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Agricultural net primary production in relation to that liberated by the extinction of Pleistocene mega-herbivores: an estimate of agricultural carrying capacity?

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Abstract

Mega-fauna (defined as animals >44 kg) experienced a global extinction with 97 of 150 genera going extinct by ∼10 000 years ago. We estimate the net primary production (NPP) that was liberated following the global extinction of these mega-herbivores. We then explore how humans, through agriculture, gradually appropriated this liberated NPP, with specific calculations for 800, 1850, and 2000 AD. By 1850, most of the liberated NPP had been appropriated by people, but NPP was still available in the Western US, South America and Australia. NPP liberated following the extinction of the mega-herbivores was ∼2.5% (∼1.4 (between 1.2 and 1.6) Pg yr^{-1} of 56 Pg C yr^{-1}; Pg: petagrams) of global terrestrial NPP. Liberated NPP peaked during the onset of agriculture and was sufficient for sustaining human agriculture until ∼320 (250–500) years ago. Humans currently use ∼6 times more NPP than was utilized by the extinct Pleistocene mega-herbivores.

Keywords: mega-fauna, extinctions, NPP, carrying capacity

1. Introduction

The extinction of the Pleistocene mega-fauna (defined as animals >44 kg) is generally explained as driven by human over-hunting, climate change, or a combination of the two [1]. Animals occupying entire ecological roles went extinct, with 88% of mega-herbivore genera going extinct in Australia, 84% in South America, 72% in North America, 36% in Eurasia, and 18% in Africa [1].

After this extinction episode, there was a global dearth in mega-fauna biomass [2]. This mega-fauna biomass eventually recovered to prior levels but was concentrated in humans and their livestock [2]. Humans developed agriculture, which enabled them to use a much larger percentage of NPP than hunter gatherers. [3], and have higher population densities. Between about 10 500 and 4500 BP, agriculture based on domestication of wild plants arose independently in up to nine different geographic areas [4] and on three separate continents ∼10 000 years ago [4–6]. Agriculture quickly spread [7], along with languages and cultures [4], through many regions of the world.

Agriculture has greatly expanded its range over the past 10 000 years. Humans currently use or alter the productivity of between 23 [8] and 40% [9] of global terrestrial net primary production (NPP) (∼15.6 Pg C yr^{-1}), of which 53% is harvested, 40% is from land-use-induced productivity changes, and 7% is from human-induced fires [8]. Globally, humans harvest ∼8 Pg C yr^{-1} of NPP (50% of this is for crops, 29% is for pastures, 11% is for forestry, 6% is for fires, and 4% is for infrastructure).

Global NPP is approximately ∼105 Pg C yr^{-1}, about evenly divided between land and sea [10]. The total amount of NPP can vary with global climate. For instance, between September 1997, an el Niño year, and August 2000, a la

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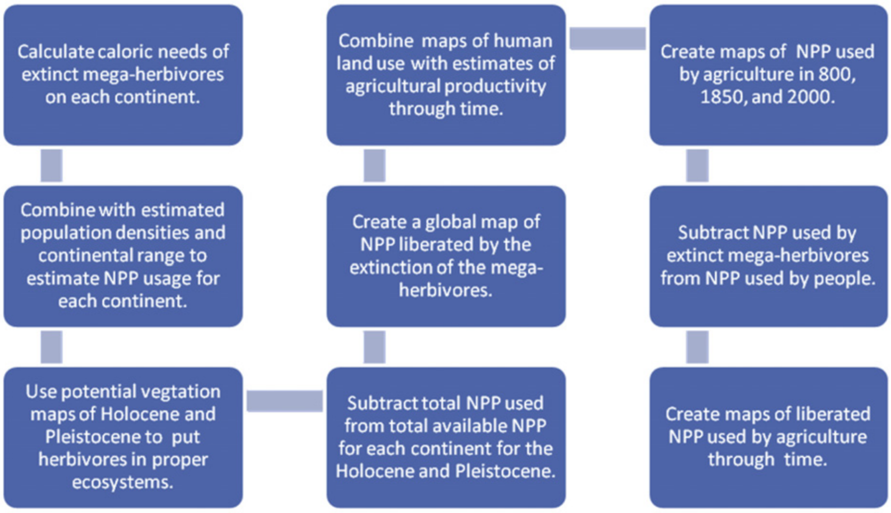

Figure 1. A flow diagram showing the methodology for calculating NPP consumed by extinct mega-herbivores and how humans appropriated this NPP through agriculture.

Niña year, global NPP varied by 6 Pg C yr^{-1} (from ~111 to 117 Pg C yr^{-1}) [11]. However, this change in NPP mainly occurred because upwelling and nutrient concentrations in the ocean were modified by climate. Global land NPP had large regional changes between these periods but did not exhibit a clear global signal, leaving year to year global terrestrial NPP fairly constant.

As humans expand their populations and usage of NPP, there is much debate how to define human carrying capacity. Some view a world in which carrying capacity may be infinitely expandable due to technological innovation [12]. Others view carrying capacity from an ecological perspective where humans share global NPP with all other heterotrophs. This definition treats NPP as limited, but susceptible to change through subsidies of water and nutrients, increased planting densities, land degradation, or climate change.

Following the crash in mega-fauna biomass, much of the NPP that had been consumed by these animals may have become available for consumption, since the herbivores evolved to consume this NPP were no longer there. People now consume NPP through agriculture in regions where these mega-herbivores would have grazed had they not become extinct. Although humans can subsidize plant NPP, this is a very recent phenomena, and the NPP liberated following the extinction of the Pleistocene mega-herbivores may have represented a large resource to early man.

To estimate historical agricultural NPP as a fraction of the NPP that was previously utilized by mega-herbivores, we need the history of agricultural NPP, as well as estimates of consumption of NPP by mega-herbivores. We calculate the NPP that was consumed by mega-herbivores based on estimates of animal density and size, and of the scaling of food requirements with size and subtract this from potential Holocene and Pleistocene NPP. We compare this to global maps of past (800 and 1850 AD) [13] and current (2000 AD) agricultural NPP [14], and we estimate integrated globally averaged NPP utilization of extinct mega-herbivores and humans from 100 000 years ago to today. We ask the following questions:

(1) When and where did people consume the NPP liberated by the extinction of the mega-herbivores?
(2) Did historical agricultural NPP exceed that liberated by the extinction, and if so, when?

2. Material and methods

2.1. NPP usage by extinct Pleistocene mega-herbivores

We calculate NPP usage for each individual extinct species using animal biomass data from Smith *et al* (2003) [15] ($N = 5731$ species) following the procedure of Barnosky (2008) [2] (figure 1). We used only herbivore species and did not use species in the orders Carnivora or Insectivora for our NPP calculations. To calculate caloric intake as a function of animal mass we used the metabolic mass equivalent scaling law where M is the mass of the animal [16]:

$$\text{Metabolic rate} = M^{0.75}.$$

We used the following relationship to estimate animal densities (number km^{-2}) based on average large (>100 kg) mammal herbivore individual mass [17]

$$\text{Log}_{10}(\text{density}) = -0.44 \times \log_{10}(M) + 1.01.$$

Following Barnosky (2008) [2], we assume that each species had a range of ~8% of the continental area (Australia, Africa, Eurasia, North America, and South America, geographic ranges sizes were set to 7.8%, 8.6%, 8.1%, 8.2%, and 7.2% of the respective continental areas) [2, 18]. We multiplied the caloric needs of an individual of each species by its density and estimated continental range to get total liberated calories per continent, divided this by 3 kcal g^{-1} dry plant matter [19] and assumed a 22.4% assimilation efficiency [20], summed for

Table 1. Yield estimates for maize and wheat through time.

	Wild	4000–2000 years ago	50 years ago	Today
Wheat	0.5–0.8 t/ha [31]	1.5–2 t/ha [32]	1–2 t/ha [33]	2–4 t/ha [33]
Maize	0.16–0.39 t/ha [34]	0.5–0.6 t/ha [35]	2.3–4.5 t/ha [33]	4.8–9.4 t/ha [33]

all extinct species to calculate liberated NPP. Discarded plant mass represents a quarter to half of the mass consumed for elephants [21], which we estimate at 30% of food NPP for all extinct mega-herbivores. To get per cent liberated NPP for each continent, we divide total continental liberated NPP by the continent's total potential NPP on grassland (for extinct savanna animals) and forest (for extinct forest animals) [8] for the Holocene and the Pleistocene [22]. We use the Carnegie–Ames–Stanford approach (CASA) to calculate present day NPP [10], results from the Lund–Potsdam–Jena dynamic vegetation model to calculate potential vegetation NPP [8], and results from Crowley (1995) [22] to calculate Pleistocene potential vegetation NPP [22]. We assume each species has the same continental range (∼7–9%) during the Holocene and the Pleistocene. To better understand temporal changes in NPP, we integrate globally averaged liberated NPP, starting from estimated extinction dates on different continents: Australia (50 000 BP), Africa (45 000 BP), Eurasia (12 000 BP), North America (12 000 BP), South America (10 000 BP) [1].

2.2. NPP usage by humans

We calculate human-used NPP in two ways: one based on population estimates from 10 000 years ago to the present [23], and one based on land use maps from 800, 1850 [13], and 2000 AD [14]. To calculate NPP based on human population estimates we assume an average human caloric intake of 2200 kcal day^{-1}. In 2000 AD, humans harvested a net 8.16 Pg C yr^{-1} NPP [8] to support ∼6 billion humans. This is a 20% efficiency (6×10^9 people × 2200 calories per person per day × 365 days/3 g per kcal). We assumed that all population growth after 10 000 years ago was in agricultural populations [24].

To estimate yield changes since the origin of agriculture, we use yield changes through time for two important crops, maize and wheat [25]. We estimate changing agricultural efficiency by comparing yields of maize and wheat from ∼10 000, 3000, 50 BP and current day (table 1). We assume a linear change in yield between each period. We assume that yields in the new world had the efficiency of maize, and yields in the old world had the efficiency of wheat. Based on 1850 demographic trends, we assume that the old world had 95% of the population and the new world had 5% of the population. Agricultural efficiency increases with time with 95% of the population having the efficiency of wheat and 5% having the efficiency of corn.

For the years 800, 1850, and 2000, we convert percentage land use to NPP for each grid cell. In agricultural regions, people currently consume ∼48% of potential vegetation NPP (on average 296 g C m^{-2} yr^{-1} harvested of 611 g C m^{-2} yr^{-1} potential NPP) [8]. In pastoral regions, people currently consume ∼8% of potential vegetation NPP (on average 41 g C m^{-2} yr^{-1} harvested of 486 g C m^{-2} yr^{-1} potential NPP) [8]. In the past, agriculture was less efficient [26]. We assume NPP harvested globally in agricultural regions in 800 and 1850 is similar to NPP currently harvested regionally in sub-Saharan Africa. The harvest factor (crop residue/primary crop harvest) for grains, rice, and corn in sub-Saharan Africa was 2.4 compared to 1.9 averaged over the globe (table 7 of the supporting information of Haberl *et al* (2007) [8]). Based on this ratio, if people, on average, harvest 296 g C m^{-2} yr^{-1} of NPP currently [8], in 800 and 1850 they would harvest 228 g C m^{-2} yr^{-1} (296/(2.4/1.9)), or 37% of potential NPP.

2.3. Sensitivity analysis

We varied our assumptions to estimate reasonable upper and lower bounds of our calculations. We varied potential NPP digested by people between 18 and 22%, from 20% (8.16 Pg C yr^{-1} NPP [8] for ∼6 billion humans), population ratios of new and old world (2–15% of global population residing in the new world), total human population estimates (increasing and decreasing early populations by 10%), mega-herbivore food assimilation efficiency [20] (20–25% of eaten NPP digested), mega-herbivore food wastage (10–40% of eaten NPP), and average continental area occupied by mega-fauna (7–9% of continental area). We calculated the date when humans utilized globally averaged liberated NPP for the upper and lower bound of each variable and averaged all upper bound dates and all lower bound dates separately to estimate a range.

3. Results

Liberated NPP following the extinction of the Pleistocene mega-herbivores was not evenly distributed. The uneven distribution was driven mainly by differing percentages of the continent's mega-fauna to go extinct, percentage grassland land cover, and total continental NPP (table 2). South America had the most liberated NPP, 0.48 ± 0.072 Pg C yr^{-1}, because of its high NPP and high extinction percentage (table 2). North America was next with 0.31±0.041 Pg C yr^{-1}, followed by Eurasia with 0.28 ± 0.036 Pg C yr^{-1}, Africa 0.19 ± 0.025 Pg C yr^{-1} and Australia 0.10 ± 0.013 Pg C yr^{-1}. Standard deviations are calculated as differences between the sensitivity runs. These continental averages hide much regional diversity (figure 2). North America has a large percentage liberated grassland NPP because of a combination of high total liberated NPP and small grassland range during the Pleistocene. As grasslands shrunk in South America, Australia and Eurasia during the Holocene, percentage liberated NPP increased. Percentage liberated NPP decreased substantially in North America as glaciers melted and grassland ranges expanded.

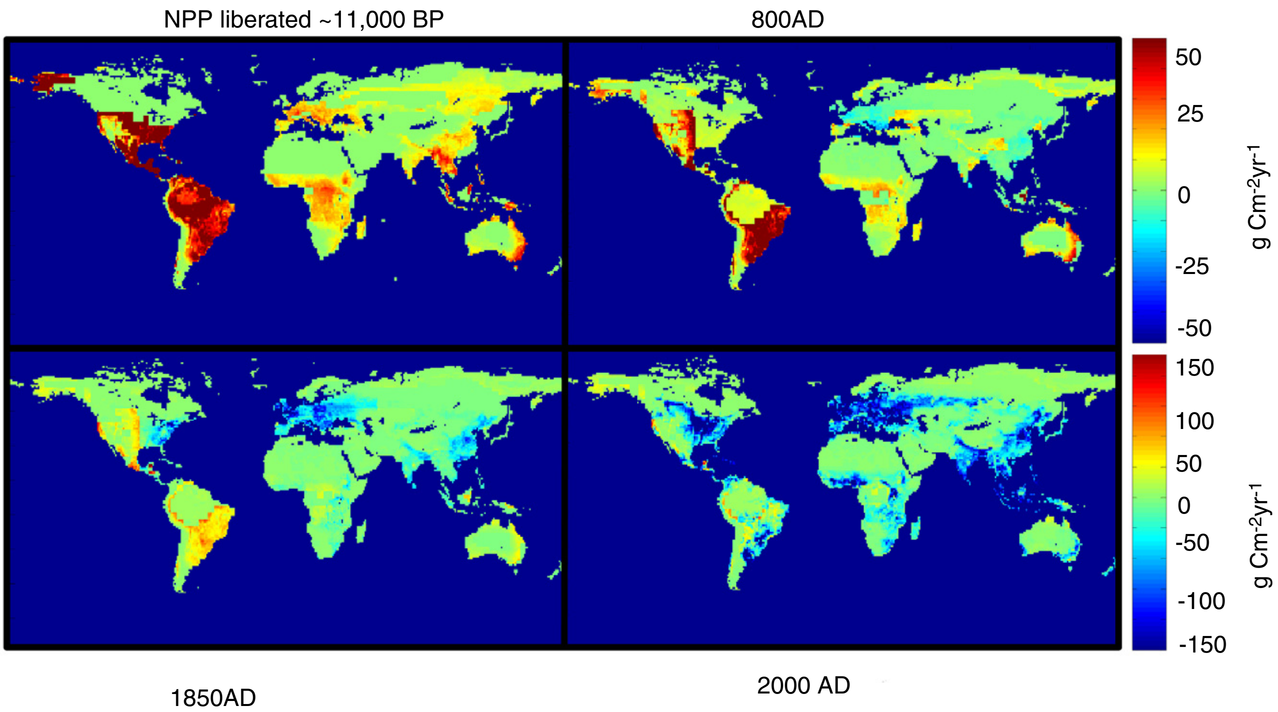

Figure 2. (top left) NPP liberated following the extinction of the mega-herbivores. Liberated NPP subtracted from agricultural and pastoral NPP in 800 AD (top right), 1850 AD (bottom left), 2000 AD (bottom right). Rectangular borders appear because of differences in model resolution.

Table 2. Percentage of mega-fauna to go extinct [1], per cent of continental area covered by grasslands in the Pleistocene [22], NPP (±sd between sensitivity studies) liberated following the extinction of the mega-herbivores, liberated grassland NPP divided by total grassland NPP in the Pleistocene and Holocene for each continent.

	Eurasia	North America	South America	Australia	Africa
Extinction per cent [1] (%)	36	72	84	88	18
Per cent grassland in Pleistocene [22] (%)	52	23	87	81	58
Liberated NPP (Pg C yr^{-1})	0.28 ± 0.036	0.31 ± 0.041	0.48 ± 0.072	0.10 ± 0.013	0.19 ± 0.025
% liberated grassland NPP Pleistocene (%)	3	38	4	4	2
% liberated grassland NPP Holocene (%)	4	11	6	6	2

To understand how people used this liberated NPP spatially, we subtracted global maps of liberated NPP from maps of NPP used by humans in agricultural and pastoral regions during current (2000 AD) [14] and historical (800 and 1850 AD) [13] times. Agricultural regions and regions of liberated NPP often overlap (figure 2). By 800 AD, much liberated NPP had been utilized in Eurasia and the Americas because agricultural land use was concentrated in these regions, but much of the rest of the world still had liberated NPP (figure 2). However, by 1850, populations had increased sufficiently that agriculture in much of Eurasia and parts of Africa had exceeded NPP liberated due to the extinction of the mega-herbivores. There are very few global regions today where appropriated NPP does not exceed NPP liberated following the extinction of the mega-herbivores.

To understand how people used this liberated NPP temporally, we integrated liberated NPP for the entire Earth from 100 000 BP to today. Before the origin of agriculture (∼10 000 YBP), a total of 2.5% (∼1.4 Pg C yr^{-1} (between 1.2 and 1.6 Pg C yr^{-1}) of ∼56 Pg C yr^{-1}) (figure 3) [10] of global terrestrial NPP was liberated following the extinction of the mega-herbivores. This NPP was gradually appropriated by people following the origin of agriculture. Liberated NPP peaked when agriculture developed and was on average completely utilized by humanity by ∼320 years ago (between ∼250 and 500 ybp). Present day agriculture utilizes ∼6 times more NPP than was used by the extinct mega-herbivores.

4. Discussion

Agriculture-based societies use a much higher percentage of NPP than hunter gatherer societies, who use, on average, only 0.01–0.001% of NPP in a given area [3]. Once human society could use a similar percentage of NPP as herbivores, total mega-fauna biomass (including humans) recovered to pre-extinction levels. This recovery was, however, attained almost exclusively by adding human and livestock biomass, with the biomass of non-human mega-fauna almost unchanged [2]. Before the extinctions, NPP utilization was distributed among many herbivore species, each with

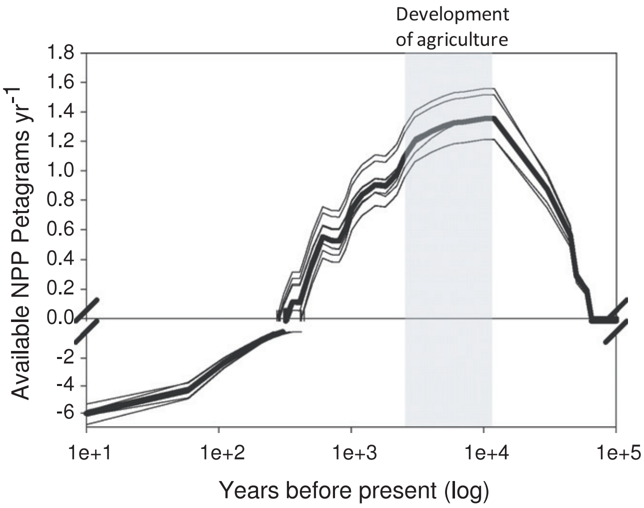

Figure 3. Globally integrated liberated NPP and NPP appropriated by people through agriculture and livestock grazing. Prior to the extinctions, 100 000 years ago, we assume no liberated NPP. The gray box indicates a window of time the agriculture is thought to have been developed independently in several regions worldwide [4]. Note the changing scale below zero on the *y* axis. Thick black line is our best estimate while the thin black lines are the results of the sensitivity studies.

a relatively narrow ecological niche. But following the extinctions, this NPP was utilized by one species, humans, who utilized this liberated NPP through agriculture and livestock.

In 800 AD, world population was approximately 220 million, and liberated NPP had been utilized in parts of Europe, India and China where populations were concentrated. By 1850 AD, global populations had increased to ~1.2 billion, and liberated NPP had been appropriated in much of Eurasia and Africa, but was still available in much of Australia, South America, and western North America. This availability of NPP may have contributed, among other reasons, to the movement of Eurasians to these regions. Today, liberated NPP has been appropriated in most of the world and NPP usage through agriculture vastly exceeds that which had been consumed by the mega-herbivores. Humans have exceeded this NPP usage by replacing natural ecosystems with agro-ecosystems that are often subsidized by irrigation and fossil fuel energy sources [2].

In our calculations, we conservatively estimate that mega-herbivores have no impact on forest and savanna distributions and assume that the Holocene distributions of the mega-herbivores are based only on Holocene potential vegetation maps. Mega-herbivores, such as elephants, however, have a large impact on tree cover in savanna regions in Africa [27]. We, therefore, may have underestimated grassland regions and the potential range of the mega-herbivores in our calculations.

In this letter, we intended to capture broad trends in how humans appropriated liberated NPP through agriculture. Our methods of estimating NPP used by mega-herbivores are subject to similar shortcomings as Barnosky (2008) [2]. Future studies could refine the methods with more accurate regional estimates of mega-herbivore continental ranges and densities and more accurate regional estimates of human appropriated NPP (HANPP). There is much regional variety in HANPP. For instance, HANPP has declined in the UK from 71% in 1800 to 68% today [28], while HANPP in the Philippines has risen from 35% in 1910 to 60% today [29].

4.1. Can this method constrain agricultural carrying capacity?

Global, terrestrial primary production in the absence of humans, would be 65.5 Pg C yr^{-1}, somewhat larger than the current global terrestrial NPP, estimated at 59.2 Pg C yr^{-1} [8]. Through agriculture, humans have decreased global NPP by ~6 Pg C yr^{-1}, partly through decreasing the length of the effective growing season and partly through degradation. Irrigation and fertilization can increase NPP, and these processes are increasingly shifting the upper limits of agricultural NPP [8]. However, this loss and gain of NPP is a relatively recent phenomena and in the early phases of the development of agriculture, the role of humans in decreasing NPP was probably small, and the liberated NPP represented a significant resource.

Herbivores will generally consume between 1 and 10% of NPP depending on the ecosystem, with larger percentages consumed in productive grasslands [30]. There is a constant arms race between plants and herbivores that keeps herbivores from consuming all plant NPP. Plants are constantly evolving strategies to avoid being eaten by herbivores such as by accumulating selenium or silica in their leaves [30]. Every defense sets the stage for a new attack by herbivores, which in turn provide a new opportunity for a defense, leading to speciation of plants and herbivores. Eventually, an ecological balance is achieved with a set percentage of NPP utilized by herbivores.

The balance of NPP consumption between herbivores and plants was removed following the extinction of the Pleistocene mega-herbivores. Prior to those extinctions, mega-herbivores consumed a certain percentage of global NPP. This percentage was determined over time as plants evolved defenses to avoid herbivory. Humans manipulate plants in their consumption of NPP in a fundamentally different way than the mega-herbivores manipulate plants in their consumption of NPP. Humans actively manipulate crop genetics by selecting the crops that provide the most edible parts and therefore, the plants that reproduce are often those with the highest portion of edible NPP. The evolutionary incentives for the plants eaten by herbivores are exactly the opposite. Plants that evolve defenses against herbivores to avoid being eaten are often those with an evolutionary advantage. Therefore, humans seem unlikely to be constrained to use the same percentage NPP as was used by the extinct Pleistocene mega-herbivores.

Human agricultural carrying capacity is related to the NPP liberated following the extinction of the Pleistocene mega-herbivores, but not as a one to one NPP trade-off. Instead, the extinction of the Pleistocene mega-herbivores may be important because agriculture and domestic animal grazing was able to flourish in the absence of competitive herbivory. The Pleistocene extinctions may also be important in helping to explain why agriculture and the grazing of livestock developed independently on several continents ~10 000 years ago. The extinction of the Pleistocene mega-herbivores may have enabled the onset of agriculture for three reasons: NPP became available for human utilization, the domestication of wild crop types was more feasible in the absence of mega-herbivore competition, and there was selective pressure on hunting societies to find a new food source as their prey went extinct.

In this letter, we show how humans have gradually taken over the NPP once consumed by the now extinct Pleistocene mega-herbivores. Humanities' relationship to agriculture is sufficiently different from normal herbivory that an exact carrying capacity based on liberated NPP is difficult to define. However, since humans currently use ~6 times more NPP than all of the extinct Pleistocene mega-herbivores, it is clear that we have moved well beyond simply filling their ecological herbivory niche through agriculture. This indicates that humanities ecological role in the planet has changed in the past centuries, now being sustained through technological innovation and non-solar fossil fuel energy sources.

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