1 **Changing NPP consumption patterns in the**
2 **Holocene: from megafauna-“liberated” NPP to**
3 **“ecological bankruptcy”**

4
5
6 **Running title** – Changing Holocene NPP consumption patterns

7 **Key words:** NPP, Holocene, HANPP, extinctions, ecological bankruptcy, anthropocene
8

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.

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 ybp-current) began at the tail end of late-Quaternary extinctions of terrestrial megafauna (Barnosky et al., 2004), a 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 2014b). 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 ~2.5% (~1.4±0.2 Pg C yr⁻¹ of 56 Pg C yr⁻¹) 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; $\#/km^2$) that consume dry matter (DM) to fulfil their metabolic requirements (MR; kg DM/ animal/day). A previous study has created global maps of theoretical NPP consumption for mammals $>1kg$ (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 $927 kg/km^2/yr$ 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 4,500 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 100W, 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, Krausmann et al., 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 8000W, 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-ton 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.

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

124 1. How much NPP energy may have become available following the extinction of the
125 megafauna?

126 2. When did humans in each country consume more NPP than the rest of the mammals in
127 that country?

128 3. When did humans in each country achieve a total energy consumption more than the total
129 NPP available in their country?

Methods

This work involves the compilation of several datasets 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 dataset 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 (SI Tables 2 and 3).

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 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; $\#/km^2$ but see (McGill et al., 2007) for a review) that consume dry matter (DM) to fulfil their metabolic requirements (based on data from the AnAge database (de Magalhaes and Costa, 2009); $kgDM/animal/day$) (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 ($NPP < 200g\ m^2\ day^{-1}$) 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 (<1kg) 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 datasets 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 ± 0.035 in a sensitivity study. For all major datasets, we explain the major uncertainties and then redo our analysis under a large range of possible values (SI Tables 2 and 3).

We compare consumption patterns of NPP between humans (through crops and pasture) and animals between 800 AD to modern times based on maps from Pongratz et al. (2008) for 800, 1700, and 1850 AD 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 to 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 center (<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 to total potential NPP per country in MJ yr⁻¹ (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 to 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:

Equation 1 – Ecologically Bankrupt = if a country’s total NPP < (human, domestic animal, wild mammal NPP consumption + total human energy use).

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 dry matter (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) 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 ± 0.035 (SI Tables 1 and 2). 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 $206 \pm 42 \text{ kg DM km}^{-2} \text{ day}^{-1}$ compared to $16 \pm 4 \text{ kg DM km}^{-2} \text{ day}^{-1}$ 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 40-60% 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 % 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 to 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 ~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.

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 consumption by people (in units of MJ yr⁻¹) to total potential NPP per country in MJ yr⁻¹ (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 (SI Table 1). For the countries that consume more energy than that produced through NPP within that country (a value of >1 in column 5 SI table 1), we calculate when these countries surpassed this mark. In Figure 4, we show the countries in the hottest colors, including mainly the US, 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 1960’s 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⁻² vs 118 ind km⁻² (excluding countries with pop density >5000ind km⁻²). 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.

313

314 **Discussion**

315 This study aimed to quantify the changes in NPP utilization across major transitions
316 of human history in the Holocene. These include a possible increase in available NPP
317 following the megafauna extinctions; a subsequent transformation of natural NPP to NPP
318 domesticated for crops and pastures in the agrarian epoch of civilization; and finally the
319 utilization of non-NPP energy sources in the industrial era. Based on recently developed
320 accurate megafauna range maps, we estimate that the Late Pleistocene-early Holocene
321 megafauna extinctions likely liberated 2.2 – 5.3% total global NPP by the start of the
322 Holocene. This is likely a conservative estimate since human hunting likely also depressed
323 densities of most surviving species (Martin and Szuter, 1999, Sandom et al., 2014). Next, we
324 find that humans, on average, began to consume more NPP than wild mammals globally by
325 ~1850 (Figure 3). Finally, ~82% of the world’s population lives in countries where more
326 energy is consumed by humans and animals than is available in NPP. This began early in
327 industrialization, with most industrialized countries already “ecologically bankrupt” by 1960.
328 Now that we have these numbers, what do they mean and why are they important?

329 We estimate that the megafauna extinctions likely liberated 2.2 – 5.3% of total global
330 NPP energy, energy that was potentially available for humans to then consume. This
331 estimate is within range of previous estimates of ~2.5% (~1.4 (between 1.2-1.6) petagrams yr⁻¹
332 of 56 Pg C yr⁻¹) of global terrestrial NPP (Doughty and Field, 2010), but now with much
333 more regional accuracy thanks to the new megafauna range maps (Faurby and Svenning
334 2015a). Here we make several modifications to our previous attempt with the most
335 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 ybp, likely only ~3-4,000 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 (Rule et al., 2012, Bakker et al., 2015).

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

386 were doing likewise. Why is it important to determine when people began to dominate
387 consumption of NPP over the natural world? In our view, this could be considered an
388 analysis of when the Anthropocene began for each individual country because dominating
389 NPP consumption clearly indicates the domination of resources of humans over the natural
390 world, one possible definition of the Anthropocene (Doughty, 2013).

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

Figures

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

440

441 **Figure 2** – A comparison (megafauna liberated minus human consumed) of NPP “liberated”
 442 following the Pleistocene extinctions (assuming 50% undigested) to that consumed by people
 443 through pasture and agriculture in (top) 800CE, (middle) 1750CE, and (bottom) 1850 in kg
 444 DM km⁻² day⁻².

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

454

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

461

463 **References**

- 464 BAKKER, E. S., GILL, J. L., JOHNSON, C. N., VERA, F. W. M., SANDOM, C. S., ASNER, G. P. & SVENNING,
 465 J. C. 2015. Combining paleo-data and modern exclosure experiments to assess the impact of
 466 megafauna extinctions on woody vegetation. *PNAS*.
- 467 BALTER, M. 2007. Seeking Agriculture's ancient roots. *Science*, 316, 1830-1835.
- 468 BARNOSKY, A. D. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions.
 469 *Proceedings of the National Academy of Sciences of the United States of America*, 105,
 470 11543-11548.
- 471 BARNOSKY, A. D., KOCH, P. L., FERANEC, R. S., WING, S. L. & SHABEL, A. B. 2004. Assessing the causes
 472 of Late Pleistocene extinctions on the continents. *Science*, 306, 70-75.
- 473 BROWN, J. H., WEST, G. B. & ENQUIST, B. J. 2000. Scaling in biology: Patterns and processes, causes
 474 and consequences. *Scaling in Biology*, 1-24.
- 475 DAMUTH, J. 1987. Interspecific Allometry of Population-Density in Mammals and Other Animals - the
 476 Independence of Body-Mass and Population Energy-Use. *Biological Journal of the Linnean
 477 Society*, 31, 193-246.
- 478 DAMUTH, J. 2007. A macroevolutionary explanation for energy equivalence in the scaling of body
 479 size and population density. *American Naturalist*, 169, 621-631.
- 480 DE MAGALHAES, J. P. & COSTA, J. 2009. A database of vertebrate longevity records and their relation
 481 to other life-history traits. *Journal of Evolutionary Biology*, 22, 1770-1774.
- 482 DIAMOND, J. & BELLWOOD, P. 2003. Farmers and their languages: The first expansions. *Science*, 300,
 483 597-603.
- 484 DILLEHAY, T. D., ROSSEN, J., ANDRES, T. C. & WILLIAMS, D. E. 2007. Preceramic adoption of peanut,
 485 squash, and cotton in northern Peru. *Science*, 316, 1890-1893.
- 486 DOUGHTY, C. E. 2010. The development of agriculture in the Americas: an ecological perspective.
 487 *Ecosphere*, 1.
- 488 DOUGHTY, C. E. 2013. Preindustrial Human Impacts on Global and Regional Environment. *Annual
 489 Review of Environment and Resources*, Vol 38, 38, 503-527.
- 490 DOUGHTY, C. E. & FIELD, C. B. 2010. Agricultural net primary production in relation to that liberated
 491 by the extinction of Pleistocene mega-herbivores: an estimate of agricultural carrying
 492 capacity? *Environmental Research Letters*, 5.
- 493 FAURBY, S. & SVENNING, J. C. 2015a. Historic and prehistoric humandriiven extinctions have
 494 reshaped global mammal diversity patterns.
- 495 FAURBY, S. & SVENNING, J. C. 2015b. Resurrection of the island rule – human-driven extinctions
 496 have obscured a basic evolutionary pattern. .
- 497 FIELD, C. B., BEHRENFELD, M. J., RANDERSON, J. T. & FALKOWSKI, P. 1998. Primary production of the
 498 biosphere: Integrating terrestrial and oceanic components. *Science*, 281, 237-240.
- 499 GILL, J. L., WILLIAMS, J. W., JACKSON, S. T., LININGER, K. B. & ROBINSON, G. S. 2009. Pleistocene
 500 Megafaunal Collapse, Novel Plant Communities, and Enhanced Fire Regimes in North
 501 America. *Science*, 326, 1100-1103.
- 502 HABERL, H., ERB, K. H., KRAUSMANN, F., GAUBE, V., BONDEAU, A., PLUTZAR, C., GINGRICH, S.,
 503 LUCHT, W. & FISCHER-KOWALSKI, M. 2007. Quantifying and mapping the human
 504 appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the
 505 National Academy of Sciences of the United States of America*, 104, 12942-12945.
- 506 HARTE, J. 1988. *Consider a spherical cow. A course in environmental problem solving*, Sausalito,
 507 California, University Science Books.
- 508 IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4.

- KRAUSMANN, F., ERB, K. H., GINGRICH, S., HABERL, H., BONDEAU, A., GAUBE, V., LAUK, C., PLUTZAR, C. & SEARCHINGER, T. D. 2013. Global human appropriation of net primary production doubled in the 20th century. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 10324-10329.
- KRAUSMANN, F., FISCHER-KOWALSKI, M., SCHANDL, H. & EISENMENGER, N. 2008a. The Global Sociometabolic Transition. *Journal of Industrial Ecology*, 12, 637-656.
- KRAUSMANN, F., SCHANDL, H. & SIEFERLE, R. P. 2008b. Socio-ecological regime transitions in Austria and the United Kingdom. *Ecological Economics*, 65, 187-201.
- MALHI, Y. 2014. The Metabolism of a Human-Dominated Planet. In: GOLDIN, I. (ed.) *Is the Planet Full?* : Oxford University Press.
- MARTIN, P. S. & SZUTER, C. R. 1999. War zones and game sinks in Lewis and Clark's west. *Conservation Biology*, 13, 36-45.
- MCGILL, B. J., ETIENNE, R. S., GRAY, J. S., ALONSO, D., ANDERSON, M. J., BENECHA, H. K., DORNELAS, M., ENQUIST, B. J., GREEN, J. L., HE, F. L., HURLBERT, A. H., MAGURRAN, A. E., MARQUET, P. A., MAURER, B. A., OSTLING, A., SOYKAN, C. U., UGLAND, K. I. & WHITE, E. P. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, 10, 995-1015.
- PETERKEN, G. 1977. Habitat conservation priorities in British and European woodlands. *Biol Conserv*, 11(3), 223-236.
- PONGRATZ, J., REICK, C., RADDATZ, T. & CLAUSSEN, M. 2008. A reconstruction of global agricultural areas and land cover for the last millennium. *Global Biogeochemical Cycles*, 22.
- RAMANKUTTY, N., EVAN, A. T., MONFREDA, C. & FOLEY, J. A. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*, 22, -.
- REES, P. A. 1982. Gross Assimilation Efficiency and Food Passage Time in the African Elephant. *African Journal of Ecology*, 20, 193-198.
- ROEBROEKS, W., CONARD, N. J. & VANKOLFSCHOTEN, T. 1992. Dense Forests, Cold Steppes, and the Paleolithic Settlement of Northern Europe. *Current Anthropology*, 33, 551-586.
- RULE, S., BROOK, B. W., HABERLE, S. G., TURNEY, C. S. M., KERSHAW, A. P. & JOHNSON, C. N. 2012. The Aftermath of Megafaunal Extinction: Ecosystem Transformation in Pleistocene Australia. *Science*, 335, 1483-1486.
- SANDOM, C., FAURBY, S., SANDEL, B. & SVENNING, J. C. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B-Biological Sciences*, 281.
- SMIL, V. 2013. *Harvesting the Biosphere: What We Have Taken from Nature*, MIT press.
- SMITH, B. D. 1997. The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. *Science*, 276, 932-934.
- VITOUSEK, P. M., EHRLICH, P. R., EHRLICH, A. H. & MATSON, P. A. 1986. Human Appropriation of the Products of Photosynthesis. *Bioscience*, 36, 368-373.
- WOLF, A., DOUGHTY, C. E. & MALHI, Y. 2013. Lateral Diffusion of Nutrients by Mammalian Herbivores in Terrestrial Ecosystems. *Plos One*, 8.