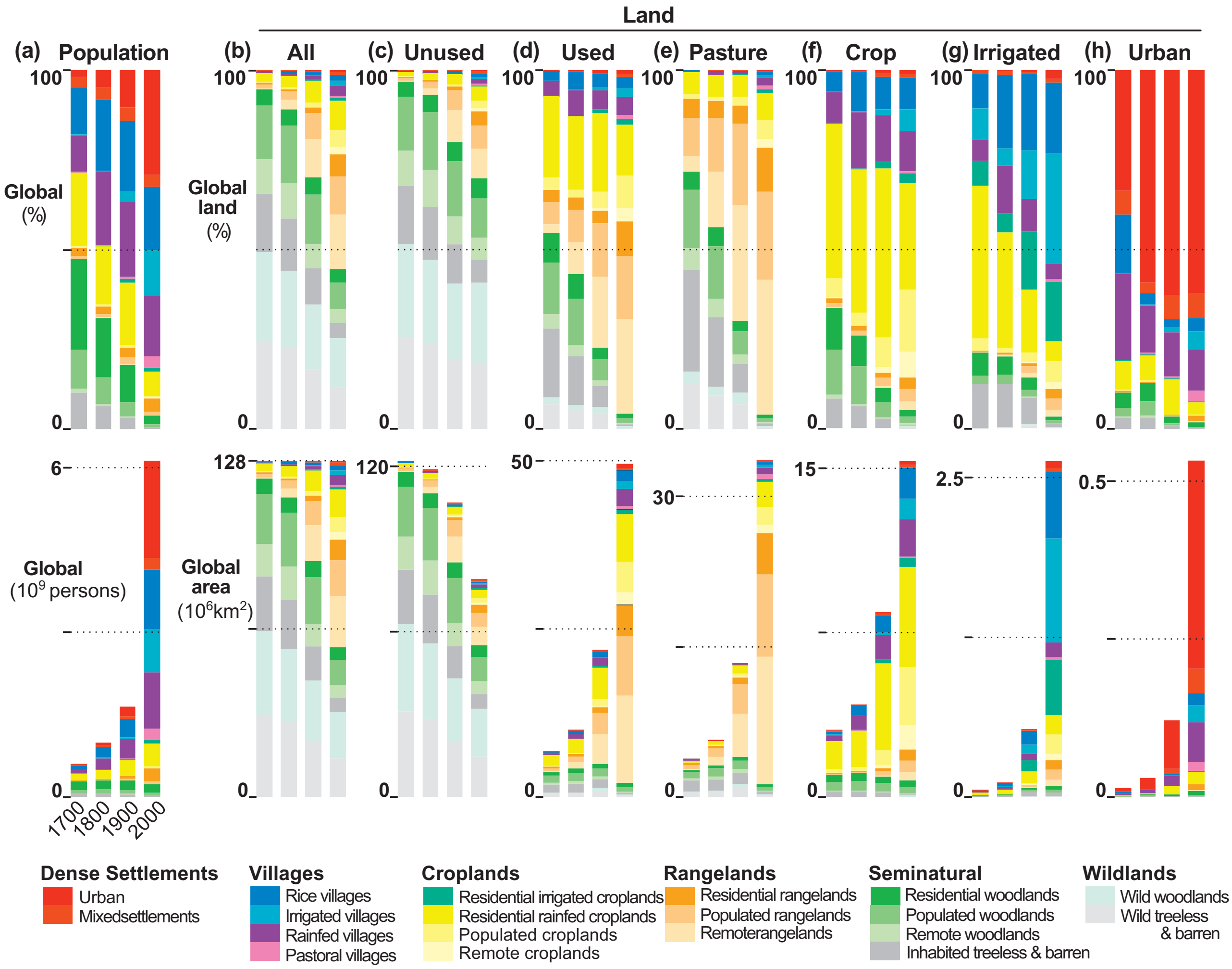

Figure 3 Global changes in anthromes, 1700–2000, relative to global population (a) and land use (b–h). Global percentages for each time period are at the top, absolute values at the bottom (scales differ for each variable, as marked), for global population (a), all ice-free land (b), unused lands (c; lands not in use for agriculture or urban settlements), used lands (d; crops + pasture + urban), pasture land (e), cropped land (f), irrigated land (g) and urban land (h).

regions almost entirely transformed and others almost uninfluenced by direct human activity (Figs 2 & 6). The maps in Fig. 6 summarize and illustrate these differences and their dynamics in a general way. In 1700, most of earth's land was already moderately transformed by human populations and land use (Fig. 6a). In subsequent centuries, land use intensified, accelerated and spread in highly dynamic and often contradictory patterns (Fig. 6b, c, d), such that even while most regions were being transformed at their most rapid rates in history, others, such as eastern North America and the northern fringes of the former Soviet Union experienced attenuation of human influence, especially in the 20th century (Fig. 6d). And while regions experiencing the most intensive transformation, to villages and croplands (Fig. 6f), tended also to have the longest periods of human habitation and land use (Fig. 6g), this was not always the case, most notably, in the grasslands of central North America, which experienced major transformation (Fig. 6f) but were mostly unused for agriculture and urban settlements prior to 1800 (Fig. 6a, b).

Even after 300 years of extensive anthropogenic transformation, more than 60% of the terrestrial biosphere remains unused directly for agriculture or urban settlements (Fig. 3c). Of these unused lands still remaining on earth in 2000, only about 40% are wildlands (see Appendix S5; Fig. 7). The other 60% are embedded within dense settlements (1%), villages (3%), croplands (7%), rangelands (19%) and seminatural anthromes (29%). Taken together, these embedded unused lands (Fig. 6h) represent an extent of human-altered terrestrial ecosystems that is substantially greater than that of all of earth's remaining wildlands combined, accounting for about 37% of all ice-free land (19% in used anthromes, 18% seminatural). Still, the global extent, type, duration and intensity of anthropogenic transformation of these embedded unused lands is a challenge to determine. Estimating the extent of older anthromes, with more than 300 years since their transformation from wildlands (Fig. 6g), and with significant areas (> 20%) of their land remaining unused (Fig. 6i), reveals that potentially ancient novel anthropogenic ecosystems now

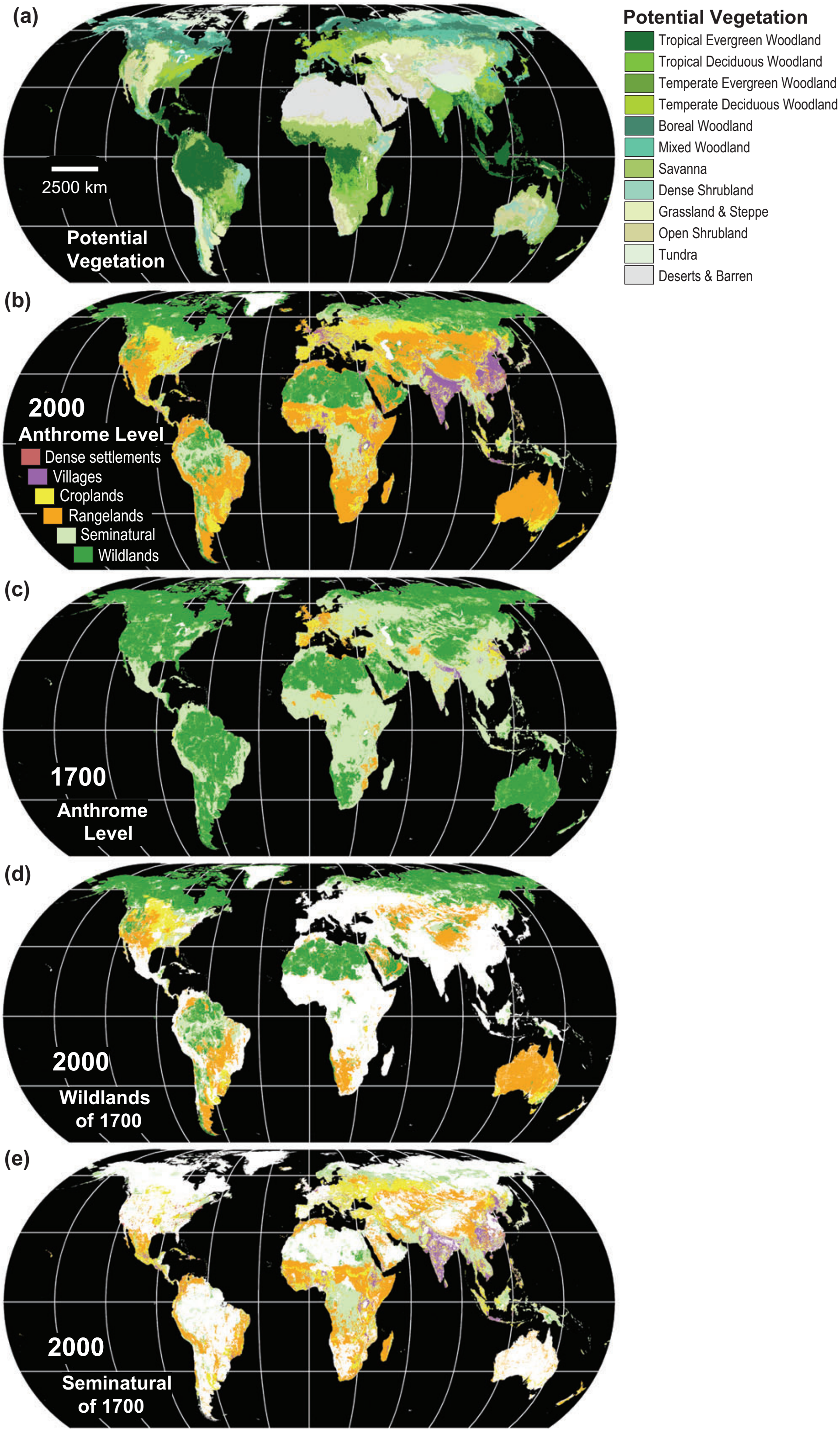

Figure 4 Potential natural vegetation biomes (a; Ramankutty & Foley, 1999) and their anthropogenic transformation from 1700 to 2000 (b–d). Levels of anthrome transformation of the terrestrial biosphere in 2000 (b) and in 1700 (c) are illustrated, along with the year 2000 anthrome levels of 1700s-era wildlands (d) and seminatural anthromes (e). White spaces in (d) and (e) are non-wild and non-seminatural areas, respectively, in 1700. Eckert IV projection.

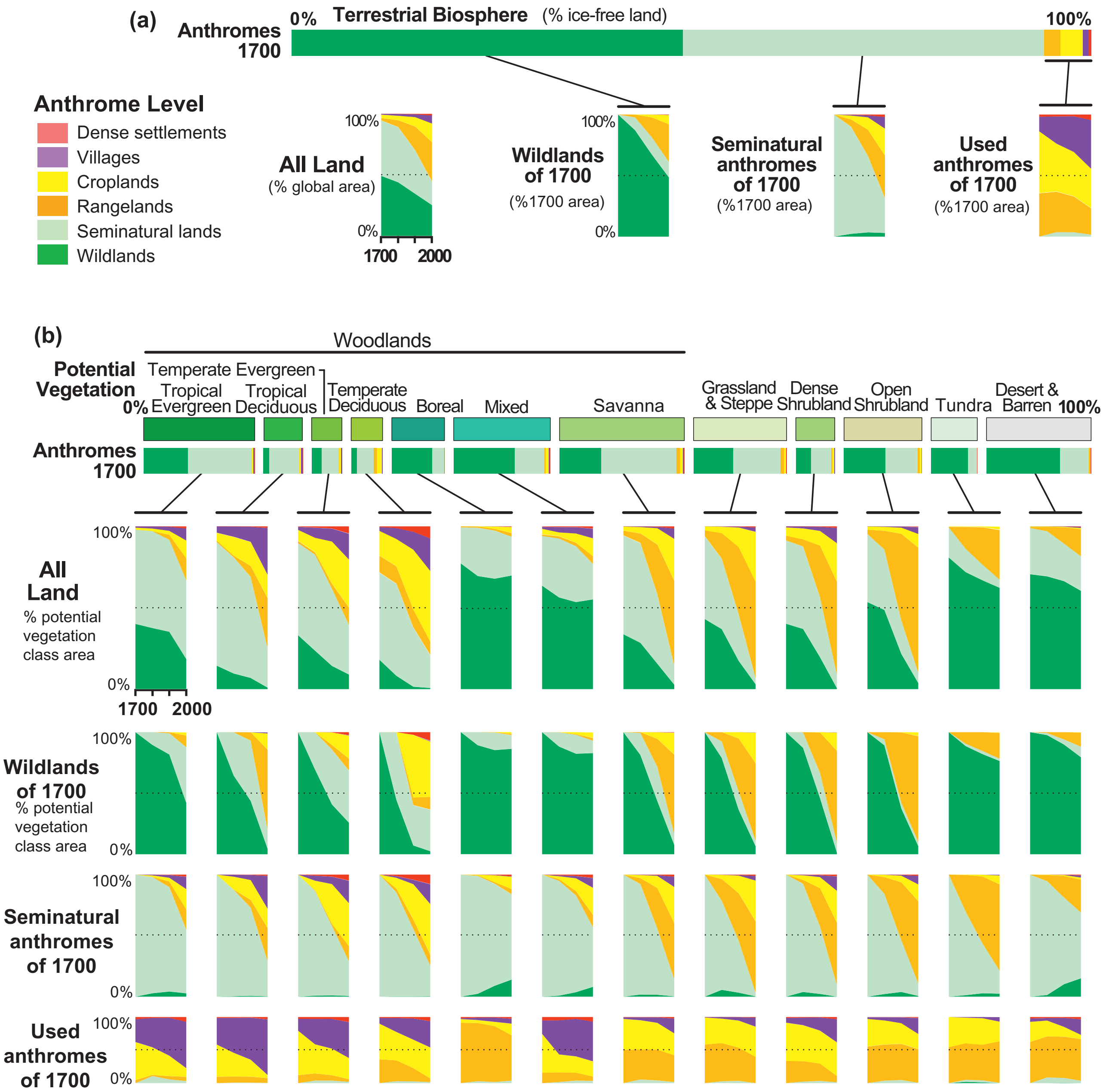

Figure 5 Transformation of the terrestrial biosphere (a) and potential natural vegetation biomes (b; Ramankutty & Foley, 1999) from 1700 to 2000. Year 1700 anthrome levels across the entire terrestrial biosphere (a) and within each potential vegetation biome (b) are depicted using horizontal bars at the top of (a) and (b); bars sum to 100% of global ice-free land area. Anthrome-level changes from 1700 to 2000 across the terrestrial biosphere (a) and within each potential vegetation biome (b) are illustrated by vertical area charts representing all land (all land; a on left; b in top row), and the 1700s areas of wildlands, seminatural anthromes and used anthromes (on right in a; lower rows in b).

cover more than 19% of all ice-free land (11% in used anthromes, 8% in seminatural). The degree to which earth's remaining unused lands are present in wildlands versus embedded within different anthromes is illustrated for different biomes and regions in Fig. 7(a) and (b), respectively. From this, it is clear that only the cold and dry biomes (boreal, shrublands, deserts), and the global regions with large extents of these (North America, Australia and New Zealand, the Near East and Eurasia) still have large extents of wildlands. Most of Earth's unused lands are now embedded within the agricultural and settled landscapes of seminatural, rangeland, cropland and village anthromes.

DISCUSSION

Anthromes as descriptors of the biosphere

Limits to anthrome classification

Anthromes, like biomes, are generalizations useful for understanding global patterns of ecosystem form and process.

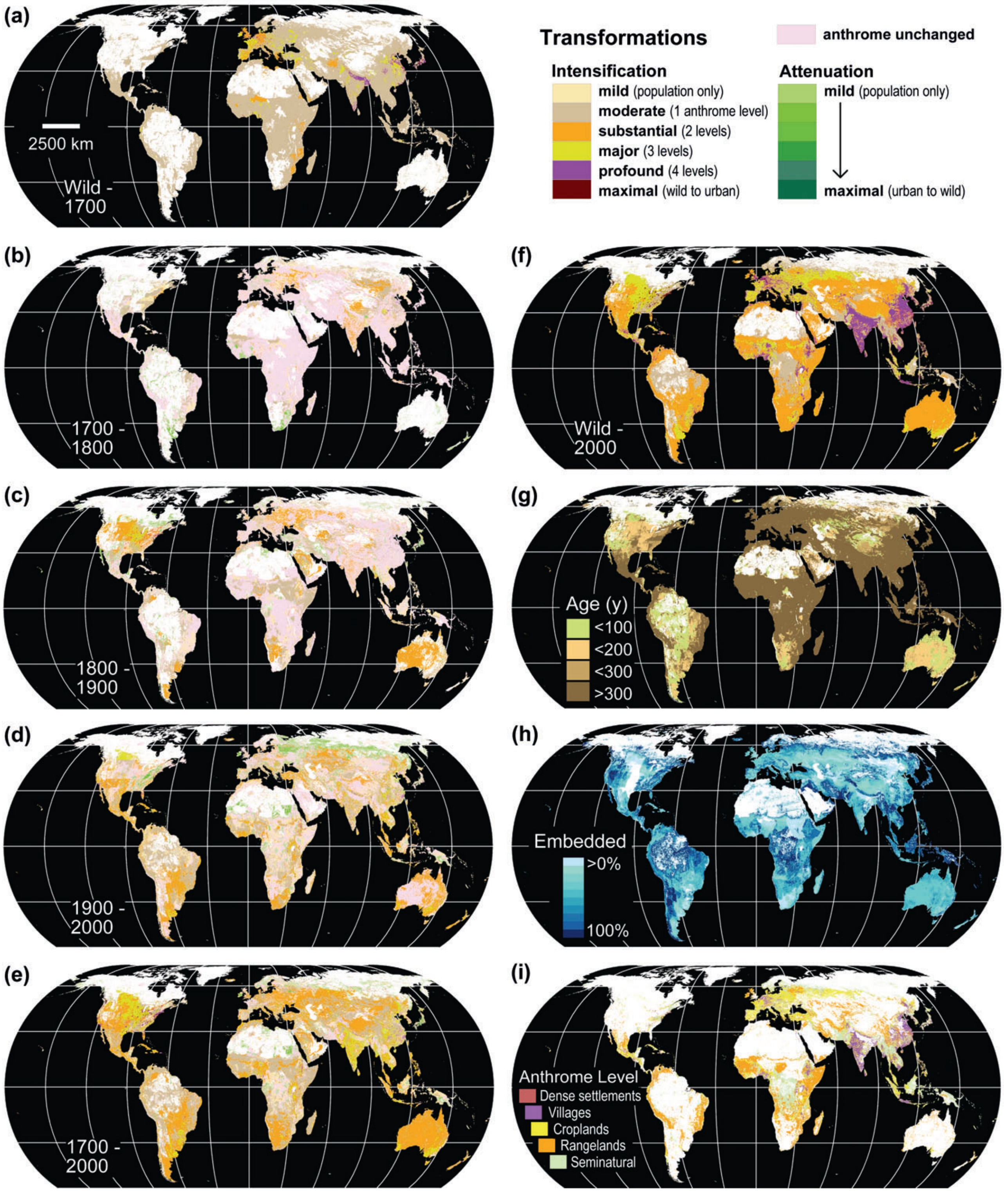

Figure 6 Global patterns of anthropogenic transformation and novel ecosystem development, 1700–2000. Anthropogenic land transformations are highlighted using an index of transformation calculated by subtracting anthrome classes between time periods (legend at upper right), for all change up to 1700 (a), between 1700 and 1800 (b), 1800 and 1900 (c), 1900 and 2000 (d), 1700 and 2000 (e) and for all change up to 2000 (f). Time since conversion to anthromes (g), percentage of anthrome area consisting of embedded unused lands (h; lands not used for agriculture or settlements, not including wildlands), and the anthrome level of all cells with > 20% cover by unused lands with at least 300 years elapsed since their conversion from wild biomes (i). Eckert IV projection.

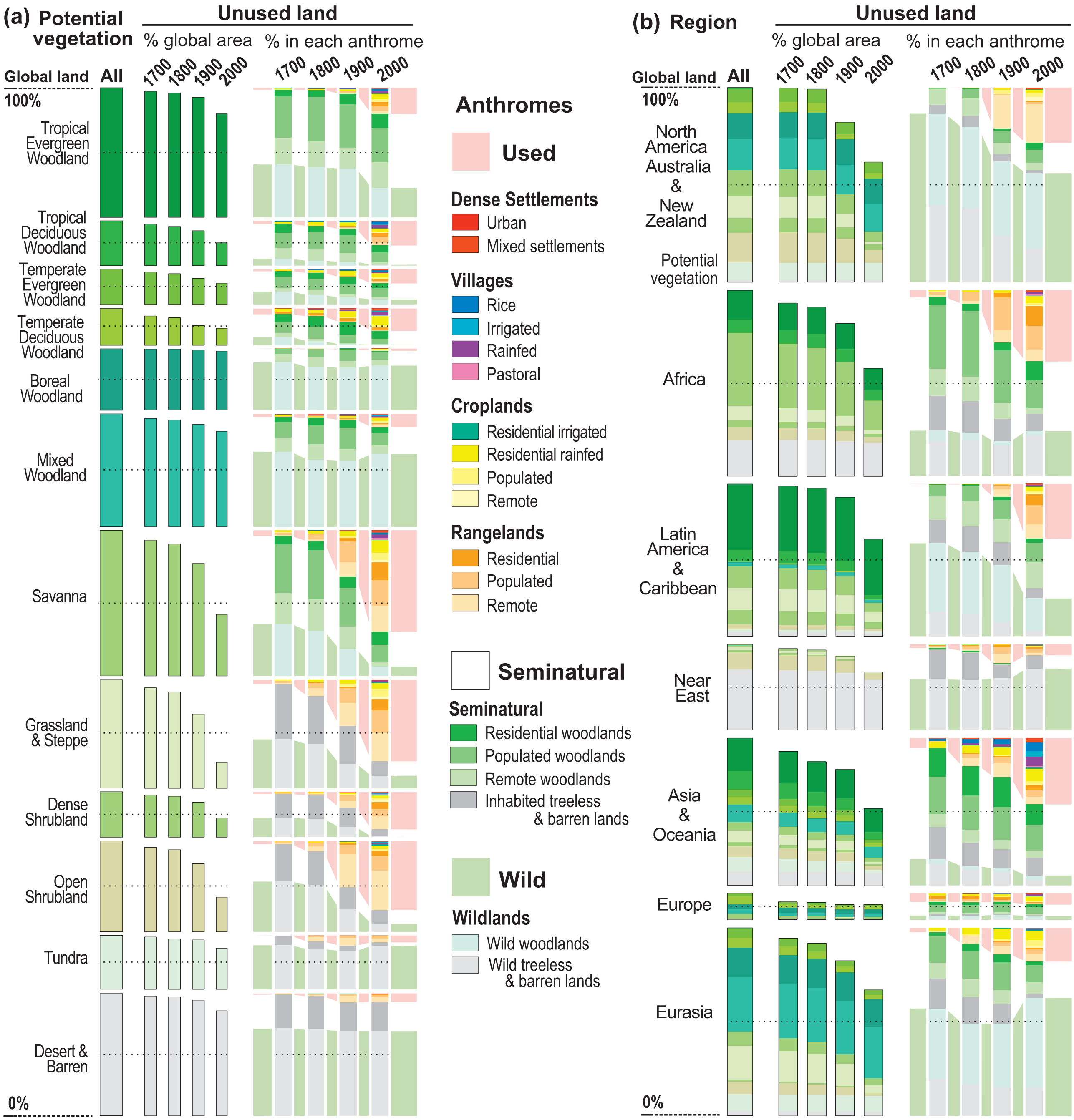

Figure 7 Changes in unused land areas and their distribution among anthromes from 1700 to 2000 within potential natural vegetation biomes (a) and regions (b). Unused land areas (lands not used for agriculture or settlements) within potential vegetation biomes (a) and regions (b) are depicted as a percentage of global ice-free land at the left in (a) and (b) The relative areas of potential vegetation biomes are highlighted in (b) using the same colours as in (a); columns sum to 100% of global land. Changes in the distribution of unused lands among anthromes over time are illustrated at right within each potential vegetation biome (a) and region (b) as a percentage of the total unused land area at each time (sum = 100% of unused land area within each biome or region at each time). Trends in the combined areas of 'used anthromes' are highlighted by red shading and wildlands by green shading; seminatural anthromes are left blank.

Moreover, anthromes provide a simple framework for assessing and modelling both past and future global biotic and ecological patterns in the light of the extent, intensity and duration of their modification by humans. Still, anthromes, like biomes or any other global classification system, are built on subjective trade-offs between detail and simplicity and usually require a variety of practical compromises to make their mapping possible using available data. One example of such a trade-off is our use of *a priori* classification thresholds, which force the division of lands into different categories at a given value of a variable, even when they may differ only slightly. An important case in point is the distinction between wildlands and the remote woodlands, rangelands and croplands anthromes, which can differ only because of very small differences in population density and land use (see Appendix S3). It is therefore necessary that any anthrome classification, including this one, be applied with full knowledge of these limitations and with consideration of the fact that other anthrome classifications are possible. Different systems would undoubtedly yield different results, depending both on differences in the classification model and on the data used as input.

On the positive side, our current anthrome system proved to have more in common with the original system of Ellis & Ramankutty (2008) than the two classic biome systems we used in this study had with each other (see Appendix S4). Moreover, the degree of variation introduced by our choice of model, data and the spatial resolution of analysis, while significant, was quantifiable and fairly predictable, with the largest effects caused by changing spatial resolution, and with all of these variations being substantially less than those caused by changes over time (see Appendix S4). For example, in comparison with our standard area estimate for the year 2000, the global wildlands estimate varied by about ± 20% across datasets and models, but was lowered by 79% at the coarsest resolution of analysis, with our standard 1700 estimate being 95% lower than for 2000.

Interpreting the ecology of anthromes

The ecological properties of anthrome classes must also be interpreted with some caution. For example, while the pasture land use that defines rangelands anthromes is usually indicative of enhanced herbivory and disturbance by livestock populations, there are also cases where the ecological effects of pasture land use on the form and diversity of vegetation can be quite small, such that rangelands may closely resemble wildlands within a particular biome (Steinfeld *et al.*, 2006). Further, unlike classic biomes, which attempt to represent fairly homogeneous forms of vegetation, anthromes represent complex mixtures of different land uses and land covers that are far harder to characterize in simple terms (Ellis & Ramankutty, 2008). Moreover, the same statistical characteristics of human populations and land use that define a particular anthrome can yield quite different ecosystems in different biomes, such as remote rangelands classified within woodlands versus shrublands or deserts.

The same anthrome class may also differ in important ways during different periods in human history. A key example is provided by seminatural woodlands – woodlands with relatively low levels of land use and human populations (Table 1; see Appendix S3). In 1700 and especially before, most seminatural woodlands were probably managed by shifting cultivators, leaving most of their forest vegetation in relatively early stages of recovery from land clearing and brief use for agriculture (Hurtt *et al.*, 2006; Ruddiman & Ellis, 2009). By 2000, however, shifting cultivation was far less common, leaving seminatural woodlands in regions with heterogeneous terrain allowing only partial use of land for agriculture, as in much of Southeast Asia (Fig. 1), and in areas experiencing agricultural abandonment, such as the eastern United States and northern Europe (Fig. 6d). In both cases these anthromes probably support forests in much later successional stages, and often with human settlements underneath the forest canopy (Rudel *et al.*, 2005).

Scientific understanding of anthrome ecology

Difficulties in interpreting the global ecological patterns created and sustained by direct human interactions with ecosystems result from our very limited scientific understanding of coupled human and ecological systems (Turner *et al.*, 2007; Ellis & Ramankutty, 2008). Certainly our understanding of these systems is far inferior to our understanding of the global ecological patterns produced by biophysical processes alone. While observations from remote sensing have revolutionized our ability to see the global patterns and dynamics of vegetation and other land covers across the earth's surface, the causes of these patterns and their dynamics are not directly observable from above, or even from the ground, without intensive local research efforts aimed at understanding both ecological and human systems (Rindfuss *et al.*, 2004; Turner *et al.*, 2007; Ellis *et al.*, 2009). Given that such efforts are extremely costly and time-consuming, global strategies are required to allocate such local observations effectively (Ellis *et al.*, 2009). By stratifying the global ecological patterns created by humans, anthrome classification may serve both as an aid in selecting global samples of local land change processes for observation and in the synthesis of these observations into theory, helping to build a global ecology that incorporates humans as sustained shapers and managers of local and global ecosystem form and function.

Anthropogenic transformation of the biosphere, 1700–2000

When did the terrestrial biosphere become anthropogenic?

Historical analysis of changes in anthrome extent and composition confirm that the terrestrial biosphere shifted from a primarily wild to a primarily anthropogenic state between 1700 and 2000 and that rapid intensification of land use in the 20th century finally pushed the biosphere into its present anthropogenic state (Fig. 2a). Still, it is important to recognize that while about half of this transition was caused by the anthropogenic transformation of lands that were still wild in 1700 (Figs 4d & 5a) the other half was caused by intensification of land use in the seminatural anthromes that already covered nearly half of the terrestrial biosphere in 1700 (Figs 4e & 5a). The ecological significance of more than 45% of earth's ice-free land being inhabited and used at lower levels in 1700 should not be underestimated, as about 60% of earth's tropical and temperate woodlands were included in this seminatural area, and these were most likely inhabited primarily by shifting cultivators who may have cleared almost this entire area, one small patch at a time, at some point in history or pre-history (Ruddiman & Ellis, 2009). Moreover, even areas without significant human populations or use of land for crops or pasture in 1700 and later, and therefore considered 'wild' in this analysis, may still have been significantly altered ecologically by prior use of land and by intensive and systematic foraging by sparse human populations (Cronon, 1983). It is also important to note that the lion's share of global land transformation since 1700 was the result of increasing pasture areas and the consequent rise of rangelands anthromes (Fig. 2a). This may have had relatively light impacts on ecosystem form and process even in comparison with the conversion of wildlands to seminatural remote woodlands, if these were managed by shifting cultivators. Nevertheless, by almost any standard, the extent of human populations and their use of land in the 20th century supports the conclusion that, by 2000, most of the terrestrial biosphere was transformed into predominantly anthropogenic ecological patterns combining lands used for agriculture and urban settlements and their legacy; the remnant, recovering and other managed novel ecosystems embedded within anthromes.

How did the terrestrial biosphere become anthropogenic?

The largest global change in land use over the past 300 years was the near sixfold increase in the global extent of pastures from 1800 to 2000 (Figs 2a & 3e). This vast increase in pastures drove the emergence of new rangelands anthromes across the wild and mostly dryer biomes of the Americas, Australia, Central Asia and southern Africa (Figs 1 & 4d) and in the seminatural anthromes of the mostly moister wooded biomes of sub-Saharan Africa, Central America and Eurasia (Fig. 4e). The other major driver of biospheric transformation was the rapid expansion of crops and croplands into the wild grasslands of North and South America, the shrublands and wild woodlands of southern Australia (Fig. 4d) and the seminatural grasslands of Eurasia (Fig. 4e).

While these tremendous expansions in land use might seem the most important anthropogenic changes in the terrestrial biosphere during the Industrial Revolution, given that together they covered nearly 50% of global land, it should not be forgotten that over the same period these were combined with dramatic intensifications in land use. Land-use intensification caused the most intensively used anthromes to expand in every century, not only in terms of the increasing global extents of villages and dense settlements, but also by increasing the areas of the more densely populated anthrome classes within each anthrome level (Figs 1, 2a & 6f). The precipitous decline in both wildlands and seminatural anthromes in all but the coldest and driest biomes must therefore be interpreted as the combined result of both land-use expansion and land-use intensification (Figs 2a & 5b). As a consequence, the terrestrial biosphere is now used far more intensively than it ever has been, though some attenuation of land use did occur during the 20th century due to agricultural abandonment in northern Eurasia, the eastern United States and parts of sub-Saharan Africa (Fig. 6d).

Implications of an anthropogenic biosphere

Conserving nature in anthromes

At this point in history, about 40% of all ice-free land on earth is in direct use for agriculture or urban settlements (Fig. 3d). An additional 37% of ice-free land is not currently used for these purposes, but is embedded within anthromes having these uses (Figs 6i & 7). This leaves wildlands in the minority, a mere 22% of global ice-free land area, with about 85% of these located only in the cold and dry biomes of the world, a result confirming earlier estimates (Sanderson *et al*., 2002).

As most of earth's land not currently in use for agriculture or urban settlements is now embedded within anthromes, it is the ecology of these embedded 'unused lands' that should now matter most in conserving the species and ecosystems we value. The critical challenge, therefore, is in maintaining, enhancing and restoring ecological functions in the remnant, recovering and managed ecosystems formed by land use and its legacies within the complex multifunctional anthropogenic landscape mosaics that will be the predominant form of terrestrial ecosystems today and into the future (Hobbs *et al*., 2006).

There is growing evidence that some lands used directly for agricultural production can sustain high levels of biodiversity, similar to those of lands unused for agriculture or settlements, especially in ancient agricultural regions (Ranganathan *et al*., 2008; Chazdon *et al*., 2009). Moreover, depending on how the mosaic structure of landscapes is managed to enhance connectivity and habitat values, it is possible to sustain high levels of wild native biodiversity even in urban and village anthromes where built-up lands and intensive cropping systems predominate (Ricketts, 2001; Fahrig, 2003; Lindenmayer *et al*., 2008; Chazdon *et al*., 2009). Yet efforts to sustain and enhance biodiversity in anthromes can be challenged by trade-offs between conservation values and the benefits of using land for agricultural production and settlements (Chazdon *et al*., 2009). Despite this challenge, anthromes composed entirely of agricultural and settled lands are rare; landscape mosaics containing substantial areas of unsettled agricultural land are the global norm (Fig. 6h). As a result, global efforts to conserve, enhance and restore biodiversity within anthromes may be possible without directly challenging these land uses. Success in this effort will require that novel anthropogenic ecosystems be the focus of expanded research, monitoring and conservation efforts in most terrestrial biomes, as their optimal management, landscape and community structure, habitat connectivity, ecosystem processes and dynamics remain poorly understood and cannot be reliably predicted from past trends or historical environmental constraints (Hobbs *et al*., 2006; Lindenmayer *et al*., 2008; Chazdon *et al*., 2009; Jones & Schmitz, 2009).

Global observing systems and models appropriate for an anthropogenic biosphere

Existing global land-use and population data, vegetation models, remote sensing platforms and other data acquisition systems and models are certainly useful for investigating current, historical and future ecological patterns across the terrestrial biosphere. Indeed, the present study made use of these to investigate current and historical patterns, and similar methods may help push this investigation into pre-history. But this remains a mere descriptive sketch. There remain tremendous uncertainties in our understanding and ability to model even current global patterns of ecosystem function and biodiversity across the anthropogenic biosphere.

Solid theoretical and predictive global models of coupled human and ecological system dynamics are only now being developed (e.g. Bouwman *et al.*, 2006; Bondeau *et al.*, 2007), and most tend to focus on land-cover interactions with climate, rather than ecosystems (e.g. Brovkin *et al.*, 2006; Olofsson & Hickler, 2008). We need human systems models that are as theoretically strong, predictive and useful as the best current biophysical models of natural biospheric pattern, process and dynamics, and we need these models to be coupled together to produce useful predictions of global ecological patterns, processes and dynamics.

The remedy is clear, but both expensive and logistically challenging: a human biosphere observing and modelling system built on standardized global observations of coupled human and ecological systems in the field. Global remote sensing is a tremendous asset in this effort but it is simply incapable of observing the causes of human and ecological dynamics. We need standardized observations across the global spectrum of anthropogenic ecosystems that integrate ecological measurements and social surveys of human practices at the relatively fine spatial scales at which these interact (Alessa & Chapin, 2008; Ellis *et al.*, 2009). Ultimately, based on these observations, we can build strong theoretical and applied models of anthropogenic ecosystem dynamics at local, regional and global scales. Given that most of the terrestrial biosphere is now anthropogenic, the future of all species, including ours, will depend on understanding and modelling the past, present and potential future ecology of our anthropogenic biosphere as we continue to directly alter and manage it.

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REFERENCES

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

Bondeau, A., Smith, P.C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-Campen, H., Müller, C., Reichstein, M. & Smith, B. (2007) Modelling the role of agriculture for the 20th century global terrestrial carbon balance. *Global Change Biology*, **13**, 679–706.

Bouwman, A.F., Kram, T. & Klein Goldewijk, K. (2006) *Integrated modelling of global environmental change: an overview of Image 2.4*. Netherlands Environmental Assessment Agency, Bilthoven, The Netherlands.

Brovkin, V., Claussen, M., Driesschaert, E., Fichefet, T., Kicklighter, D., Loutre, M.F., Matthews, H.D., Ramankutty, N., Schaeffer, M. & Sokolov, A. (2006) Biogeophysical effects of historical land cover changes simulated by six earth system models of intermediate complexity. *Climate Dynamics*, **26**, 587–600.

Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Breugel, M.V. & Philpott, S.M. (2009) Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica*, **41**, 142–153.

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

Dansereau, P.M. (1957) *Biogeography: an ecological perspective*. Ronald Press Company, New York.

Dearing, J., Battarbee, R., Dikau, R., Larocque, I. & Oldfield, F. (2006) Human–environment interactions: learning from the past. *Regional Environmental Change*, **6**, 1–16.

DeFries, R.S., Asner, G.P. & Houghton, R.A. (2004) *Ecosystems and land use change*. Geophysical Monograph Series. American Geophysical Union, Washington, DC.

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

Ellis, E.C., Neerchal, N., Peng, K., Xiao, H.S., Wang, H., Yan, Z., Li, S.C., Wu, J.X., Jiao, J.G., Ouyang, H., Cheng, X. & Yang, L.Z. (2009) Estimating long-term changes in China’s village landscapes. *Ecosystems*, **12**, 279–297.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487–515.

Feddema, J.J., Oleson, K.W., Bonan, G.B., Mearns, L.O., Buja, L.E., Meehl, G.A. & Washington, W.M. (2005) The importance of land-cover change in simulating future climates. *Science*, **310**, 1674–1678.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., III, Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

Hansen, D.M. & Galetti, M. (2009) Ecology: the forgotten megafauna. *Science*, **324**, 42–43.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holdridge, L.R. (1947) Determination of world plant formations from simple climatic data. *Science*, **105**, 367–368.

Hurtt, G.C., Frolking, S., Fearon, M.G., Moore, B., Shevliakova, E., Malyshev, S., Pacala, S.W. & Houghton, R.A. (2006) The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Global Change Biology*, **12**, 1208–1229.

Jones, H. & Schmitz, O. (2009) Rapid recovery of damaged ecosystems. *PLoS ONE*, **4**, e5653.

Kareiva, P., Watts, S., McDonald, R. & Boucher, T. (2007) Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, **316**, 1866–1869.

Kirch, P.V. (2005) Archaeology and global change: the Holocene record. *Annual Review of Environment and Resources*, **30**, 409–440.

Klein Goldewijk, K. (2001) Estimating global land use change over the past 300 years: the HYDE database. *Global Biogeochemical Cycles*, **15**, 417–433.

Klein Goldewijk, K. & van Drecht, G. (2006) HYDE 3: current and historical population and land cover. *Integrated modelling of global environmental change. An overview of IMAGE 2.4* (ed. by A.F. Bouwman, T. Kram and K. Klein Goldewijk), pp. 93–111. Netherlands Environmental Assessment Agency (MNP), Bilthoven, The Netherlands.

Küchler, A.W. (1949) A physiognomic classification of vegetation. *Annals of the Association of American Geographers*, **39**, 201–210.

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R. *et al*. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters*, **11**, 78–91.

Monfreda, C., Ramankutty, N. & Foley, J.A. (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles*, **22**, GB1022.

Oak Ridge National Laboratory (2006) *LandScan global population database*. Oak Ridge National Laboratory, Oak Ridge, TN. Available at: http://www.ornl.gov/landscan/ (accessed 28 July 2008).

Olofsson, J. & Hickler, T. (2008) Effects of human land-use on the global carbon cycle during the last 6,000 years. *Vegetation History and Archaeobotany*, **17**, 605–615.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, **51**, 933–938.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.

Ramankutty, N. & Foley, J.A. (1999) Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles*, **13**, 997–1027.

Ranganathan, J., Daniels, R.J.R., Chandran, M.D.S., Ehrlich, P.R. & Daily, G.C. (2008) Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences USA*, **105**, 17852–17854.

Rea, L.M. & Parker, R.A. (1997) *Designing and conducting survey research: a comprehensive guide*. Jossey-Bass, San Francisco.

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

Rees, W.G. (2008) Comparing the spatial content of thematic maps. *International Journal of Remote Sensing*, **29**, 3833–3844.

Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, **158**, 87–99.

Rindfuss, R.R., Walsh, S.J., Turner, B.L., II, Fox, J. & Mishra, V. (2004) Developing a science of land change: challenges and methodological issues. *Proceedings of the National Academy of Sciences USA*, **101**, 13976–13981.

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

Rudel, T.K., Coomes, O.T., Moran, E., Achard, F., Angelsen, A., Xu, J.C. & Lambin, E. (2005) Forest transitions: towards a global understanding of land use change. *Global Environmental Change – Human and Policy Dimensions*, **15**, 23–31.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.

Shelford, V.E. (1932) Basic principles of the classification of communities and habitats and the use of terms. *Ecology*, **13**, 105–120.

Siebert, S., Döll, P., Feick, S., Hoogeveen, J. & Frenken, K. (2007) *Global map of irrigation areas version 4.0.1*. Johann Wolfgang Goethe University, Frankfurt am Main, Germany/Food and Agriculture Organization of the United Nations, Rome, Italy. Available at: http://www.fao.org/nr/water/aquastat/irrigationmap/index.stm (accessed 22 September 2008).

Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., Rosales, M. & De Haan, C. (2006) *Livestock's long shadow: environmental issues and options*. Food and Agriculture Organization of the United Nations, Rome.

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

Turner, B.L., II, Lambin, E.F. & Reenberg, A. (2007) The emergence of land change science for global environmental change and sustainability. *Proceedings of the National Academy of Sciences USA*, **104**, 20666–20671.

UNFPA (2007) *State of world population 2007: unleashing the potential of urban growth*. United Nations Population Fund, New York.

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

Whittaker, R.H. (1970) *Communities and ecosystems*. Macmillan, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Analyses based on Olson biomes (Olson *et al.*, 2001; Acrobat file).
Appendix S2. Irrigated areas 1700–2000: methodology and data sources (Acrobat file).
Appendix S3. Anthrome classification algorithm (Acrobat file).
Appendix S4. Anthrome classification sensitivity to data inputs, model thresholds and spatial resolution (Acrobat file).
Appendix S5. Statistical data for anthromes and biomes and their transformations (Excel file).

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BIOSKETCH

This research was conducted by members of the anthromes working group, an informal international collaboration of researchers dedicated to investigating, understanding and modelling human transformation and management of the terrestrial biosphere past, present and future.

Author contributions: E.C.E conceived the initial idea, conducted the anthrome analysis and led the writing; K.K.G. prepared the land-use and population datasets; S.S. produced the irrigation datasets; D.L. and N.R. developed early versions of the anthrome classification system; N.R. developed an initial version of Appendix S3. All authors contributed to the analysis and to revising the manuscript for publication.

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