

# Changing NPP consumption patterns in the Holocene: From megafauna-‘liberated’ NPP to ‘ecological bankruptcy’

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## Abstract

There have been vast changes in how net primary production (NPP) has been consumed by humans and animals through the Holocene. Here we ask: how much NPP energy may have become available following the megafauna extinctions? When did humans, through agriculture and livestock, consume more NPP than wild mammals? When did humans and wild mammals use more energy than was available in total NPP in each country? The megafauna extinctions potentially liberated ~2.2–5.3% of global NPP that early humans eventually consumed. By 1850, humans began to consume more than wild mammals (globally averaged). Currently, >82% of people live in ‘ecologically bankrupt’ countries where all plant production could not satisfy our energy demands. To summarize, we began the Holocene with an NPP energy surplus, became the dominant consumers of NPP over the natural world by the start of the Industrial Revolution, but now consume more total energy (including fossil fuels) than is available in NPP in most countries.

## Keywords

Anthropocene, ecological bankruptcy, extinctions, HANPP, Holocene, NPP

## Introduction

Animal life on Earth is, and has always been, almost entirely sustained by energy ultimately derived from consumption of net primary production (NPP). However, the Holocene, the most recent 0.002% of Earth’s history, has witnessed greater changes in these consumption patterns than possibly any other geological period. The Holocene (11,500 years BP–current) began at the tail end of late-Quaternary extinctions of terrestrial megafauna (Barnosky et al., 2004), a

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disruption which opened up a resource niche for other animals to consume this plant-derived energy, effectively liberating the NPP that was formerly consumed by megafauna (Doughty and Field, 2010). During these extinctions, animals occupying entire functional guilds went extinct, with 88% of megafauna genera going extinct in Australia, 84% in South America, 72% in North America, 36% in Eurasia, and 18% in Africa (Barnosky et al., 2004). After this extinction episode, it is argued that there was a global dearth in megafauna biomass for some time (Sandom et al., 2014). Megafauna biomass did eventually recover to prior levels but is now concentrated in humans and livestock (Barnosky, 2008).

Pleistocene megafaunal consumption of NPP has been previously estimated as  $\sim 2.5\%$  ( $\sim 1.4 \pm 0.2$  Pg C/year of 56 Pg C/year) of global terrestrial NPP (Doughty and Field, 2010). Other analyses argued that both Barnosky (2008) and Doughty and Field (2010) underestimated megafauna biomass (Smil, 2013), leading to larger estimates of unconsumed NPP. However, there were significant limitations to all previous calculations since none used well-constrained range maps for the now-extinct megafauna. Recently such range maps have been produced by Faurby and Svenning (2015a) using a methodology that estimated megafauna distributions as they would have today been in the absence of any local or global extinctions (the study does not estimate animal density).

The change in NPP consumption following the Pleistocene extinctions is related to a similar question: how much NPP do contemporary wild mammals consume? We often do not know exact population densities for specific animals, but as for the Pleistocene megafauna, theoretical population densities and consumption rates can be calculated using scaling theory (Brown et al., 2000). Scaling theory relates an animal's size with a range of animal attributes such as metabolic rate, energy demand, and population density. Therefore, we can estimate theoretical NPP consumption by wild mammals by estimating the population density of animals (PD; #/km<sup>2</sup>) that consume dry matter (DM) to fulfil their metabolic requirements (MR; kg DM/animal per day). A previous study has created global maps of theoretical NPP consumption for mammals >1 kg (Wolf et al., 2013).

If we are interested in the percentage reduction of NPP consumption following the megafauna extinctions, a pertinent question is whether total consumption of NPP by a particular species increases with animal size. A large animal clearly eats more than a small one, but it also has lower population density and both theory and data suggest that total NPP species consumption does not increase with animal size. A previous study suggested little mass dependence of biomass consumption because energy usage per area does not scale with body size (Wolf et al., 2013). For instance, herbivory in Kruger National Park by mammalian herbivores >1 kg was not related to species body size (average consumption was 927 kg/km<sup>2</sup> per year or 0.37% of the standing crop biomass per herbivore) (Wolf et al., 2013). The theoretical explanation for this phenomena is termed the 'law of energy equivalence', which argues that the population-level biomass consumption should be equal across a range of animal sizes (Damuth, 2007). Therefore, total consumption of NPP by animals per unit area should, to first order, be a function of the total number of species present or the biodiversity. There are of course exceptions to this law with a single species capable of eating a large percentage of NPP. However, when scaled across all species there is no relationship in the data between mean animal size and mean per area consumption rates and we would predict that each loss of a species would decrease consumption by a roughly equal amount.

The second major change in the consumption of NPP arose with the development of agriculture and the domestication of animals. Between about 10,500 and 4500 BP, agriculture based on the domestication of wild plants arose independently in many different geographic areas (Diamond and Bellwood, 2003). Recent studies have pushed back the dates in which agriculture developed independently in both North and South America, and pushed forward the dates of onset in the Near

East so all three are currently thought to have begun ~10,000 years ago (Balter, 2007; Dillehay et al., 2007; Smith, 1997). It remains an active research topic how much NPP was historically consumed by humans in the form of crops, pastures and rangelands. There are now estimates of this past NPP consumption since 800 CE (Pongratz et al., 2008). In that study, the past three centuries of agriculture and pasture maps were created using published agricultural maps and earlier periods were created using population data as a proxy for agricultural activity. In combination, estimates of total wild animal NPP consumption and human NPP consumption since 800 allow us to investigate when human consumption of NPP surpassed total wild animal NPP consumption. The question is germane because it provides a boundary condition for identifying a sustainable long-term NPP consumption level on Earth.

The third major change in NPP consumption patterns followed the Industrial Revolution, when, for the first time in Earth's history, animals (humans and their livestock) were supported in increasing measure by energy not derived from recent photosynthesis. This process began with the Industrial Revolution in Britain in the 19th century and slowly spread through the rest of the world. A recent study tried to quantify this energy usage using metabolic scaling theory to compare our social metabolism to our actual metabolism (Malhi, 2014). For instance, the average hunter-gatherer has a metabolism of 100 W, about what the mean human size would predict based on scaling theory. However, hunter-gatherers have other energy needs such as for fire for cooking and warmth. When this total metabolism (metabolism + social energy) is accounted for, hunter-gatherers have a social metabolism of ~300 W, roughly three times their physiological metabolism. Likewise, the pre-industrial agrarian human (using 18th-century agrarian Austria as an example and derived using land use, material and energy flows, such as domestic extraction, imports and exports, as well as socio-economic variables such as GDP and population) has a social metabolism of 2000 W (Krausmann et al., 2008a, 2008b), mainly derived from NPP usage through agriculture, equivalent to the physiological metabolism of a 2.5-tonne rhino. Using a similar set of calculations, a modern industrial human has an average (with a great deal of variability based on individual circumstances) social metabolism of 8000 W (Krausmann et al., 2008a), which is equivalent to the physiological metabolism of a 10-tonne mammal. This is double the size of an African elephant, and greater than any extant land mammal.

This present study takes that analysis one step further and asks, if we, as industrial humans, with our average social metabolism of 8000 W, were forced to only utilize NPP energy as we have had to during most of human history, when in history would each country have an energy consumption equivalent to the available NPP within that country? Another way of asking this question is if we literally consumed NPP as a population of 10-tonne social metabolic animals, at what point in history would we have completely consumed all available NPP energy in each respective country? This is directly relevant because a country that could not sustain consumption in the absence of non-sustainable energies is clearly more ecologically vulnerable to resource depletion than a country that could change its source of energy if necessary.

In order to quantitatively understand these three energy transitions of the Holocene (hunter-gatherer, agricultural, industrial), we chart the history of NPP consumption and total energy use to ask the following three specific questions:

1. How much NPP energy may have become available following the extinction of the megafauna?
2. When did humans in each country consume more NPP than the rest of the mammals in that country?
3. When did humans in each country achieve a total energy consumption more than the total NPP available in their country?

## Methods

This work involves the compilation of several data sets including new megafauna range maps (Faurby and Svenning, 2015a), global mammal NPP consumption maps (Wolf et al., 2013), historical crop and pasture NPP consumption maps (Pongratz et al., 2008), the Carnegie–Ames–Stanford approach (CASA) to calculate present-day NPP (Field et al., 1998), modern crop and pasture NPP consumption values (Ramankutty et al., 2008), and modern country by country historical energy, population, alternative energy usage and area data from the World Bank (<http://data.worldbank.org/>). Below we give further descriptions of each data set and how we fit them together to answer each of the three questions listed above. There are other sources for these data and we explore the impact of this and other potential errors in a detailed sensitivity study (Supplementary Tables 2 and 3, available online).

Although estimates of megafauna NPP consumption have been published previously (Doughty and Field, 2010), they lacked the critical range estimates for each species. However, a recent study has solved this issue by estimating present-natural sensu (Peterken, 1977) distributions (Faurby and Svenning, 2015a), the distributions as they would have been today without any extinctions or regional extirpations. Range maps for prehistoric extinct species were created using a co-occurrence approach, where their distributions are estimated based on those of the extant species with which the extinct animals co-occurred. Climate variations between the Holocene and Pleistocene were therefore indirectly taken into account because it was assumed that each extinct species would have responded to the late-Quaternary climatic changes in a similar way to the species with which they used to co-occur. To evaluate the accuracy of the co-occurrence approach, the ranges of 39 extant species in North America (11 terrestrial species of Artiodactyla and 28 terrestrial species of Carnivora) were estimated using this approach and compared to their historical (pre-Columbus) distributions. The simulated distributions of species was very similar to the actual historical distributions of those species (with a correlation of  $\rho = 0.856$ ) which gives confidence that the extinct megafauna species are accurately predicted (Faurby and Svenning, 2015a). There have been large reductions in the ranges of extant mammals too and historical range maps were employed if they were available as estimates of the present-natural (no human-caused decline) distributions. However, if not available, the maps were created by combining historic knowledge and climate maps. For instance, climatic convex hull modelling (based on average temperature, winter temperature and annual precipitation) combined with overall biogeographical constraints was used to estimate the potential range of many of the extant species.

We estimate total wild animal NPP consumption for each species based on body size, species range maps (described above), and scaling theory. We used the International Union for the Conservation of Nature and Natural Resources (IUCN) spatial database on mammal species and their ranges (IUCN, 2010) to develop a gridded, global estimate of mammal ranges for all terrestrial mammals of which we have information on body mass on almost all (Faurby and Svenning, 2015b). Based on these range maps, we use species mass and scaling theory to estimate the population density of animals (based on data from Damuth 1987; #/km<sup>2</sup> but see McGill et al., 2007, for a review) that consume DM to fulfil their metabolic requirements (based on data from the AnAge database; de Magalhaes and Costa, 2009; kg DM/animal per day) (Damuth, 1987). The product of population density and metabolic rate equals a population consumption rate of dry matter of NPP. We do not calculate NPP consumption by animals in desert regions (NPP < 200 g/m<sup>2</sup> per day) because our mass–animal density relationships do not appear accurate in such low productivity systems and we get unreasonably high consumption values relative to NPP (improved species abundance distribution predictions could improve this in the future; McGill et al., 2007).

The data available to us give a measure of gamma diversity, that is, the total species diversity in a 1° grid. The relevant metric for our study is however the alpha diversity, namely the average species diversity in a grid. This distinction is important to us, because in some regions, the gamma diversity of small (< 1 kg) species in a 1° grid is substantial, and has the potential to overwhelm herbivory calculations. To address this uncertainty, we vary the number of small mammals in this study to reflect different assumptions about the alpha diversity of these animals, up to a maximum value given by the gamma diversity. We attempt to propagate this error in a sensitivity study. Using our data sets we calculate that metabolic consumption has an error on the slope (mean animal biomass versus consumption on a logarithmic scale) of 0.008 and population density has an error on the slope of 0.027. We therefore vary the slope of our regression by  $\pm 0.035$  in a sensitivity study. For all major data sets, we explain the major uncertainties and then redo our analysis under a large range of possible values (Supplementary Tables 2 and 3, available online).

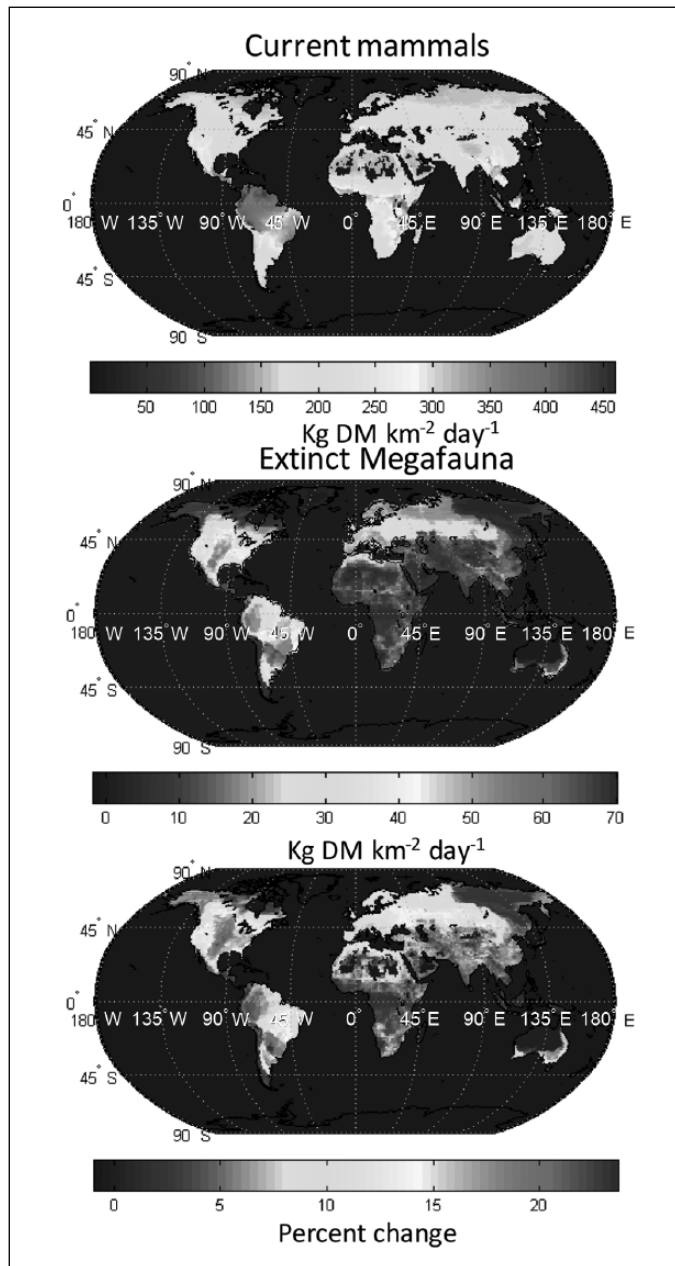
We compare consumption patterns of NPP between humans (through crops and pasture) and animals between AD 800 to modern times based on maps from Pongratz et al. (2008) for AD 800, 1700 and 1850 and for modern crop and pasture values based on Ramankutty et al. (2008) (Pongratz et al., 2008; Ramankutty et al., 2008). We sum total NPP consumed (human plus mammal) and determine what percentage is human consumption at each time slice. Human NPP consumption is estimated through crop production, not human metabolism.

Next, we add energy consumption to our estimates of total NPP consumption by humans and animals and compare this with present-day NPP using the Carnegie–Ames–Stanford approach (CASA) (Field et al., 1998). To calculate energy use and population per country since 1960, we use data from the World Bank data centre (<http://data.worldbank.org/>) for energy use in units of oil consumption per capita. This is defined by the World Bank as: ‘primary energy before transformation to other end-use fuels, which is equal to indigenous production plus imports and stock changes, minus exports and fuels supplied to ships and aircraft engaged in international transport’. We focus on energy consumption following the ‘Great Acceleration’ of 1960 when there are good energy and population data from the World Bank for most countries. We convert this total energy usage to MJ per capita (using an energy density for oil of 46 MJ/kg) and compare this with total potential NPP per country in MJ/year (using the energy density for biomass of 16 MJ/kg) (Harte, 1988). We calculate total mean NPP produced in each country and multiply this by the country’s area, also based on data from the World Bank. We then convert NPP consumed by wild animals, crops, and livestock to MJ and add this to total energy used in MJ and compare this with total potential NPP in MJ for each country. This analysis excludes countries where the World Bank’s energy data were flagged as incomplete or otherwise problematic. Based on our previous calculations of total human, domestic animal and wild mammal NPP consumption as well as total human energy consumption we have created a term we call ‘ecologically bankrupt’ which we define as:

$$\text{Ecologically Bankrupt} = \text{if a country's total NPP} < (\text{human, domestic animal, wild mammal NPP consumption} + \text{total human energy use}) \quad (1)$$

## Results

We first estimate theoretical consumption of NPP by both existing mammals and by the now-extinct megafauna (Figure 1) by using range maps and body mass to estimate total consumption of dry matter for each species. We estimate DM consumption per unit area based on the equation  $DM = 1.84 * M^{-0.008}$  which multiplies the expressions for population density  $87.6 * M^{-0.724}$  ( $N = 366$ )



**Figure 1.** Estimated potential NPP consumption ( $\text{kg DM}/\text{km}^2$  per day) by current mammals (top), extinct megafauna (middle), and the percentage decreased mammal consumption following the extinctions and range reductions (bottom).

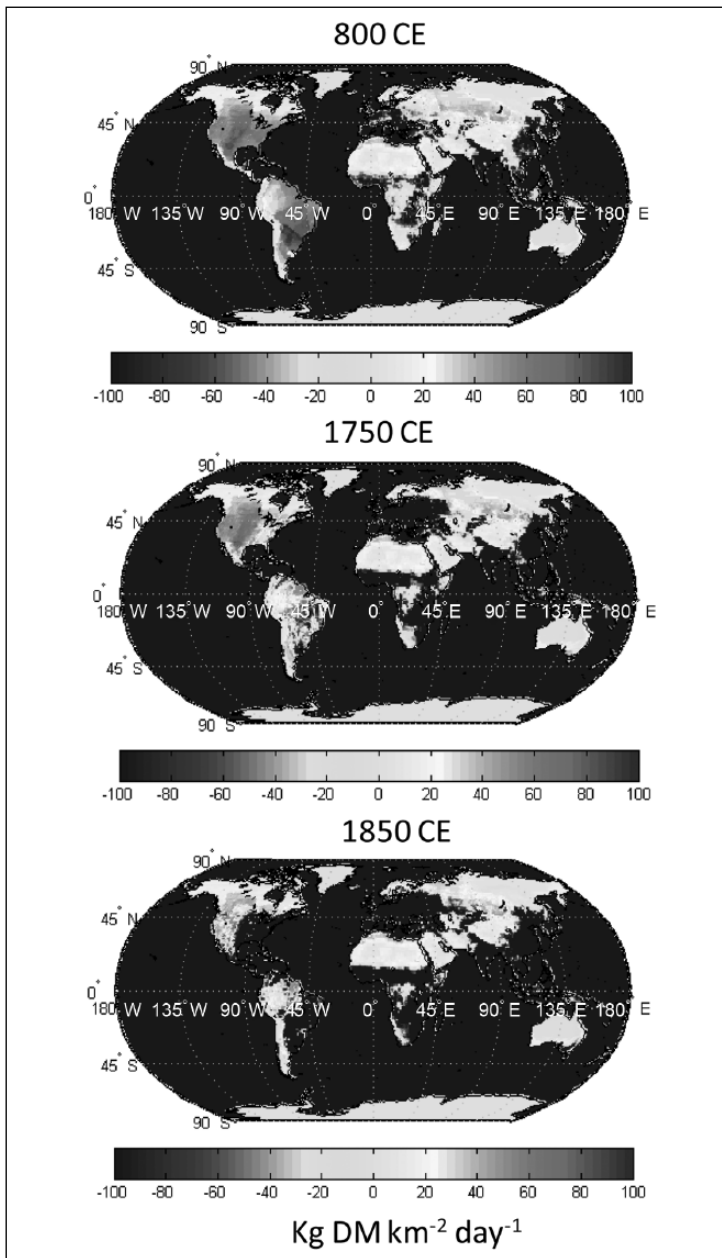
and metabolic rate  $0.021 * M^{0.716}$  ( $N = 131$ ) (see Wolf et al., 2013, for original data). The low coefficient for our equation ( $-0.008$ ) indicates NPP consumption is largely size independent, and total consumption will be a linear function of the total number of species. In a sensitivity study, we

vary this coefficient by the error of our slope of  $\pm 0.035$  (Supplementary Tables 1 and 2, available online). Hotspots of NPP consumption by the now-extinct megafauna include the grasslands of North and South America, and to a lesser extent, much of Europe (Figure 1, middle). This compares to current consumption hotspots of tropical forest regions with high numbers of species (Figure 1, top). We estimate a global mean consumption by current mammals is  $206 \pm 42$  kg DM/km<sup>2</sup> per day compared with  $16 \pm 4$  kg DM/km<sup>2</sup> per day by the extinct animals, i.e. the loss of megafauna has caused a decline in global NPP consumption of  $\sim 7\%$ . Hence consumption averages  $\sim 9.4 \pm 1.9\%$  of total global NPP by living mammals and  $\sim 1.8 \pm 0.5\%$  by the extinct megafauna (after removing unproductive desert regions). This is the global average of NPP consumed by living (9.4%) and extinct mammals (1.8%) as a percentage of total NPP. However, animals are not perfectly efficient eaters, with large animals such as elephants only digesting  $\sim 20\%$  of consumed food (Rees, 1982), with smaller animals being more efficient. Therefore, if we estimate that between 40% and 60% of food passes through the system of large herbivores without being digested, then our estimate of megafauna consumption increases to 2.2–5.3% of global NPP. There is much regional variability in these numbers with, for instance, consumption of NPP in the grasslands in South America declining by  $>20\%$  following the extinctions, with other regions seeing almost no change at all (Figure 1, bottom).

To get a better sense of the quantity of NPP ‘liberated’, we compared this NPP not consumed by megafauna with that subsequently consumed by people through agriculture and grazing of livestock (Figure 2). We find that in 800 CE, almost 9000 years after most of the extinctions, much of the planet still had ‘liberated NPP’, and that human consumption had not yet matched this liberated NPP. Only population-dense regions of Europe, India and China had consumed the NPP, with much liberated NPP still available especially in the Americas (although this may be due to underestimated pre-Hispanic American human population densities: see Pongratz et al., 2008, for details). This ‘liberated’ NPP energy was gradually consumed by people through agriculture leaving little beyond 1850.

We then compare how human consumption of NPP compares with theoretical wild animal consumption of NPP over four periods of time (800, 1700, 1850, and 2000 CE) (Figure 3). We do not calculate *total* NPP consumption, because we do not include the important role of smaller animals such as birds, reptiles, and insects. Therefore, we call our consumption estimates ‘wild mammal’ consumption. Although human appropriated NPP (HANPP) has been calculated many times previously (Haberl et al., 2007; Vitousek et al., 1986), it has never been compared with consumption by other consumers of NPP such as wild animals. In other words, we are not estimating what percentage of total planetary NPP humans consume, but what percentage of total mammal NPP consumption is consumed by people. When we averaged together, the average percent of total global NPP consumption by humans is 8% in 800, 19% in 1700, 30% in 1850, and 58% by 2000. Consumption of NPP accelerated towards modern times and there was a greater change between the periods of 1700 and 1850 than between 800 and 1700.

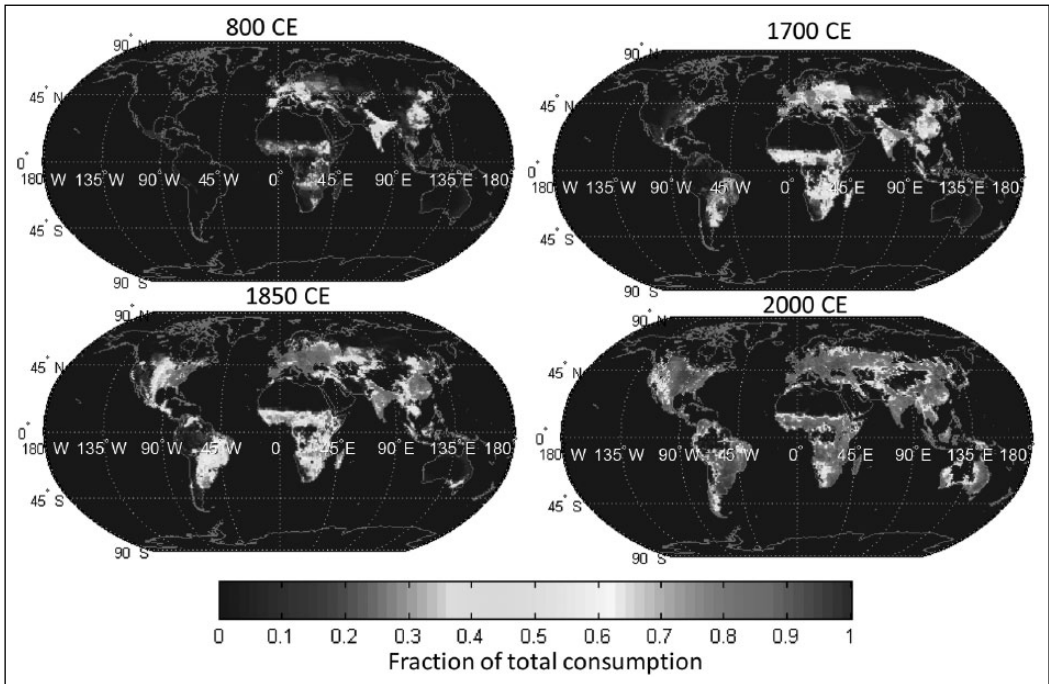
By 800 CE, humans and associated domesticates accounted for a low percentage ( $< 20\%$ ) of total NPP consumption (humans and all mammals) in most of the world, but a relatively high percentage  $> 50\%$  of total consumption in India, Europe, and China. This percentage is a function of spatially variable wild animal consumption (itself mainly a function of the number of species present), percent of area used for human pasture and agriculture lands, and total country NPP. In 1700 CE, most countries increased their percentage NPP consumption by  $\sim 20\%$  relative to the year 800, but this was not uniform. By 1850, most NPP consumption was primarily by humans and associated domesticates, with the exception of parts of South America, Canada, Australia and Russia. By 2000 CE, almost everywhere was heavily dominated ( $> 80\%$  NPP) by human and domestication consumption.



**Figure 2.** A comparison (megafauna liberated minus human consumed) of NPP 'liberated' following the Pleistocene extinctions (assuming 50% undigested) to that consumed by people through pasture and agriculture in (top) 800 CE, (middle) 1750 CE, and (bottom) 1850 CE in kg DM/km<sup>2</sup> per day.

Next, we consider total energy consumption following the Industrial Revolution, but focus especially on the period following the 'Great Acceleration' of 1960 when there is more consistent energy and population data from the World Bank for most countries. We compare total energy

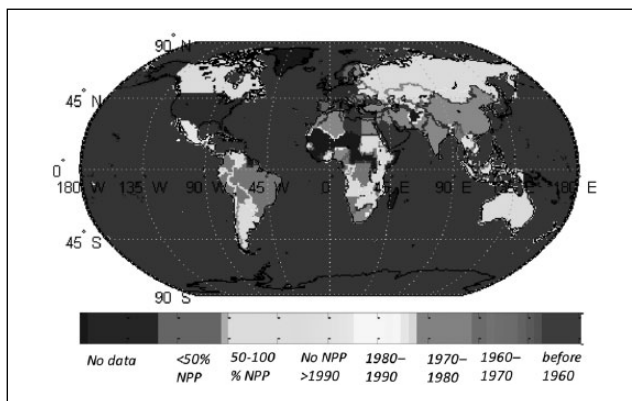




**Figure 3.** Percentage of consumed NPP that is appropriated by humans compared with that consumed by all mammals (pasture and crop NPP divided by wild animal consumption, pasture and crop NPP) in 800 CE (top left), 1700 CE (top right), 1850 CE (bottom left), and 2000 CE (bottom right).

consumption by people (in units of MJ/year) to total potential NPP per country in MJ/year (using the energy density of biomass of 16 MJ/kg). We then convert NPP consumed by large wild animals, crops and livestock to MJ and add this to total energy used in MJ and compare this to total potential NPP in MJ for each country (Supplementary Table 1, available online). For the countries that consume more energy than that produced through NPP within that country (a value of  $> 1$  in column 5 Supplementary Table 1, available online), we calculate when these countries surpassed this mark. In Figure 4, we show the countries in the hottest colors, including mainly the USA, Western Europe and Japan, were already what we call energetically bankrupt (i.e. where there is currently not enough NPP energy produced by that country to supply all the current demands by both human and wild mammals) at the start of the 1960s when the World Bank records begin. Next came India, China, Mexico, South Africa and Indonesia in the 1970s. This was later followed by eastern European countries.

There are a number of countries that are not yet energetically bankrupt (these countries have enough NPP energy to supply all the current energy demands both human and animal). Countries with more than 50% of NPP available are colored blue (Figure 4). Not surprisingly, these include large countries with relatively low population densities such as Brazil, Canada, Australia, and the Democratic Republic of the Congo. In fact central Africa seems to have the lowest total percentage NPP consumption, with the Congo (12%), Democratic Republic of the Congo (19%), and Gabon (14%) the lowest. In the Americas, Bolivia and Brazil are the lowest with both at 38%. Of Western democracies, Canada is the lowest at 60%. Mean population density of countries with no remaining NPP is 149 ind/km<sup>2</sup> versus 118 ind/km<sup>2</sup> (excluding countries with pop density  $> 5000$  ind/km<sup>2</sup>).



**Figure 4.** Countries whose total energy usage (animals, people's energy, crops and pasture) is greater than total NPP produced by each country. Colors show the decade in which the countries became energetically 'bankrupt'. Darkest blue indicates there is no energy data available from the World Bank, darker blue indicates < 50% of NPP consumed, and lighter blue indicates that between 50% and 100% of NPP consumed.

Globally, 5.4 billion people live in countries with no remaining NPP and 1.2 billion people still have NPP, so approximately 82% live in ecologically bankrupt countries.

## Discussion

This study aimed to quantify the changes in NPP utilization across major transitions of human history in the Holocene. These include a possible increase in available NPP following the megafauna extinctions; a subsequent transformation of natural NPP to NPP domesticated for crops and pastures in the agrarian epoch of civilization; and finally the utilization of non-NPP energy sources in the industrial era. Based on recently developed accurate megafauna range maps, we estimate that the Late Pleistocene–early Holocene megafauna extinctions likely liberated 2.2–5.3% total global NPP by the start of the Holocene. This is likely a conservative estimate since human hunting likely also depressed densities of most surviving species (Martin and Szuter, 1999; Sandom et al., 2014). Next, we find that humans, on average, began to consume more NPP than wild mammals globally by ~1850 (Figure 3). Finally, ~82% of the world's population lives in countries where more energy is consumed by humans and animals than is available in NPP. This began early in industrialization, with most industrialized countries already 'ecologically bankrupt' by 1960. Now that we have these numbers, what do they mean and why are they important?

We estimate that the megafauna extinctions likely liberated 2.2–5.3% of total global NPP energy, energy that was potentially available for humans to then consume. This estimate is within range of previous estimates of ~2.5% (~1.4 (between 1.2 and 1.6) petagrams/year of 56 Pg C/year) of global terrestrial NPP (Doughty and Field, 2010), but now with much more regional accuracy thanks to the new megafauna range maps (Faurby and Svenning, 2015a). Here we make several modifications to our previous attempt with the most substantial being improved maps from Faurby and Svenning (2015a) of extinct megafauna distributions and better consumption estimates based on scaling theory from Wolf et al. (2013).

Why is it important to know the size of the increased quantity of NPP available following the extinctions? One of the most interesting questions is whether this 'liberated' NPP aided humans during a critical stage of our development. If the extinctions liberated a large amount of NPP, then

rationally it seems this may have had a bigger impact on early human development than if only a small amount of NPP were liberated (Sandom et al., 2014). Prior to the development of agriculture and during the Pleistocene extinctions, we were a successful expansionist carnivore species. However, following the extinction of our prey, changes were necessary. It was argued (Doughty, 2010) that the megafauna extinctions may have accelerated the onset of agriculture, specifically in the Americas where the extinctions were most profound. The Americas saw the largest impact of megafauna extinction on liberated NPP, and recent evidence suggests agriculture began more rapidly there, arising in several regions in North and South America independently ~10,000 years BP, likely only ~3000–4000 years following the arrival of people (Balter, 2007; Dillehay et al., 2007; Smith, 1997). Reduced NPP competition from the megafauna would have helped the rise of agriculture for three potential reasons: net primary production (NPP) became available for human utilization, the domestication of wild crop types was more feasible in the absence of mega-herbivore competition, and hunting societies became more sedentary as their prey went extinct, the first step towards agriculture (Doughty, 2010).

One complication to this hypothesis is fire, as there is evidence that megafauna extinctions sometimes, but not always, increase fire occurrence (which also consumes NPP) (Gill et al., 2009; Rule et al., 2012) but not all studies find such evidence (Sandom et al., 2014). Most liberated NPP was from grassland ecosystems where most megafauna were thought to exist. Prior to the development of tools to clear forests, grasslands were the regions where agriculture could most easily exist, so the availability of NPP in these regions may have been especially important. Likewise, additional NPP in forests may not have helped early humans at all because of the difficulty in accessing this NPP (Roebroeks et al., 1992). Would the NPP previously consumed by megafauna simply have been consumed by the remaining small herbivores? This is a highly uncertain issue, but there are a few reasons to think that it would not. The first is simply size. For instance, forest elephants and other large herbivores have unique patterns of consumption where, in the case of forest elephants, they break small trees to access forage and this is unlikely to be replicated by smaller animals (an effect not included in our analysis). The absence of megafauna generally leads to an increase in biomass of ecosystems (Bakker et al., 2015; Rule et al., 2012).

Another reason it is interesting to understand the quantity of NPP liberated following the extinctions is it may help us understand the natural carrying capacity of the planet. If a set amount of NPP had become available, then only once we surpassed this quantity could we surpass the ‘natural’ carrying capacity of the planet. When did we consume this NPP energy? Previously, we had estimated that we had consumed this quantity around the start of the Industrial Revolution (Doughty and Field, 2010). Using estimates from Pongratz et al. (2008), we estimate that by 800, 1.4% of global potential NPP was consumed by crops and pasture and by 1700, 4.3% was consumed. This is the approximate range of our estimate of 2.2–5.3% global NPP consumed by the extinct megafauna, so ‘liberated NPP’ may have been consumed by between 1700 and 1850 CE.

We compared when people, through crops and agriculture, began to consume more NPP than wild animals in 800, 1700, 1850 and 2000 CE. We estimate that by 1850 CE people in most countries had begun to consume more NPP than the wild animals. Again there are large geographic differences, but by 1700s much of Eurasia (outside of Siberia) had people consuming more NPP than wild mammals and by the 1850s many parts of the world were doing likewise. Why is it important to determine when people began to dominate consumption of NPP over the natural world? In our view, this could be considered an analysis of when the Anthropocene began for each individual country because dominating NPP consumption clearly indicates the domination of resources of humans over the natural world, one possible definition of the Anthropocene (Doughty, 2013).

Finally, we estimate when people and wild animals consume more energy in each country than is available in total NPP within that country. To state this in another way, we estimate our reliance on non-sustainable energies. If such non-sustainable energies ran out, which countries could maintain their consumption patterns? This could be achieved either through alternative energies or reverting back to using only NPP energy, as animals have had to do throughout Earth's history. Those that could not maintain their consumption demonstrate ecological fragility which we have termed 'ecologically bankruptcy'. Bankruptcy clearly has a negative connotation and energy use has traditionally had a positive association with development. We are not arguing that energy use is negative, just as financial credit in a market economy is not necessarily negative. However, just like for credit, when it is important to understand when people have spent beyond their means, it is likewise important for countries to realize they have surpassed their ecological means. Fossil fuels, therefore, in our analogy, act as a credit card, imitating ecological solvency. A nation unable to continue their consumption patterns once non-sustainable energies run out is certainly more fragile than one that can. Many ecologically bankrupt countries handle this problem through globalization, i.e. via importing energy from other countries. It is perhaps not surprising that most countries consume more energy than is produced from the NPP contained within their borders and this emphasizes that globalization is so ingrained in the functioning of the planet that individual countries could not exist without international co-operation.

Can humanity counter trends of increasing use of NPP by increasing total global NPP through the use of fertilizers and irrigation? Irrigation and fertilizer can increase NPP, however, it seems unlikely that humans can increase total global NPP through such methods because Haberl et al. (2007) calculated that humans have reduced global NPP by 9.6% mainly by decreasing below-ground productivity in crops. Humans have shifted allocation in crops to parts we use, such as starchy grains, but away from parts we do not use, such as root structures, resulting in a net decline in total NPP. However, there are reasons for hope and humanity is becoming more efficient in our use of NPP. For example, from 1910 to 2005 the human population grew fourfold and economic output increased 17-fold, but global HANPP has only doubled (Krausmann et al., 2013). This same paper predicted that HANPP might only grow to 27–29% by 2050, but if we decide to convert to bioenergy to provide our energy, this could increase to 44%.

Overall, the Holocene has seen remarkable changes in consumption patterns of NPP. It began with a potential available NPP of 2.2–5.3% that we could potentially 'grow' into. This excess was eventually consumed through agriculture and we began to consume more NPP than wild animals in most of the world by 1850. We now consume enough energy that > 82% of us live in countries where even using all available NPP would not provide sufficient energy. To continue the economic analogy, we began with an energy surplus, became the dominant consumers of NPP over the natural world before the Industrial Revolution, but now find ourselves ecologically bankrupt in most regions.

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