Exploring a natural baseline for large-herbivore biomass in ecological restoration

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Title: Exploring a natural baseline for large-herbivore biomass in ecological restoration

Running title: Large-herbivore biomass and NPP

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Abstract

1. Large herbivores provide key ecosystem processes, but have experienced massive historical losses and are under intense pressure, leaving current ecosystems with dramatically simplified faunas relative to the long-term evolutionary norm. Hampered by a shifting baseline, natural levels of large-herbivore biomass are poorly understood and seldom targeted. This “Decade of ecosystem restoration” calls for evidence based targets for restoring the natural diversity and biomass of large-herbivores.

2. We apply the scaling of the consumer-producer relationship to a global dataset of large herbivore density in natural areas. The analyses reveal that African ecosystems generally have much higher large-herbivore biomass and also the strongest consumer-producer relationship. For Europe, Asia and South America there are no significant relationships with primary productivity indicative of impoverished faunas. Compared to expectations from the African scaling relation, large-herbivore biomass in ecosystems outside Africa is considerably lower than expected.

Synthesis and application. Ecological restoration and rewilding entails restoration of a natural grazing process. Our findings indicate that many nature reserves are depleted in large-herbivore biomass, judged from their primary productivity. Meanwhile overexploitation by seasonal livestock grazing takes place in other areas. It is thus difficult, but urgent, to reach scientific consensus regarding a natural baseline for large-herbivore biomass. Until such agreement has been reached, we recommend to manage, or rewild, large herbivores in year round near-natural grazing and without predefined density targets, but following natural and fluctuating resource availability with minimal management intervention. The establishment of experimental rewilding sites with reactive herbivore management is needed to further advance our understanding of natural grazing density.

Introduction:

Large-herbivore grazing is widely recognized as an important process for biodiversity, but there is considerable debate about appropriate densities of wild large-herbivores and natural levels of grazing and browsing intensity. Perceptions of overabundance and unnaturally high densities of large-herbivores (e.g., Ickes 2001; Gortázar et al. 2006; Mosley & Mundinger 2018) influence wildlife management, whereas meat or dairy production targets influence stock in agro-environmental schemes and specific species, habitat or landscape targets influence conservation grazing management. The continued global loss of biodiversity calls for an alternative approach to ecosystem grazing. Contrary, trophic rewilding (Bakker & Svenning 2018) and ‘naturalistic grazing’ (Jepson, Schepers & Helmer 2018), have no fixed herbivore density target,
but allow fluctuations according to resource availability and with minimal management intervention. To avoid the danger of managing for preconceived conservation targets, notably when promoting natural processes and species interactions for self-regulating biodiverse ecosystems, we consider a long-term natural baseline for large-herbivore biomass for ecosystem restoration and biodiversity.

Most extant species evolved in prehistoric ecosystems shaped by natural processes and where large herbivores contributed by diversification of biotic resources and the abiotic environment to the benefit of other species (MacFadden 1997; Weil 2005; Galetti et al. 2018). Many terrestrial mammals, notably megafauna (≥44.5 kg) have gone extinct during the late-Quaternary, leaving depauperate assemblages in most areas (Sandom et al. 2014a; Ripple et al. 2015). The remaining species have been displaced, hunted, and eradicated, resulting in wild terrestrial mammals only accounting for 4% of total mammal biomass today (Bar-On, Phillips & Milo 2018).

The historical legacy and contemporary high human influence on ecosystems makes it difficult to make even a qualified guess at a natural baseline for large-herbivore biomass. However, the close association between consumer and producer biomass has been formulated as a general scaling law in ecology (Cebrian 2015) describing how energy flows between trophic levels, e.g., predator-prey biomass relationships (Hatton et al. 2015). Hatton et al. (2015) reported that for ecosystems representing near-natural conditions, across trophic levels, ecosystems and ecosystem productivity, there is a strong correlation between producer and consumer biomass typically following a scaling law with an exponent close to ¾. Scaling laws have also been demonstrated for the relationships between consumer biomass and productivity typically with an exponent of c. 1.5-2 (Coe, Cumming & Phillipson 1976; East 1984; Fritz & Duncan 1994).

We expect large-herbivore biomass in intact (or near-intact) ecosystems to follow a scaling relationship with primary productivity. Given the more intact terrestrial mammal faunas in protected areas in Africa (Sandom et al. 2014a), we hypothesize that African ecosystems will express a strong relationship between productivity and large-herbivore biomass whereas ecosystems from the continents more heavily influenced by humans, including past megafauna loss, are expected to show a poorer relationship and have lower herbivore biomass in general. Here, we use empirical global data on large-herbivore biomass and Net Primary Production (NPP), and ecological theory to explore the scaling relationship across continents and discuss a natural baseline for terrestrial large-herbivore biomass. We compare our findings to rewilding projects seeking to restore large herbivores and discuss implications for restoring ecosystems with both intact mammal assemblages and biomass.

Exploring the relationship between large-herbivore biomass and primary productivity
We collated published empirical data on large-herbivore biomass (kg/km²) from Hatton et al. (2015), Rodriguez et al. (2014) and from personal communication (Fløjgaard et al. 2021). Hatton et al. reports wild large-herbivore biomass (≥5 kg) for 73 protected areas. Opposite to Hatton et al. we included the biomass of megaherbivores (i.e., herbivores ≥1000 kg, e.g., elephants, rhinos, and hippos) and migratory species (species with seasonal, long-distance movement of individuals) weighted by the fraction of the year they spend in the ecosystem. Rodriguez et al. reports contemporary ungulate biomass of all species in the orders Perissodactyla, Artiodactyla or Proboscidea for 95 natural areas (national parks and protected areas with some degree of traditional pastoralism). We ensured no data overlap between Rodriguez et al and Hatton et al. From Rodriguez et al., we included the livestock biomass because grazing livestock in pastoralist systems also rely on the local primary production. In total, we included 289 data points from 146 ecosystems across Africa, Asia, Europe, North America and South America (Fløjgaard et al. 2021). GPS positions were checked using Google maps satellite images and place names. Doubtful positions were checked against primary literature and either placed accordingly or moved to reserve centers. We used data from the years 1926-2009 as well as data from unknown years. There are temporal mismatches between some data points and the net primary productivity data because NPP has generally increased over the last decades (Nemani et al. 2003). The temporal mismatch is most pronounced for Africa with the oldest data points, wherefore, we do a sensitivity analysis to explore the effect of this mismatch on model fit and interpretation on a data subset where only African biomass data from the same range of years as the NPP data are used (n = 14). As an additional sensitivity analysis, we analyzed subsets of African data points including only herbivores larger than 20 kg (n=21) and for ecosystems with megaherbivores present (n=20) reported from Hatton et al. to investigate the role of large-bodied mammals.

Primary productivity was estimated using satellite-derived products (Zhao et al. 2005; Zhao, Running & Nemani 2006) (NPP retrieved from http://files.ntsg.umt.edu/data/NTSG_Products/MOD17/GeoTIFF/MOD17A3/GeoTIFF_30arcsec/). These products give the average of yearly NPP from 2000 to 2015 in 30 arc seconds (global). As the exact size of the area pertaining to the biomass estimate is unknown, we explore model fits using mean and median NPP in 1, 5, 10, 50 and 100 km buffers surrounding the given coordinate of the ecosystem as an indication of the robustness of the patterns.

For ecosystems with the same name, we use the average biomass and NPP (the same ecosystem can have slightly different coordinates depending on the source). Consistent with Hatton et al., we use ordinary least squares (OLS) to fit the loge-transformed biomass and NPP data. The detailed analysis can be obtained from the available R-script (R Core Team 2017) and data file in Fløjgaard et al. (2021). For comparison, we show...
Empirical findings of large-herbivore biomass

There are orders of magnitude of differences in large-herbivore biomass between ecosystems and continents (Figs. 1-2). African and Asian ecosystems have the highest biomass, whereas North and South America have the lowest. European ecosystems are highly variable, with rewilding sites standing out with high large-herbivore biomass at intermediate NPP exceeding large herbivore biomass even in most African and Asian ecosystems with equivalent NPP (Fig. 2).

A regression fitted to log-transformed data records a significant, but relatively poor relationship between large-herbivore biomass and NPP using the global data set (best-fit model: $R^2=0.10$, n=146, $P < 0.001$, Table 1). Across African ecosystems (Fig. 1), large-herbivore biomass follows a much stronger relationship to ecosystem NPP with the following scaling relationship: $\text{Biomass} = 3.64E^{-04} \times \text{NPP}^{1.23}$ (best-fit model: $R^2=0.44$, n=48, $P < 0.001$, Table 1). Subsetting the African data to either only ecosystems with megaherbivores present, or using only species with body mass $\geq 20$ kg in the biomass estimates increases model fit (Table 1).

Subsetting the African data to the years 2000-2015 to increase temporal matching with NPP reduces the dataset to n=14 and reduces the slope, but hardly influences model fit (Table 1). For the other continents than Africa, a significant positive relationship between large-herbivore biomass and NPP was only recorded for North America, with a scaling pattern of $\text{Biomass} = 4.49E^{-07} \times \text{NPP}^{1.51}$ ($R^2=0.35$, n=32, $P < 0.001$, Table 1). Asia, Europe and South America do not have significant relationships between large-herbivore biomass and NPP, and South American large-herbivore biomass displays a consistently negative relationship with NPP (Table S1, Fig. 1).

Discussion

Our results confirm a strong scaling relationship between large herbivore biomass and NPP in protected areas in Africa, and weaker or non-existing relationships outside Africa. Large-herbivore biomass in Asian ecosystems is most similar to Africa, particularly at low-intermediate levels of NPP. The Pleistocene megafaunal attrition was least severe in Africa followed by Asia (Sandom et al. 2014a) and these are the only continents to still host native megaherbivores. At intermediate-high NPP, there is a lower large-herbivore biomass in Asia than Africa, possibly attributed to higher contemporary anthropogenic pressures on large herbivores (Sanderson et al. 2002). Notably, suppressed fire regimes, causing a decrease in palatable forage in woodlands (Karanth & Sunquist 1992), habitat contraction and species’ persistence in
less productive refuges (Suraprasit et al. 2020; Teng et al. 2020), and poaching (Srikosamatara 1993) may contribute to lowered large-herbivore biomass in Asia.

Europe, North and South America suffered greater losses in the late-Quaternary megafauna extinction (Sandom et al. 2014a) and extant faunas experience high contemporary human impacts in Europe and North America (Sanderson et al. 2002). The introduction of livestock to rangelands in South America (where supplementary feeding, irrigation and fertilization are rare) has increased large-herbivore biomass by an order of magnitude compared to surrounding unmanaged ecosystems (Oesterheld, Sala & McNaughton 1992), indicating that the biomass of wild large herbivores is well below carrying capacity. Dense forest cover in the most productive ecosystems in South America could also be a contributing factor to the – seemingly – low biomass at high NPP. In North America, extant species may persist at low densities due to fragmented habitat, continued hunting and culling and recovery lag from past persecution. A simulation study showed that bison in Yellowstone NP has not yet reached the estimated mean food-limited carrying capacity of the area (Plumb et al. 2009). In all these cases, the lack of mega herbivores on these continents means the remaining large herbivores are more susceptible to predation, potentially limiting large-herbivore biomass (Hopcraft et al. 2012).

High large-herbivore biomass in European rewilding projects also suggest contemporary, limiting factors in other nature areas. European large-herbivore biomass ranges from a minimum of 190 kg/km² to 16,000 kg/km² with a notable bimodal distribution between rewilding sites and other nature areas (see RewEu and Europe, respectively, in Fig. 2). The high biomasses are found in rewilding areas that practice ‘naturalistic grazing’ or trophic rewilding. In practice, this approach leads to large-herbivore populations being primarily regulated by primary productivity. Interestingly, these rewilding sites reach large-herbivore biomasses exceeding the median, but within the maximum, observed in African and Asian ecosystems at intermediate NPP (Fig. 2). This may reflect the lack of predation in rewilding areas, yet, it could also reflect that large herbivores are reduced to some extent even in African ecosystems through regulatory hunting or poaching (e.g., Fayrer-Hosken et al. 2000; Robson et al. 2017). For historical reference, palaeoecological data from Europe and Asia, reveal relatively high biomass estimates, e.g., the mammoth steppe is estimated to have had a megafauna biomass of 10,500 kg/km² (Zimov et al. 2012) and in Last interglacial Britain an equivalent of ≥2.5 fallow deer/ha were estimated for half the study locations (Sandom et al. 2014b), i.e., ≥15,000 kg/km² assuming 60 kg individuals.

It has been argued that predation can reduce the densities of large herbivores and that reintroduction of predators may solve perceived overabundance (e.g., Warren 2011). Evidence that predators generally and substantially regulate total herbivore densities is at best equivocal and varies across ecosystems (Skogland...
large- and megaherbivores in those ecosystems. Work from Africa suggest that rather than reducing overall herbivore biomass, predation causes it to shift from smaller herbivores to the largest species (le Roux et al. 2019). Our finding of a scaling relationship and generally high large-herbivore biomass in African ecosystems with generally fairly complete predator faunas also suggest that predation does not reduce herbivore biomass to low levels in near-natural ecosystems (Table 1).

**Perspectives for applying a large herbivore biomass baseline in restoration**

Our results clearly highlight that in many ecosystems outside Africa large-herbivore biomass is far below long-term natural levels. Decision makers and managers of large herbivores in nature areas designated to ecosystem restoration, should reflect on the following: Current management actions to down-regulate populations potentially reflect a shifting baseline. At the other extreme, we see a risk of exceeding the natural baseline for large-herbivore biomass when practicing seasonal livestock grazing for agricultural purposes leading to suppression of pollinators and herbivore invertebrates. Both overgrazing and absence of grazing (whether by abandoned livestock grazing or suppressed large herbivore biomass in nature areas) impose threats to biodiversity (Sartorello et al. 2020). We therefore recommend practicing year round ‘naturalistic grazing’ with no specified large-herbivore density, but resource-limited populations with minimum management intervention. Despite a thorough scientific foundation (ICMO2 2010) this practice is known to stir animal welfare debates, and may over time jog our understanding of wild animal welfare (Capozzelli, Hecht & Halsey 2020). A practical solution to this challenge may be that large herbivores are removed or culled in the event that they fall below predefined body condition or animal welfare criteria, notably in small, fenced nature areas. Reactive regulation (culling to avoid forthcoming starvation) comes closer to naturalistic grazing than proactive regulation (culling to a set population density well below carrying capacity) but the two may also be combined.

The consumer-producer relationships presented here, however useful for exploring a natural baseline, are limited by uncertainties in available data and the contingencies of long term population management and should not be used for predicting or extrapolating large-herbivore biomass targets for specific areas. Instead, we recommend local experimental rewilding of sites with ‘naturalistic grazing’ which in turn can help informing targets of appropriate large herbivore densities in agro-environmental schemes, where self-regulating populations are not possible.

We have presented a macroscale study and more attention is needed to address issues of spatial and temporal scale and ecosystem context. Further progress in establishing reliable baselines would strongly benefit from large-scale and open-ended field experiments where diverse assemblages of large herbivores
are allowed to respond to primary productivity, seasonality, and other ecological conditions without population regulation according to predefined management targets.

References:


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Conflict of Interest

All authors declare no competing interests.

Authors’ contribution

C.F. and R.E. conceived the idea. C.F. collated the data and carried out the statistical analyses. All authors contributed to developing the concept and writing.

Data Availability Statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.2rbnzs7pb (Fløjgaard et al. 2021).

Supporting Information: Additional tables and figures
Figure 1. The scaling relationship of large-herbivore biomass and NPP.

Log-log linear regression lines of large-herbivore biomass as a function of primary productivity (mean NPP at 1 km buffer scale for all groups, see Table S1). The colors of points and lines show that the relationships and data for the global data and subset by continent. Grey shading shows the 95% CI and dashed lines are insignificant regressions (p>0.05).
Table 1. Summary of ordinary least squares log-log models for large herbivore biomass as a function of primary productivity (NPP).

Rows represent geographic regions and the primary productivity (NPP) measure, i.e. median or mean and the scale of the buffer (radius in km) surrounding the ecosystem center coordinate. All models with 1 km buffer mean NPP and any other buffer scales yielding significant best-fit models (highest $R^2$ in Table S1) are shown. Africa, mega denotes a subset of data including only ecosystems with megaherbivores (>1000 kg) present, Africa, yrs≥2000 is a subset including only biomass data from the same time period as the NPP, and Africa ≥20 kg is a subset of data where only animals larger than 20 kg were included in the biomass estimates. Model significance is indicated by ns, non-significant, * p<0.05, ** p<0.01, and *** p<0.001. The intercept and slope can be used to formulate the scaling law according to Biomass = intercept x NPP$^{slope}$. N denotes the number of data points in the model and current biomass gives the current mean and standard deviation of large-herbivore biomass within the regions.

<table>
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<tr>
<th>Continent</th>
<th>NPP calculation and buffer scale</th>
<th>$R^2$</th>
<th>Intercept (ln)</th>
<th>Intercept</th>
<th>slope</th>
<th>n</th>
<th>Current biomass, mean (kg/km²)</th>
<th>Current biomass, sd (kg/km²)</th>
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Figure 2. Biomass of large herbivores across low (<500 000 kgC/km²/yr NPP), medium (500 000-1 000 000 kgC/km²/yr NPP) and high (>1 000 000 kgC/km²/yr NPP) productivity (1 km mean NPP) ecosystems by continent. The European data is represented separate for rewilding sites (RewEu), i.e., ecosystems practicing natural grazing, i.e., animals in (often fenced) nature reserves are allowed to increase and are only regulated to avoid winter starvation, and Europe denoting data from national parks and other nature areas. The box plot visualizes the median, the first and third quartiles (hinges), 1.5 * IQR (Interquartile range, whiskers), and all data points.