



# Herbivory baseline estimates in Spanish protected areas, and environmental implications

Rubén Serrano-Zulueta · Guillermo Pardo ·  
Ferran Pauné · Agustín del Prado ·  
Pablo Manzano

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## Abstract

**Context** There are no estimations of herbivory baselines in Spain. Due to the bioclimatic conditions, ungulates have maintained Open Ecosystems until the Holocene. Pastoral tradition later fulfilled the niche of wild grazers, but this role is not considered in environmental assessments of grazing livestock.

**Objectives** We attempted to better understand the scale of herbivory in Spain. We aimed to estimate the weight of current wild herbivory and evaluate the role of domestic herbivory in these baselines. We applied them to improve the allocation of environmental impacts and emissions from grazing livestock.

**Methods** We inferred an equation relating Net Primary Productivity (NPP) with ungulate biomass and enteric CH<sub>4</sub> with data from 11 Spanish Protected Areas. We estimated theoretical baselines in Spain using other literature sources. We applied the equations to the Spanish open ecosystems that are currently grazable. We also estimated the proportion of grazing livestock that would be part of such baseline.

**Results** We found relationships between NPP and ungulate biomass and enteric CH<sub>4</sub> emissions. However, current abundances are several times below the estimated baselines and the carrying capacity. There are major constraints for herbivore populations to reach their baseline state, particularly the absence of migration and the extinction of grazers among wild herbivores. Structural maintenance of Open Ecosystems should therefore be complemented by domestic grazers that cannot be replaced by the extant wild, mostly browser, ungulates.

**Conclusions** We concluded that Spain is widely susceptible to being populated by herbivores that generate Open Ecosystems as baseline landscapes. Current grazing livestock accounts for a significant part of them, so baselines must be included in their environmental assessments. For the case of Spain,

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R. Serrano-Zulueta · G. Pardo · A. del Prado ·  
P. Manzano (✉)  
Basque Centre for Climate Change (BC3), Leioa, Spain  
e-mail: pablo.manzano@helsinki.fi

F. Pauné  
Universitat de Vic - Universitat Central de Catalunya, Vic,  
Spain

A. del Prado · P. Manzano  
Ikerbasque — Basque Foundation for Science, Bilbao,  
Spain

P. Manzano  
Global Change and Conservation Lab, Organismal  
and Evolutionary Biology Research Programme, Faculty  
of Biological and Environmental Sciences, University  
of Helsinki, Helsinki, Finland

P. Manzano  
Faculty of Biological and Environmental Sciences,  
Helsinki Institute of Sustainability Science (HELSUS),  
University of Helsinki, Helsinki, Finland

we propose a minimum baseline equivalent to 36% of current grazing livestock biomass and 23% of their enteric CH<sub>4</sub> emissions.

**Keywords** Open Ecosystems · Herbivory baselines · Environmental assessment · Land abandonment · Carrying capacity

## Introduction

Ecological baselines can be defined as the natural impacts of biotic interactions in absence of human activity (Jenkins and Brian Bedford 1973; Arcese and Sinclair 1997). In landscape ecology, factors that shape ecosystem structure are still unclear (Adie and Lawes 2023). The traditional approach conceptualizes closed forests as a baseline, or climax state, of most ecosystems (Pausas and Bond 2019). However, research in the last decades is tending to geographically and climatically expand the consideration of Open Ecosystems as alternative climactic landscapes (Bond 2005; Archibald et al. 2019; Ellis et al. 2020). In Open Ecosystems, top-down biomass regulators like herbivory and fire shape the landscapes in large areas, such as the Eurasian temperate forest (Vera 2000; Bond 2005; Karp et al. 2021; Adie and Lawes 2023). Alternate states between Open and Close Landscapes are natural (Adie and Lawes 2023), discarding a fix, unique state across time (Moncrieff et al. 2016). However, with intrinsic spacious-temporal variability and a long human activity, it is difficult to define herbivory baselines of potential Open Ecosystems (Hempson et al. 2017). The dynamics of herbivory and fire have been discussed theoretically, but there are limitations to quantifying them (Hempson et al. 2017; Manzano and White 2019; Archibald et al. 2019; Adie and Lawes 2023).

Spain is largely suitable to be populated by wild megaherbivores such as ungulates, linked to baselines for landscape configuration (Acevedo et al. 2012; Ellis et al. 2020; Adie and Lawes 2023). Megaherbivores have been abundant since at least the Pleistocene (Álvarez-Lao and García 2011), and possibly for the last 15 million years (Bond 2019). During the last millennia, when most megaherbivores have already disappeared, the Spanish landscape has remained largely Open (Ellis et al. 2020). This may include structural alternate states of Open and Close

canopies, being especially relevant in areas with more significant rainfall (approximately > 800 mm/yr) where fire is a more important regulator than herbivory (Archibald et al. 2019; Adie and Lawes 2023). Currently, most of Spain has the environmental conditions to be a temperate savanna (Bond 2005; Archibald et al. 2019; Launchbaugh and Strand 2021), and its potential landscape is structurally similar to that (Johnsen et al. 2019). Phenotypical characteristics of Spanish dominant trees like *Quercus spp.* are indeed adapted to top-down regulation, i.e., an open landscape (Adie and Lawes 2023). With human expansion, livestock progressively replaced wild herbivores, maintaining high densities that fulfil part of megafauna's previous ecological role (Smith et al. 2016; Manzano et al. 2023a). Therefore, baseline herbivory intensities at landscape level in Spain can be very significant.

In Open Ecosystems, some natural and anthropic processes linked to both wild and domestic herbivores are, to a large extent, mutually equivalent. This includes, among others, the configuration of the landscape and the vegetation structure, and GHG fluxes (Smith et al. 2010; Hristov 2012; Kim et al. 2013; Smith et al. 2016; Manzano and White 2019). Herbivore densities have hence great implications for burning environmental questions such as biodiversity maintenance or climate change. For the latter, estimations indicate that about 14.5% of the global anthropogenic greenhouse gas (GHG) emissions could be allocated to livestock, from which 39% is attributed to enteric fermentation (Gerber et al. 2013)—most of them linked with grazed systems (Opio et al. 2013). Understanding ecological herbivory baselines and their wide-ranging implications can disentangle how much of the herbivore disturbances could be associated to man-made impacts, and how much to natural ecological processes. They are, however, more difficult to establish in managed, yet semi-natural ecosystems (i.e., those combining natural and human elements), as e.g. pastoralist systems, than in anthropized landscapes that are more decoupled from natural ecological dynamics (Manzano et al. 2021). In both cases, though, assuming an ecological baseline with widespread closed-canopy forests and reduced herbivory levels can distort the perception of current landscapes and the understanding of past and future scenarios, negatively affecting land management strategies (Moncrieff et al. 2016), with implications

for climate change (Malhi et al. 2022). Although not currently considered, herbivory baselines could have an important role in the ongoing debate on grassland-based animal food systems (Manzano et al. 2023b; Thompson et al. 2023), a hot research topic that still has no clear or easy solutions (Opio et al. 2013).

Discussions on the best livestock systems are highly influenced by the methodologies and assumptions used to assess the impacts of livestock activity (O'Brien et al. 2012; Curran 2014; McAuliffe et al. 2018; Manzano et al. 2023b). It has conventionally been assumed that wild herbivory numbers have always been much lower than current livestock ones—i.e., wild emissions being negligible when compared with those from livestock. Environmental accounting tools applied to agricultural systems have therefore regarded all environmental impacts from livestock as anthropogenic, leading to a high direct impact attribution of GHG emissions per kg of product (Gerber et al. 2011). But domestic grazing herbivores can indeed fulfil ecological roles that are equivalent to wild herbivores, and their densities can also be equivalent (Manzano et al. 2023a). At the same time, some authors have demanded that the consideration of baselines can be important in environmental assessment (Pardo et al. 2023) and policy-making (Moncrieff et al. 2016), for example, when supporting or limiting pastoralism (Manzano et al. 2023a). In sum, new methodological approaches demand delving into a specific framework for Open Ecosystems that explicitly includes and quantifies baseline values (Manzano and White 2019).

In this study, our main overall objective is to understand the weight of the Spanish herbivory in an ecological baseline scenario, given the natural status of Open Ecosystems in the country. Additionally, we aim to better understand the ecological state of current Protected Areas (PAs) in relation to wild herbivory and apply baseline values to refine GHG assessments of livestock systems that include herbivory processes, i.e. grazing livestock producing enteric methane (CH<sub>4</sub>).

## Methods

The baseline concept and assumptions involved

Interpretations of ecological baselines vary, since landscapes are very heterogeneous and evolve over time (Moncrieff et al. 2016). Most baselines are either based on the Pleistocene or the Holocene period. Whereas the Pleistocenic approach goes back to the presence of mostly extinct megaherbivores, which eventually got substituted by domestic animals, the Holocenic approach considers animal domestication as a potential part of the baseline (Corson et al. 2022; Fraanje and Garnett 2022). Considering that pastoral tradition in Spain has played an important role in social, ecological and economic terms for, at least, 2500 years (Garzón 1992; San Miguel et al. 2017) and that most landscapes could be defined as the Open Ecosystems that pastoralism contributes to shaping, both baseline approaches (i.e., Pleistocenic and Holocenic) could be relevant in Spain. In this study, we use current wild herbivore biomass as a proxy for wild herbivory baselines in a Holocenic approach. To do so, and since PAs are a proxy for ecological baselines (Jenkins and Brian Bedford 1973; Arcese and Sinclair 1997), we use wild herbivore biomass of different PAs in Spain to estimate baselines for herbivory.

Estimations of current wild herbivore biomass density in Spanish PAs

Data from ungulate abundances (individuals/km<sup>2</sup>) in Spanish PAs were collected from multiple sources (see Supplementary Information). Beyond reviewing literature, technicians from PAs were directly contacted in cases when data were not easily available. Ungulates present in each PA were extracted from Cátedra de Parques Nacionales (2019). In this study, we included all National Parks in peninsular Spain, excluding Sierra de las Nieves because of its recent gazetting as a National Park (BOE 2021) (Table 1). We also included three Natural Parks, which limit human intervention in the regulation of wild populations through their legal status: Sierras de Cazorla, Segura y Las Villas (BOJA 2017), Los Alcornocales (BOJA 2012), and Capçaleres del Ter i Freser. Due to their strict protection status, and their relative distance to, or isolation from, densely

**Table 1** Site conditions of the studied PAs

| Protected area                          | A    | MAT  | P    | Bio           | Dom | Mig |
|---|------|------|------|---------------|-----|-----|
| Aigüestortes i Estany de Sant Maurici   | 144  | 1,9  | 1443 | Alpine        | Yes | No  |
| Cabañeros                               | 415  | 13,6 | 466  | Mediterranean | No  | Yes |
| Capçaleres del Ter i Freser             | 147  | 3,6  | 1372 | Alpine        | Yes | No  |
| Doñana                                  | 545  | 18,0 | 514  | Mediterranean | Yes | No  |
| Guadarrama                              | 1670 | 7,2  | 1037 | Alpine        | Yes | No  |
| Los Alcornocales                        | 179  | 16,5 | 781  | Mediterranean | Yes | No  |
| Monfragüe                               | 159  | 15,6 | 511  | Mediterranean | No  | No  |
| Ordesa y Monte Perdido                  | 624  | 4,2  | 1281 | Alpine        | Yes | No  |
| Picos de Europa                         | 351  | 7,6  | 1064 | Alpine        | Yes | No  |
| Sierra Nevada                           | 867  | 7,5  | 789  | Alpine        | Yes | No  |
| Sierras de Cazorla, Segura y Las Villas | 2104 | 12,0 | 505  | Mediterranean | Yes | No  |

Variables: *A* Area (km<sup>2</sup>), *MAT* Mean Annual Temperature (°C), *P* Annual rainfall (mm/yr), *Bio* Biome, *Dom* Competition with domestic livestock, *Mig* Enabling conditions for seasonal migration

populated areas, most National Parks and many PAs in Spain are currently the areas closest to a theoretical climax state. They are subjected to represent the landscapes with least human intervention countrywide (only occasional animal supplementation, restricted to scarcity periods, and occasional population controls due to the absence of predators).

Population densities (individuals/km<sup>2</sup>) were converted into biomass densities (kg/km<sup>2</sup>). For this purpose, Typical Animal Mass (TAM) was used, as proposed by Gavrilova et al. (2019) in the latest IPCC (2019) report on Guidelines for National Greenhouse Gas Inventories. This approach is useful to avoid overestimating the biomass by assuming the Adult Mass (AM) as the average body weight, which ignores that young individuals make up an important proportion of the population. Therefore, TAM data were collected for domestic species that could be considered similar in weight and digestive systems to wild species (Gavrilova et al. 2019). Data for AM for wild and domestic species were extracted from literature for both ruminants (Pérez-Barbería 2017) and monogastrics (Jones et al. 2009). TAM of the domestic equivalent was then scaled by the ratio between AM of the wild and domestic species (Eq. 1). Detailed calculations and TAMs are available in the Supplementary Information.

**Equation 1** Arithmetic equations to calculate wild Typical Animal Mass (TAM) using Adult Mass (Jones et al. 2009; Pérez-Barbería 2017) and TAM from similar domestic animals (Gavrilova et al. 2019).

$$AM(\text{wild and domestic}) = \frac{\text{Male AM} + \text{Female AM}}{2}$$

$$\text{Wild TAM} = \text{Domestic TAM} \frac{\text{Wild AM}}{\text{Domestic AM}}$$

Establishing the relationship between NPP and herbivore biomass in PAs

In low anthropized Open Ecosystems (e.g. PAs), large herbivore abundance can be modelled from bioclimatic parameters such as mean temperature and precipitation (Rodríguez et al. 2014) or NPP (Zhu et al. 2018). NPP is just significantly correlated with herbivory biomass under correct ecosystem functioning, i.e., with complete herbivore guilds including grazers, intermediate feeders and browsers (Coe et al. 1976; Hofmann 1989; Kiffner & Lee 2019; Fløjgaard et al. 2022).

Net primary productivity values (NPP, expressed in kg C/m<sup>2</sup>.year) were hence extracted for the areas occupied by the PAs used in this study, using data from the MOD17A3HGF product of Terra MODIS NPP over Peninsular and Balearic Spain, for the 2000–2021 period (Running and Zhao 2021). Mean NPP for this period was estimated using QGIS, version 3.22.1. We then correlated the local NPP values at each PA with the herbivore biomass density of each PA—calculated according to the previous Methods subsection above. We obtained a descriptive equation of the relationship through Least Square linear regressions.

## Comparison of NPP-herbivore biomass density in PAs with previous studies

Comparing different methods to estimate herbivory baselines can be useful to understand the optimal state of Open Ecosystems, to discuss the current state of PAs in relation to the baselines, and to better understand the drivers of herbivore densities. In order to compare our approach with other studies, we applied two simple models (Rodríguez et al. 2014; Zhu et al. 2018) to estimate the wild herbivory baselines of the PAs.

Zhu et al. (2018) provides a theoretical relation between grass NPP and grazing biomass. We deduced the equation:  $\text{Biomass} = 9038.1 \cdot \text{NPP} - 77.23$  (units are  $\text{kg}/\text{km}^2$  for biomass and  $\text{kg C}/\text{km}^2$  for NPP). The model of Rodríguez et al. (2014) (Eq. 2) uses mean annual temperature (MAT) and annual rainfall (P), extracted from Fick and Hijmans (2017). It is constructed from worldwide empirical megaherbivore abundances in Open Ecosystems, mainly feeding on African savannas that are warmer than usual Spanish conditions, posing limitations to its use in the present work. The model climatic range was P: 93–1612 mm/yr; MAT: 13.4–29.1 °C. All alpine parks were excluded for falling out of this climatic range, with lower MATs, i.e., Aigüestortes i Estany de Sant Maurici, Capçaleres del Ter i Freser, Guadarrama, Ordesa y Monte Perdido, Picos de Europa, Sierra Nevada and Sierras de Cazorla, Segura y Las Villas. The model was run with those PAs that fitted into the P and MAT range. The yielded herbivore carrying capacity, or maximum theoretical wild herbivore biomass, was correlated with the NPP of each PA that fitted in the model's climatic range. The resulting equation was compared with the equations from the previous section.

**Equation 2** Climate-based model based on Rodríguez et al. (2014) to estimate ungulate carrying capacity of Open Ecosystems. CC = carrying capacity ( $\text{kg}/\text{km}^2$ ); P = Annual rainfall (mm/yr); MAT = Mean Annual Temperature (°C).

$$CC = \text{Min}(18.3 \cdot P - 3993, 1634 \cdot \text{MAT} - 12502)$$

Apart from these two relations, we compared Spanish wild biomass with data provided by Fløjgaard et al. (2022) and Pedersen et al. (2023). The

results were used to contextualize the Spanish baseline, and two different approaches were consequently proposed: current ecosystem functioning, and theoretical levels (or baseline)—with two equations relating NPP and potential wild ungulate biomass density. In light of the results, an equation of current ecosystem functioning was built through all PAs with similar ecological conditions (i.e., excluding Cabañeros and Monfragüe), and theoretical levels were represented by the model by Zhu et al. (2018). See results sections for further details.

## Scaling up wild herbivore biomass to grazeable areas in Spain

We estimated potential wild herbivore biomass for grazeable areas in Spain using, again, NPP data from Terra MODIS NPP (see above) and equations from both scenarios obtained in the previous step. Grazeable areas are defined as potential open landscapes (Bond et al. 2005) under current land use suitable for herbivory (Díaz Gaona et al. 2014).

Land use information was obtained from European Union (2018). In order to avoid distortions in estimating NPP from anthropogenic land uses, we removed agriculture and intensive monospecific forestry. Vast inner sedimentary basins created by Spain's largest rivers are dominated by agricultural use, where current NPP is generally low (mean  $0.406 \pm 0.154 \text{ kg C}/\text{m}^2/\text{yr}$ ). Due to the massive use of some plantations in the twentieth century, some mountain areas were filtered according to their dominating tree species (MTERD 2020). Excluded coniferous species were: *Eucalyptus* spp, *Pinus radiata*, *P. pinea*, *P. halepensis* in all the country and *P. pinaster* in the Atlantic region.

Land uses included in the modelling were: broad-leaved forest, mixed forest, natural grassland, moor- and heathland, sclerophyllous vegetation, and sparsely vegetated areas. Coniferous forest not previously excluded, and transitional woodland/shrub, were also considered. Mountain areas are overrepresented, as they are usually covered by rangelands or autochthonous forests. Overrepresentation of other plantations of *Pinus sylvestris*, *P. nigra*, *P. uncinata* or *P. pinaster* in the Mediterranean area is greatly compensated by the underrepresentation of autochthonous presence for the excluded coniferous species. The Canary Islands were also excluded from



this study. The area considered as grazable constitutes  $1.48 \cdot 10^5 \text{ km}^2$ , or 29.9% of the total Spanish national territory, excluding the Canary Islands (Fig. 1).

Estimations of enteric  $\text{CH}_4$  from wild herbivory

Clauss et al. (2020) (Eq. 3) was used to estimate enteric  $\text{CH}_4$  from herbivore densities observed in PAs. In that work, scaling relationships in mammalian species are developed between  $\text{CH}_4$  (l/d) and body mass (kg) according to different groups—ruminants and hindgut fermenters, among other herbivore groups not considered in our study.  $\text{CH}_4$  output was converted into mass units applying density of the gas phase ( $0.716 \text{ kg/m}^3$ ).

**Equation 3** Equations to estimate  $\text{CH}_4$  emissions (E) from Clauss et al. (2020). Units: TAM = kg; E =  $1 \text{ CH}_4/\text{yr}$ .

$$E = 0.539 \cdot \text{TAM}^{1.00} \text{ for ruminants}$$

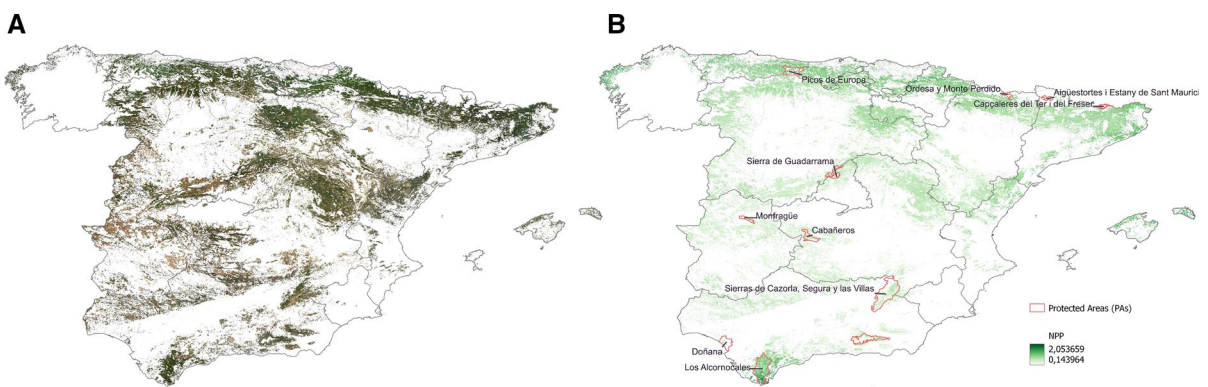
$$E = 0.512 \cdot \text{TAM}^{0.79} \text{ for hindguts}$$

After estimating emissions in PAs, we obtained a descriptive equation of the current relationship between NPP and  $\text{CH}_4$ , following the same approach as with biomass. The baseline was calculated by multiplying current emissions through the factor between baseline and current biomass (5 in average). These equations were applied to grazeable areas at country-wide level to get a baseline of enteric  $\text{CH}_4$  emission in Spain.

Estimation of enteric  $\text{CH}_4$  emissions from current grazing-based livestock in Spain

A selection of enteric  $\text{CH}_4$  emissions data was extracted from the Spanish guidelines for reporting GHG inventories (MAPA 2023). These reports show detailed information on how Spain calculates direct GHG emissions for UNFCCC reporting in its national inventory. They comprehensively indicate how the IPCC (2019) methodology framework is carried out to estimate N and P excretion and  $\text{CH}_4$  output from enteric fermentation, which originates from the main livestock species in Spain.

Within the cattle, sheep, goats and pigs' species, we extracted the emissions data and the body mass that were allocated to animals that have been under grazing management. For simplicity purposes, we did not include horses. Within these documents and for each province in Spain, there are assumptions based on literature and expert opinion on how many animals of the total population and type (e.g. disaggregated by age) graze for each year of the time series (1990–2020), and what % of the annual dry matter of feed is consumed under grazing. Considering these feeding management and animal type characteristics, emissions from enteric  $\text{CH}_4$  and N, P excretion were calculated and body mass is indicated per animal of each type and management.



**Fig. 1** Areas potentially populated by large wild herbivores, given current land uses in potentially open areas. **A** is an orthophoto (USGS 2006) and **B** represents NPP ( $\text{kg C/km}^2$ ). PAs are drawn in red

## Results

### Current and potential ungulate biomass and enteric CH<sub>4</sub> emissions in Spanish PAs

Current animal biomass densities in Spanish PAs range from 304 kg/km<sup>2</sup> in Aigüestortes i Estany de Sant Maurici, to 4222 kg/km<sup>2</sup> in Cabañeros, while NPPs range from 0.340 kg C/m<sup>2</sup>·yr in Aigüestortes to 1.117 kg C/m<sup>2</sup>·yr in Los Alcornocales (Table 2). A lower herbivore biomass is linked to mountain locations, with an abundance of rocky outcrops and limited availability of forage in winter. Meanwhile, higher biomass is related to Open Ecosystem areas sensu (Bond (2019), with an important presence of *Quercus spp.* As expected, enteric CH<sub>4</sub> emissions, ranging from 36 kg CH<sub>4</sub>/km<sup>2</sup>·yr to 615.6 kg CH<sub>4</sub>/km<sup>2</sup>·yr, are generally proportional to biomass, influenced by the predominant forage digestion type of the herbivores. For example, at PAs with a higher proportion of ruminants, emissions are proportionally higher. It is the case of Sierras de Cazorla, Segura y Las Villas, where the biomass value is 6.6 times the one for CH<sub>4</sub>, while in Sierra Nevada, with a high proportion of wild boar (a hindgut fermenter), this ratio was 15.3.

Neither biomass nor emissions were related with NPP when all PAs are considered together ( $R^2 = -0.085$ ,  $p = 0.649$  and  $R^2 = -0.094$ ,  $p = 0.716$ ). However, two PAs stand out due to their high herbivory rates: Monfragüe and Cabañeros. Their outlier character can be explained by their differential ecological functioning in relation to the rest of the PAs.

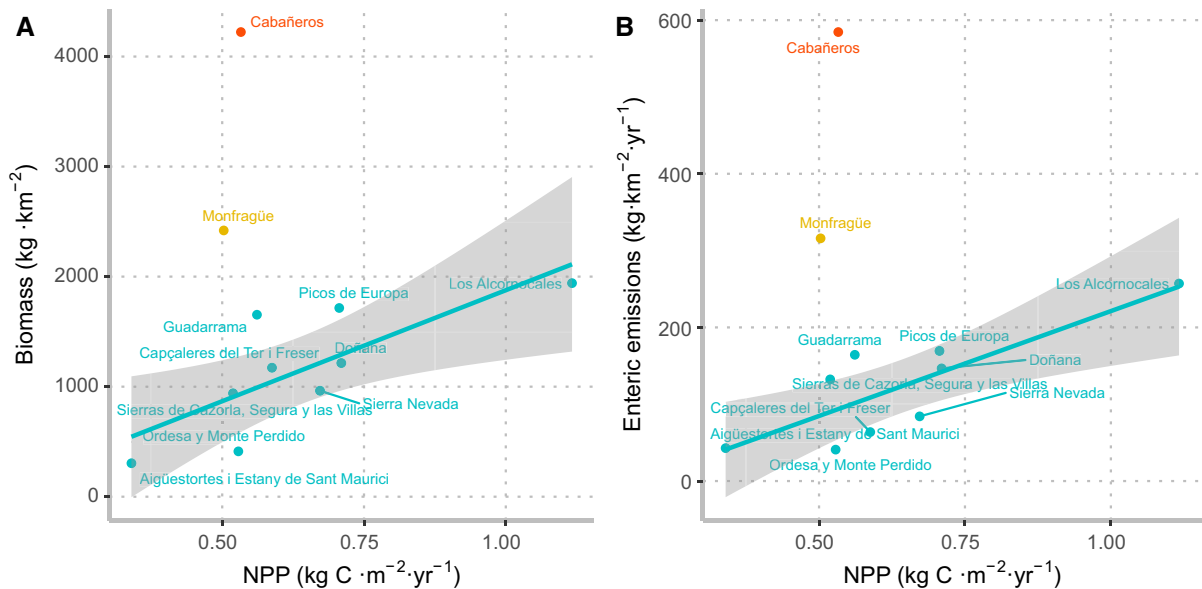
Contrary to the rest of the PAs, Monfragüe has practically no livestock grazing inside its limits, so competition for forage with domestic ungulates is negligible. Cabañeros does not host livestock grazing either, and allows for seasonal migration of wild herbivores, accommodating higher herbivory levels. This is made possible by two marked, distinct landscape units conformed by (i) an extensive flat valley at an altitude of between 600 and 700 m.a.s.l. dominated by grassy vegetation, which constitutes an optimal forage base in winter but dries up in summer, and (ii) a steeper, shrubby area ranging from 700 to 1400 m.a.s.l. that provides suboptimal foraging resources during summer time (ESA 2022). Differential ecological conditions are hence important in Monfragüe and Cabañeros when contextualizing herbivory at the national level. When these two cases are excluded, a significant relation was found between NPP and biomass ( $R^2 = 0.523$ ;  $p = 0.017$ ; Fig. 2A), similar to the relation between NPP and enteric CH<sub>4</sub> ( $R^2 = 0.619$ ,  $p = 0.007$ ; Fig. 2B).

### Comparison of NPP-herbivore biomass density in PAs with previous studies

We compared our empirical data with the theoretical model by Zhu et al. (2018), and the empirical model by Rodríguez et al. (2014) applied to the PAs that climatically fitted in its range of conditions (Fig. 3). The resulting regression line from Rodríguez et al. (2014) was: Biomass (kg/km<sup>2</sup>) = 8957.92 · NPP – 33.82 (kg C/km<sup>2</sup>);  $p = 0.04261$ ;  $R^2 = 0.8749$ ). Both equations highly overlap, but contrast with

**Table 2** Biomass, enteric CH<sub>4</sub> and NPP in selected Spanish PAs

| Protected Area                          | Biomass (kg/km <sup>2</sup> ) | Enteric CH <sub>4</sub> (kg/km <sup>2</sup> ·yr) | NPP (kg C/m <sup>2</sup> ·yr) |
|---|-------------------------------|--|-------------------------------|
| Aigüestortes i Estany de Sant Maurici   | 304.2                         | 47.0   | 0.340                         |
| Cabañeros                               | 4222.6                        | 615.6  | 0.533                         |
| Capçaleres del Ter i Freser             | 1172.2                        | 267.4  | 0.588                         |
| Doñana                                  | 1214.5                        | 143.2  | 0.710                         |
| Guadarrama                              | 1653.8                        | 142.4  | 0.561                         |
| Los Alcornocales                        | 1940.8                        | 266.4  | 1.117                         |
| Monfragüe                               | 2419.6                        | 321.8  | 0.503                         |
| Ordesa y Monte Perdido                  | 412.1                         | 36.0   | 0.528                         |
| Picos de Europa                         | 1715.1                        | 142.7  | 0.706                         |
| Sierra Nevada                           | 963.2                         | 63.6   | 0.672                         |
| Sierras de Cazorla, Segura y Las Villas | 939.7                         | 142.8  | 0.519                         |



**Fig. 2** Relationship between NPP and herbivory in different PAs, measured in terms of biomass and enteric CH<sub>4</sub>. Cabañeros and Monfragüe are considered as outliers. Equations are: Biomass = 2017.22 · NPP—140.8; and Enteric emis-

sions = 273.07 · NPP—51.83, respectively. Standard error of the estimates and correlation indexes were, respectively, 390 and 0.523 for Biomass and 44.0 and 0.620 for Enteric emissions

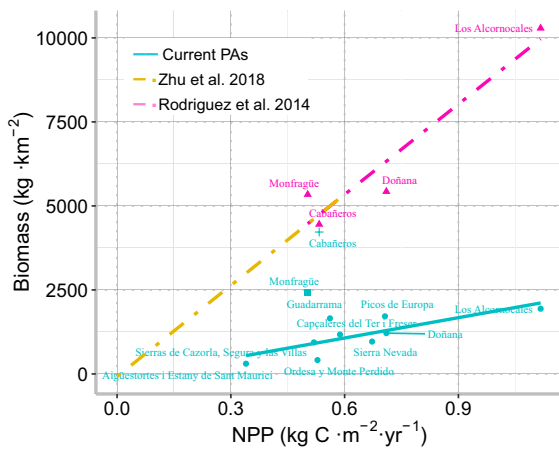
a current low wild herbivory biomass from most Spanish PAs. However, current wild herbivory in Cabañeros—4222 kg/km<sup>2</sup>—is very close to densities expected from Zhu et al. (2018) (4740 kg/km<sup>2</sup>) and Rodriguez et al. 2014 (4451 kg/km<sup>2</sup>). The rest of PAs, such as Monfragüe, Doñana or Los Alcornocales, display current wild herbivore densities that are well below such estimations. These latter values are closer to further Pleistocene baselines reported for Open Ecosystems worldwide, which are at the range of 10 t/km<sup>2</sup> (Manzano et al. 2023a). In light of these results, the ecological conditions of Cabañeros could be the best available wild baseline in Spain, thanks to a lack of competition with pastoralism, and to the possibilities for herbivore migration that its biophysical configuration offers. This would mean that current densities in most PAs are around 80% lower than natural baselines, close to estimations of Pedersen et al. (2023), suggesting that the current vegetation consumption rate in Spain is between 50 and 75% lower than the baseline. Such reductions are observed in most regions worldwide due to anthropic factors, with a diverse casuistic that prevents a thorough relation between NPP and herbivore biomass. However, the capacity

to sustain larger herbivory baselines all across Europe is proven by many rewilding experiments hosting herbivore biomasses close to African and Asian sites, suggesting that actual baselines are some orders of magnitude above currently observed densities in PAs (Fløjgaard et al. 2022) (Fig. 4).

#### Scaling up wild herbivore biomass and enteric emissions to grazeable areas in Spain

According to the both approaches previously presented, wild herbivore biomass in grazeable Spanish areas would be  $1.68 \times 10^8$  kg under current conditions and  $8.33 \times 10^8$  kg under baseline conditions. This means that, under natural conditions such as seasonal migration and lack of competition with livestock, wild herbivores could be almost 5 times more abundant. Baseline equation for enteric emissions was  $1313 \cdot \text{NPP} - 234.6$ . Thus, when relating NPP with enteric CH<sub>4</sub>, the total values for Spain result in  $1.78 \times 10^7$  kg /yr and  $8.79 \times 10^7$  kg/yr, respectively.





**Fig. 3** Potential ungulate biomass in current grazable Open Ecosystems in Spain under different approaches. Blue: Potential biomass according to the ecological functioning in most Current PAs excluding Monfragüe and Cabañeros, which were considered outliers. Yellow: Baseline densities based on the theoretical model from Zhu et al. (2018), using data from African, Asia and North American PAs, built with NPPs between 0 and 0.6 kgC/m<sup>2</sup>/yr. Pink: carrying capacities applying the empirical model from Rodríguez et al. (2014) to Spanish PAs that fit into its temperature and precipitation range. The equation derives from the linear regression of those carrying capacities (Cabañeros, Monfragüe, Doñana and Los Alcornocales). Equation for this model was: Biomass (kg) = 8957.92 · NPP – 33.82 (kgC/m<sup>2</sup>/yr); p = 0.04261; R<sup>2</sup> = 0.8749. Note that the equations from Zhu et al. (2018) and Rodríguez et al. (2014) almost overlap

Proportion of herbivore baseline currently taken up by grazing livestock

According to our estimates (see Supplementary Information), Spanish grazing livestock system currently accounts for a biomass of  $2.34 \times 10^9$  kg, producing  $3.87 \times 10^8$  kg CH<sub>4</sub>/yr (387 kt CH<sub>4</sub>/yr) (Fig. 5). In terms of enteric CH<sub>4</sub> emissions, this represents about 54% of the total enteric emissions reported by Spain (MAPA 2023), i.e. implying that the rest, i.e., about 46%, would be allocated to confined livestock. Within grazing livestock systems, cattle accounted for most of the biomass and CH<sub>4</sub> emissions (68 and 70%, respectively), followed by sheep (27 and 26%, respectively), goats (3 and 3%, respectively), and Iberian pigs (3 and 0.3%, respectively). Estimations on wild herbivory compared to grazing livestock are shown at Fig. 5, comparing the two approaches. In the baseline scenario, natural CH<sub>4</sub> emissions in current grazable

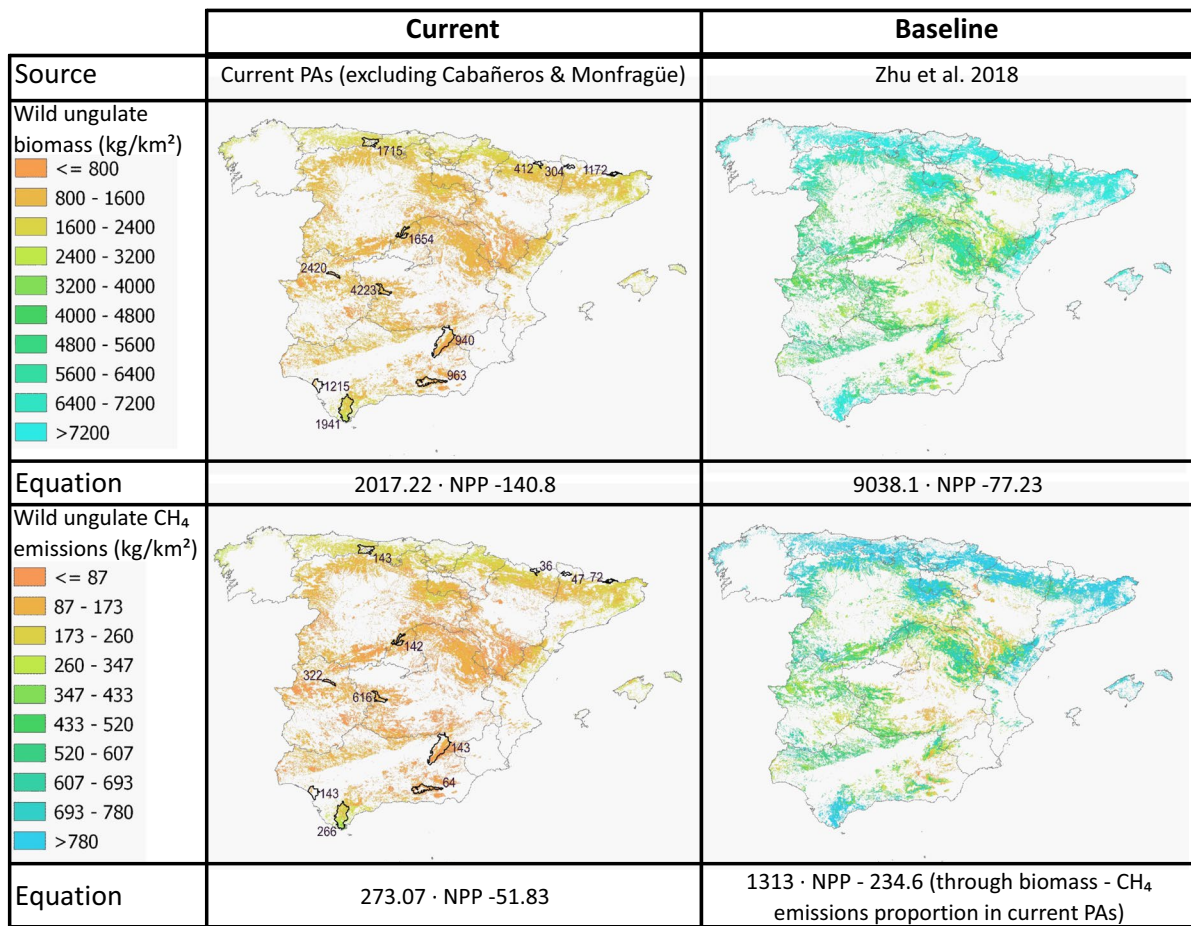
areas represent more than 20% of the current Spanish grazing livestock emissions.

Discussion

Current status of Spanish wild Open Ecosystems

In this study, we have related NPP and ungulate abundances in PAs in Spain under two different ecological scenarios with the aim to establish natural herbivory baselines. Because of alternative closed-canopy vs. tree-sparse states of Open Ecosystems that do not depend on climatic parameters (Moncrieff et al. 2016; Pausas and Bond 2019) and that condition forage resources, there are many limitations for estimating herbivory baselines. Moreover, due to coevolution, such herbivore abundance has been subjected to constant change through climate fluctuations and through human presence (Álvarez-Lao and García 2011; Rodríguez et al. 2014; Palmqvist et al. 2022). Unsurprisingly, the literature reports difficulties to estimate such baselines at a large scale in highly anthropized countries (Fløjgaard et al. 2022). We have found that such relations can be improved by contextualizing individual sampling points (in this case, PAs) by key ecological conditions that affect wild herbivores, namely competition with domestic livestock, and capacity to migrate between feeding areas that offer differential rangeland resources.

We confirm that current herbivore abundances in anthropized areas are far from the baselines (Fløjgaard et al. 2022; Pedersen et al. 2023) represented by the equation provided by Zhu et al. (2018) and represented in Spain only by Cabañeros PA, with conditions enabling seasonal migration and precluding competition with livestock. Monfragüe PA also shows intermediate abundances; without pastoralism it is also closer to the baseline, but it lacks migration options in the surrounding areas. Even if rural abandonment is making many landscapes optimal for the extant wild species (Acevedo et al. 2011), this is not translated into the recovery of baseline levels. Anthropic determinants reduce the possibility of survival and proliferation (Fløjgaard et al. 2022). For example, in the Mediterranean coast of Spain, ungulates have gone almost extinct due to strong anthropization in the last couple of centuries (Pauné 2021). In *Quercus*-dominated PAs, theoretically susceptible



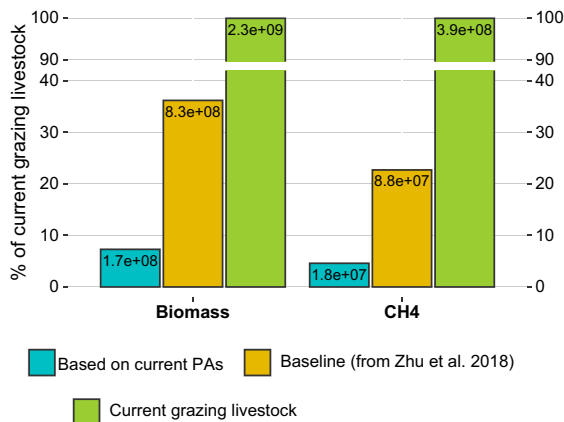
**Fig. 4** Potential wild herbivory biomass and derived CH<sub>4</sub> emissions, under approaches based on current abundances in PAs compared to theoretical baselines (through the equation of

Zhu et al. 2018). Current wild ungulate emissions (kg/km<sup>2</sup>) in PAs are also represented

to wild herbivory, like Sant Llorenç, Garraf or Ports de Tortosa y Beseit, current calculated densities are well below the baseline, yielding values below 800 kg/km<sup>2</sup>, and are consistent with mixed *Quercus* and *Pinus* vegetation at Montgrí and Montserrat PAs (Pauné 2021), even though pastoralism has almost disappeared. This is in line with densities from low productive PAs in altitudes over 1000 m.a.s.l. such as Ordesa y Monte Perdido, or Aigüestortes i Estany de Sant Maurici. It happens in spite of the high local plant productivity (Running and Zhao 2021), with a baseline above 5000 kg/km<sup>2</sup> in all of them.

Our results support the idea that wild herbivory in Spain could be much higher than current levels. Land fragmentation and the impossibility of migratory dynamics are important drivers for this (Coffin

et al. 2021; Johnson et al. 2023). In the Spanish plateaus and mountain ranges (occupying most areas of the country), migrations are particularly necessary, because they are greatly affected by seasonally extreme climatic conditions (dry and cold) that limit plant growth (Garzón 1992; Manzano-Baena and Casas 2010; San Miguel et al. 2017). Hence, carrying capacities are significantly higher where migrations are possible (Rodríguez et al. 2014; Fløjgaard et al. 2022; Manzano et al. 2023a; Pedersen et al. 2023), similar to what we here describe for Cabañeros National Park. In Spain, a great carrying capacity was observed during periods of high livestock migratory systems, like *trashumancia* (long distance) and *transterminancia* (short-distance, i.e., < 100 km). A census from 1750 (García Sanz 1994; San Miguel



**Fig. 5** Amount of current grazing livestock in Spain represented by the two different approaches, in terms of biomass and enteric emissions. Absolute values are labelled on the bars. Units for the absolute values are: kg for biomass and kg/yr for enteric emissions

et al. 2017) shows grazing livestock biomass of  $10.7 \cdot 10^3$  kg/km<sup>2</sup>, a number closer to Pleistocenic abundances than to current ones (Manzano et al. 2023a). Such migration patterns following productive opportunities are logical in wild systems too (Garzón 1992; Nandintsetseg et al. 2019) but anthropogenic influence greatly reduces daily animal mobility (Tucker et al. 2018). Currently, the impossibility to migrate is a challenge for the survival of most ungulate populations in the Mediterranean, a hazard exacerbated by climate change (Pérez-Barbería et al. 2020). Yet, migration patterns are very susceptible to other external agents, such as to supplementary feeding, which is often found in PAs with conservationist aims, as well as in many hunting estates for economic exploitation reasons (Laguna et al. 2021). The fragility of migration in anthropized landscapes, following a global crisis for such phenomena (Berger 2004), is therefore evident, as difficulties for self-regulation through ecological dynamics arise.

A paradox for overgrazed landscapes below baseline levels

Even if Cabañeros hosts densities that are below the theoretical carrying capacity described by Rodríguez et al. 2014 or Zhu et al. 2018, ungulate impacts there are reported to be dangerous for ecological conservation (López-Sáez et al. 2014; Perea

et al. 2014, 2015; Carpio et al. 2021). Such negative effects on vegetation have been attributed to an herbivore overabundance linked to low densities of carnivores, who would not exert enough top-down regulation (Bueno et al. 2009; Perea et al. 2014). While such pressure can be relevant, it may not be a primary regulator when naturally diverse herbivory guilds—that include large ungulates—manage to escape predation through migration (Fryxell & Sinclair 1988; Mduma et al. 1999; Sinclair et al. 2003; Creel et al. 2005; Nelson et al. 2012; Clark and Hebblewhite 2021). In a natural baseline scenario, the role of predator–prey dynamics as a primary determinant of potential herbivore biomass is unclear, even if it does impact elements such as grazing patterns and therefore, vegetation structure—mainly through landscapes of fear (Donadio and Buskirk 2016; Kuijper et al. 2013; Tizzani et al. 2022).

If the potential carrying capacity of Cabañeros is considered, there may be underlying causes for the observed symptoms attributed to overgrazing. Apart from overall excessive vegetation removal, they can derive from unbalanced grazing regimes, with crucial factors such as grazing selectivity, driven by consumption patterns (Augustine and McNaughton 1998; Fernández-Olalla et al. 2016; Velamazán et al. 2023) and grazing seasonality, driven by migration patterns (Abraham et al. 2022; Velamazán et al. 2023) (Table 3). Grazing selectivity is balanced in natural Open Ecosystems, with grazers, browsers or intermediate feeders (Hofmann 1989) preventing overgrazing of certain plant tissues. An excess of browser biomass can lead to problems for tree renewal through the removal of shrubby shelter structures and saplings (Fernández-Olalla et al. 2016). Conversely, grazer excess and grass removal can favour landscape closure (Kiffner and Lee 2019), leading to plant biomass accumulation that boosts other top-down regulators such as fire (Madrigal et al. 2017; Varela et al. 2020). Grazing seasonality is relevant in Spain and the Mediterranean biome in general, with contrasting production peaks that need herbivore migrations to be sustainably harvested (Garzón 1992; Manzano-Baena & Casas 2010; San Miguel et al. 2017). As discussed above, effects attributed to overgrazing can also arise from disrupted migration patterns.

In Spain, the nature of both grazing selectivity and grazing seasonality merge with a long history of

**Table 3** Summary of the different approaches for ungulate baselines in Spain. Pleistocenic and Ungulate biomass in Pleistocenic and Holocenic baselines should be similar, in case livestock is included as part of the baseline

|                       | Grazing selectivity  | Grazing seasonality  |
|-----------------------|--|--|
| Pleistocenic baseline | Diverse herbivory guilds: grazers, browsers and intermediate feeders | Diverse migratory guilds. Following production peaks<br>Predator influence through “landscapes of fear”                      |
| Holocenic baseline    | Extinction of wild grazing ungulates, replaced by livestock          | Migrations conducted by pastoralists following production peaks  |
| Based on current PAs  | Abandonment of grazing livestock<br>Unbalance: Browsers > > grazers  | Obstacles to migration, absence of migratory wild species and predators<br>Simultaneous overgrazing and undergrazing effects |

anthropic influence. Spanish wild herbivores belonging to the grazer functional type (aurochs or tarpans) went extinct as livestock expanded, so extant wild ungulates are rather browser or intermediate feeders, such as cervids. Grazers are only represented by livestock, with cattle, horse and sheep standing out (Hofmann 1989; Fernández-Olalla et al. 2016). With the ongoing rangeland abandonment process (Lasanta et al. 2017), wild browser expansion has been the dominant trend in the last decades in Spain (San Miguel et al. 2017; Valente et al. 2020). Browsers may thus be becoming overabundant while grazers are dwindling, leading to a selective predation on woody vegetation without depleting available forage (Perea et al. 2014; Fernández-Olalla et al. 2016). Grazing seasonality is also affected by herbivore guilds, as grazers tend to migrate longer distances than browsers (Teitelbaum et al. 2015; Abraham et al. 2022), driving current systems dominated by extant ungulates to have reduced mobility. Seasonal grazing patterns are also promoted by predation on wild herbivores (Fryxell and Sinclair 1988; Grigg 2007; Nelson et al. 2012), or shepherds, in the case of domestic herbivores (Manzano et al. 2020). All these characteristics are currently missing in Cabañeros and many other Spanish areas where land connectivity, predators and domestic herbivores have mostly disappeared from the landscape.

In Cabañeros, there has been an important shift in grazing patterns after it was made a protected area, from the previous livestock grazing (traditionally migratory) and anthropic land use for millennia (Morales-Molino et al. 2018). The exclusion of livestock in Cabañeros meant an important shift in selectivity and seasonality, with the loss of the exclusive grazing function and of long-distance migration. Present ungulates here are mainly red deers (*Cervus*

*elaphus*), i.e., intermediate feeders (Hofmann et al. 1989) that perform medium-distance migrations (Jarnemo 2008; Bischof et al. 2012; Nelson et al. 2012). This implies a context of high selectivity and medium seasonality context. Ecological imbalances are therefore likely to happen, similar to what happened in other past ungulate extinctions (Davoli et al. 2023) or in similar contexts of low-density browser-dominated PAs such as Guadarrama with *Capra pyrenaica* (Perea et al. 2015). A conclusion is that the function of preserving Open Ecosystems is left to grazing livestock (Fernández-Olalla et al. 2016; Lasanta et al. 2021). Correct herbivore baseline and carrying capacity estimations should therefore consider not only total biomass, but also the ecological functionality and the feasibility of reaching an equilibrium with the present herbivore species.

Including baselines in environmental assessments of grazing livestock

Herbivory, as a necessary ecological component, is often overlooked in environmental assessments and in decision-making (Veldman et al. 2015; Thompson et al. 2023). According to our results, a substantial fraction of environmental effects attributed to grazing livestock could be indeed part of the herbivory ecological baseline. A significant part of the herbivore biomass, as well as the enteric anthropogenic CH<sub>4</sub> emissions currently attributed to grazing livestock (36.2% and 22.72%, respectively), are part of the herbivory baseline. This is not negligible, considering that it represents about 13% of enteric CH<sub>4</sub> emissions reported in the Spanish GHG inventories. This means that these emissions should not be considered part of anthropogenic emissions since they would be unavoidable under ideal, correct

ecosystem functioning conditions. Importantly, these calculations are subject to large uncertainties and therefore, careful consideration must be taken, but they provide a first value estimate to a process whose quantification is currently completely missing.

An herbivory baseline implies that enteric herbivore emissions have been part of the natural fluxes in the past and have a degree of inevitability in the future, because such emissions are consubstantial to the grazing ecological niche that dominates Open Ecosystems (Manzano and White 2019). Considering a significant fraction of current herbivory as a natural process, as done in the present study, as in Pardo et al. (2023), contrasts from the conventional approach of most studies. All livestock herbivory is usually considered as purely anthropic, and so are all enteric emissions caused (e.g. Opio et al. (2013)). Studies quantifying emissions from wildlife, or taking place in abandoned grazeable landscapes, consider them a natural ecosystem flow disentangled from livestock production, or from any emissions currently considered as anthropogenic (Fiala et al. 2020; Hayek et al. 2021). This conventional approach has been possibly reached because of practical reasons. For example, the guidelines of IPCC for national GHG inventories since its first publications (IPCC 1996) consider natural emissions on managed land as anthropogenic on the basis that they are equal to those emissions on unmanaged land, which are assumed negligible—but this is something that our study puts into question. IPCC also excludes emissions from natural sources in national inventories. Semi-natural rangelands, however, are difficult to interpret. If human activity was not present in them, emissions would not be zero. There is evidence for wild ecosystem scenarios hosting very significant CH<sub>4</sub> emissions (Hristov 2012; Smith et al. 2015; Manzano et al. 2023c). In summary, it is doubtful that all CH<sub>4</sub> emissions from semi-natural rangelands can be catalogued as anthropogenic (Manzano et al. 2023b). At this point, herbivory baselines, i.e. potential ecosystem effects from wild herbivory, must be calculated to evaluate strategies that aim to reduce either global warming, biodiversity loss or other land-use-associated impacts (Manzano and White 2019; Scoones 2022).

### Challenges for estimating herbivore baselines

Our results are constrained by a significant degree of uncertainty, and there is still room to refine methodologies—e.g. for measuring wild ungulate abundance on the field. In addition, fluctuations across time are very common (Carpio Camargo et al. 2021) and animal abundances are very susceptible to disturbances, such as diseases (San Miguel et al. 2017). There are also challenges to accurately estimate grazing livestock biomass in Spain, due to the complexity of different management systems at inter-, but also at intra-farm level. Most grazing-based management combines pastoralism with supplementary feeding or the use of stubble or fallow lands, especially during scarcity periods. In addition, much of the grazing livestock included in the calculus is placed in ecosystem areas belonging to natural closed canopy forest, following Bond et al. (2005). Grazing livestock estimations may thus probably be overestimated, showing a smaller proportion of the baseline in relation to the total grazing biomass.

There are also ecological limitations to correctly envision natural herbivory baseline conditions in Spanish Open Ecosystems. Grazers are only represented by livestock in Spain (Hofmann 1989), so empirical Holocene baselines can just be simulated by (1) rewilding with wild ungulates, but also including new grazers (Cromsigt et al. 2018); (2) considering grazing livestock as part of the baselines. The absence of such empirical situations can lead to a distorted conception of baseline ecological implications. For example, current CH<sub>4</sub> emissions are proportionally lower than biomass when compared to current grazing livestock. This is possibly due to an underestimation of CH<sub>4</sub> emissions in current PAs as a consequence of the absence of wild grazer herbivores. Higher body sizes lead to higher CH<sub>4</sub> emission rates in grazers (Pérez-Barbería et al. 2017; Clauss et al. 2020), while grazers' diets, richer in fibre, would cause larger ingestion rates and a higher CH<sub>4</sub> emission per animal (Hofmann 1989; Hristov et al. 2013). Considering more grazers in the baseline could hence increase the estimations on CH<sub>4</sub> emissions.



## Conclusion

NPP is a predictor of ungulate abundance in Open Ecosystems which share similar ecological functioning. Removing constraints such as obstacles to migration, or competition from pastoralism, from current PAs could lead to a five-fold increase in wild ungulate biomass in the open ecosystems in current grazable areas in Spain. However, Spain is a country with a pastoral tradition that has replaced wild grazers to the point of extinction, and the browser expansion due to land abandonment could lead to a situation of browser overabundance in wild systems. We conclude that wild herbivory baselines must incorporate an important proportion of grazers, nowadays only represented by livestock. According to our estimations, wild herbivory baselines are at the order of 36.2% of the domestic grazing biomass, and 22.7% of their enteric GHG emissions, but these numbers are probably underestimated due to current ecological and methodological constraints.

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**Data availability** The data generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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## References

- Abraham JO, Upham NS, Damian-Serrano A, Jesmer BR (2022) Evolutionary causes and consequences of ungulate migration. *Nat Ecol Evol* 6(7):998–1006
- Acevedo P, Farfán MÁ, Márquez AL et al (2011) Past, present and future of wild ungulates in relation to changes in land use. *Landsc Ecol* 26:19–31
- Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. *J Biogeogr* 39:1383–1390
- Adie H, Lawes MJ (2023) Solutions to fire and shade: resprouting, growing tall and the origin of Eurasian temperate broadleaved forest. *Biol Rev* 98:643–661
- Álvarez-Lao DJ, García N (2011) Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula. *Quatern Int* 233:159–170
- Arcese P, Sinclair ARE (1997) The role of protected areas as ecological baselines. *J Wildl Manag* 61:587
- Archibald S, Bond WJ, Hoffmann W et al (2019) Distribution and determinants of savannas. In: Scogings PF, Sankaran M (eds) *Savanna woody plants and large herbivores*. Wiley, Hoboken, pp 1–24
- Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J Wildl Manage* 62:1165
- Berger J (2004) The last mile: how to sustain long-distance migration in mammals. *Conserv Biol*. <https://doi.org/10.1111/j.1523-1739.2004.00548.x>
- Bischof R, Loe LE, Meisingset EL et al (2012) A Migratory Northern Ungulate in the pursuit of spring: jumping or surfing the green wave? *Am Nat* 180:407–424
- BOE (2021) Ley 9/2021, de 1 de julio, de declaración del Parque Nacional de la Sierra de las Nieves. *Boletín Oficial Del Estado* 157:78572–78635
- BOJA (2012) Orden de 27 de julio de 2012, por la que se aprueba el Plan del Área Cinegética Alcornocales de Andalucía 2012–2022. *Boletín Oficial de la Junta de Andalucía* 156:56–57

- BOJA (2017) Decreto 191/2017, de 28 de noviembre, por el que se declara la zona especial de conservación Sierras de Cazorla, Segura y Las Villas (ES0000035) y se aprueban el Plan de Ordenación de los Recursos Naturales y el Plan Rector de Uso y Gestión del Parque Natural Sierras de Cazorla, Segura y Las Villas. Boletín Oficial De La Junta De Andalucía 246:19–356
- Bond WJ (2005) Large parts of the world are brown or black: a different view on the ‘Green World’ hypothesis. *J Veg Sci* 16:261–266
- Bond WJ (2019) *Open ecosystems*. Oxford University Press, Oxford
- Bueno CG, Alados CL, Gómez-García D et al (2009) Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. *J Zool* 279:195–202
- Carpio AJ, Apollonio M, Acevedo P (2021) Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. *Mamm Rev* 51:95–108
- Carpio Camargo AJ, Barasona J, Acevedo P et al (2021) Assessing red deer hunting management in the Iberian Peninsula: the importance of longitudinal studies. *PeerJ* 9:e10872
- Cátedra de Parques Nacionales (2019) *Gestión de ungulados silvestres en parques nacionales*. Universidad Politécnica de Madrid, Valsain, Segovia
- Clark TJ, Hebblewhite M (2021) Predator control may not increase ungulate populations in the future: a formal meta-analysis. *J Appl Ecol* 58:812–824
- Clauss M, Dittmann MT, Vendl C et al (2020) Review: comparative methane production in mammalian herbivores. *Animal* 14:s113–s123
- Coe MJ, Cumming DH, Phillipson J (1976) Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341–354
- Coffin A, Ouren D, Bettez N, et al (2021) *The Ecology of Rural Roads: Effects, Management, and Research*. Issues in Ecology. Report No. 23
- Corson MS, Mondière A, Morel L, van der Werf HMG (2022) Beyond agroecology: agricultural rewilding, a prospect for livestock systems. *Agric Syst* 199:103410
- Creel S, Winnie J, Maxwell B et al (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397
- Cromsigt JPGM, Kemp YJM, Rodríguez E, Kivitt H (2018) Rewilding Europe’s large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? *Restor Ecol* 26:891–899
- Curran MA (2014) Strengths and limitations of life cycle assessment. Background and future prospects in life cycle assessment. Springer, Dordrecht, pp 189–206
- Davoli M, Monsarrat S, Pedersen R et al (2023) Megafauna diversity and functional declines in Europe from the Last Interglacial (LIG) to the present. *bioRxiv*. <https://doi.org/10.1101/2023.06.12.544580>
- Díaz Gaona C, Rodríguez Estévez V, Sánchez Rodríguez M et al (2014) Estudio de los pastos en Andalucía y Castilla-la Mancha y su aprovechamiento racional con ganado ecológico. Asociación Valor Ecológico-Ecológica, Sevilla
- Donadio E, Buskirk SW (2016) Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *J Mammal* 97:966–977
- Ellis EC, Beusen AHW, Goldewijk KK (2020) Anthropogenic biomes: 10,000 BCE to 2015 CE. *Land (basel)* 9:129
- ESA (2022) Copernicus DEM - Global and European Digital Elevation Model (COP-DEM)
- European Union (2018) CORINE Land Cover 2018 (CLC2018). European Environment Agency (EEA). <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018> Accessed: 25 Nov 2022
- Fernández-Olalla M, Martínez-Jauregui M, Perea R et al (2016) Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. *J Arid Env* 129:9–15
- Fiala M, Marveggio D, Viganò R et al (2020) LCA and wild animals: results from wild deer culled in a northern Italy hunting district. *J Clean Prod* 244:118667
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315
- Fløjgaard C, Pedersen PBM, Sandom CJ et al (2022) Exploring a natural baseline for large-herbivore biomass in ecological restoration. *J Appl Ecol* 59:18–24
- Fraanje W, Garnett T (2022) *Rewilding and its implications for agriculture*. University of Oxford, Oxford
- Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. *Trends Ecol Evol* 3:237–241
- García Sanz A (1994) La ganadería española entre 1750 y 1865: los efectos de la reforma agraria liberal. *Agric Soc* 72:81
- Garzón J (1992) La trashumancia como reliquia del paleolítico. In: *Trashumancia y Cultura Pastoril en Extremadura*. Asamblea de Extremadura, Sevilla
- Gavrilova O, Leip A, Dong H, et al (2019) Emissions from livestock and manure management. In: Calvo Buendía E, Tanabe K, Kranjc A, et al. (eds) 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories 4. Agriculture, forestry and other land use, 10. IPCC, Geneva, pp 10.1–10.209
- Gerber P, Vellinga T, Opio C, Steinfeld H (2011) Productivity gains and greenhouse gas emissions intensity in dairy systems. *Livest Sci* 139:100–108
- Gerber PJ, Steinfeld H, Henderson B et al (2013) Tackling climate change through livestock - a global assessment of emissions and mitigation opportunities. Food and Agriculture Organization of the United Nations, Rome
- Grigg JL (2007) Gradients of predation risk affect distribution and migration of a large herbivore. *Montana State University, Bozeman*
- Hayek MN, Harwatt H, Ripple WJ, Mueller ND (2021) The carbon opportunity cost of animal-sourced food production on land. *Nat Sustain* 4:21–24
- Hempson GP, Archibald S, Bond WJ (2017) The consequences of replacing wildlife with livestock in Africa. *Sci Rep* 7:17196
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a

- comparative view of their digestive system. *Oecologia* 78:443–457
- Hristov AN (2012) Historic, pre-European settlement, and present-day contribution of wild ruminants to enteric methane emissions in the United States. *J Anim Sci* 90:1371–1375
- Hristov AN, Oh J, Firkins JL et al (2013) Mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options. *J Anim Sci* 91:5045–5069
- IPCC (1996) Revised 1996 IPCC Guidelines for National Greenhouse Gas Inventories. IPCC/OECD/IEA, UK Meteorological Office, Bracknell, UK
- Jarnemo A (2008) Seasonal migration of male red deer (*Cervus elaphus*) in southern Sweden and consequences for management. *Eur J Wildl Res* 54:327–333
- Jenkins RE, Brian Bedford W (1973) The use of natural areas to establish environmental baselines. *Biol Conserv* 5:168–174
- Johnsen KI, Niamir-Fuller M, Bensada A, Waters-Bayer A (2019) A case of benign neglect: Knowledge gaps about sustainability in pastoralism and rangelands. United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal
- Johnson TF, Isaac NJB, Paviolo A, González-Suárez M (2023) Socioeconomic factors predict population changes of large carnivores better than climate change or habitat loss. *Nat Commun* 14:74
- Jones KE, Bielby J, Cardillo M et al (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648–2648
- Karp AT, Faith JT, Marlon JR, Staver AC (2021) Global response of fire activity to late quaternary grazer extinctions. *Science* (1979) 374:1145–1148
- Kiffner C, Lee DE (2019) Population dynamics of browsing and grazing ungulates in the anthropocene. In: Gordon I, Prins H (eds) *The ecology of browsing and grazing II*. Ecological studies. Springer, Cham, pp 155–179
- Kim DG, Giltrap D, Hernandez-Ramirez G (2013) Background nitrous oxide emissions in agricultural and natural lands: a meta-analysis. *Plant Soil* 373:17–30
- Kuijper DPJ, de Kleine C, Churski M et al (2013) Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* 36:1263–1275
- Laguna E, Carpio AJ, Vicente J et al (2021) The spatial ecology of red deer under different land use and management scenarios: protected areas, mixed farms and fenced hunting estates. *Sci Total Environ* 786:147124
- Lasanta T, Arnáez J, Pascual N et al (2017) Space–time process and drivers of land abandonment in Europe. *Catena* (amst) 149:810–823
- Lasanta T, Nadal-Romero E, Khorchani M, Romero-Díaz A (2021) A review of abandoned lands in Spain: from local landscapes to global management strategies. *Cuadernos De Investigación Geográfica* 47:477–521
- Launchbaugh K, Strand E (2021) Rangelands of the World. In: Information & Education (I&E); Remote Sensing & GIS committees of the Society for Range Management (SRM). [https://www.webpages.uidaho.edu/what-is-range/rangelands\\_map.htm](https://www.webpages.uidaho.edu/what-is-range/rangelands_map.htm). Accessed 25 Nov 2022
- López-Sáez JA, García-Río R, Alba-Sánchez F et al (2014) Peatlands in the Toledo Mountains (central Spain): characterisation and conservation status. *Mires Peat* 15:1–23
- Madrigal J, Fernández-Migueláñez I, Hernando C et al (2017) Does forest biomass harvesting for energy reduce fire hazard in the Mediterranean basin? a case study in the Caroig Massif (Eastern Spain). *Eur J for Res* 136:13–26
- Malhi Y, Lander T, le Roux E et al (2022) The role of large wild animals in climate change mitigation and adaptation. *Curr Biol* 32:R181–R196
- Manzano P, White SR (2019) Intensifying pastoralism may not reduce greenhouse gas emissions: wildlife-dominated landscape scenarios as a baseline in life-cycle analysis. *Clim Res* 77:91–97
- Manzano P, Galvin KA, Cabeza M (2020) A global characterization of pastoral mobility types. *Open Anthropol Res Repos*. <https://doi.org/10.1002/oarr.10000335.1>
- Manzano P, Burgas D, Cadahía L et al (2021) Toward a holistic understanding of pastoralism. *One Earth* 4:651–665
- Manzano P, Pardo G, Itani MA, del Prado A (2023a) Under-rated past herbivore densities could lead to misoriented sustainability policies. *Npj Biodivers* 2:2
- Manzano P, Rowntree J, Thompson L et al (2023b) Challenges for the balanced attribution of livestock environmental impacts: the art of conveying simple messages about complex realities. *Anim Front* 13:35–44
- Manzano P, Pardo G, del Prado A (2023c) Comparable GHG emissions from animals in wildlife and livestock-dominated savannas. *Npj Clim Atmos Sci* 6:27
- Manzano-Baena P, Casas R (2010) Past, present and future of Trashumancia in Spain: nomadism in a developed country. *Pastoralism* 1:72–90
- MAPA (2023) Balance de nitrógeno e inventario de emisiones de gases. In: Guías para el cálculo del balance alimentario de nitrógeno y fósforo. <https://www.mapa.gob.es/es/ganaderia/temas/ganaderia-y-medio-ambiente/balance-de-nitrogeno-e-inventario-de-emisiones-de-gases/default.aspx>. Accessed 31 Jan 2023.
- McAuliffe GA, Takahashi T, Lee MRF (2018) Framework for life cycle assessment of livestock production systems to account for the nutritional quality of final products. *Food Energy Secur* 7:e00143
- Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: a 40-year record. *J Anim Ecol* 68:1101–1122
- Moncrieff GR, Bond WJ, Higgins SI (2016) Revising the biome concept for understanding and predicting global change impacts. *J Biogeogr* 43:863–873
- Morales-Molino C, Colombaroli D, Tinner W, Perea R et al. (2018) Vegetation and fire dynamics during the last 4000 years in the Cabañeros National Park (central Spain). *Rev Palaeobot Palynol* 253:110–122
- MTERD (2020) Mapa Forestal de España (MFE) de máxima actualidad [1:50000]. Ministerio para la Transición Ecológica y Reto Demográfico, Madrid. <https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/mfe50.aspx>. Accessed 25 Nov 2022.

- Nandintsetseg D, Bracis C, Leimgruber P et al (2019) Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates. *Ecosphere* 10:e02924
- Nelson AA, Kauffman MJ, Middleton AD et al (2012) Elk migration patterns and human activity influence wolf habitat use in the greater yellowstone ecosystem. *Ecol Appl* 22:2293–2307
- O'Brien D, Shalloo L, Patton J et al (2012) Evaluation of the effect of accounting method, IPCC v. LCA, on grass-based and confinement dairy systems' greenhouse gas emissions. *Animal* 6:1512–1527
- Opio C, Gerber P, Mottet A et al (2013) Greenhouse gas emissions from ruminant supply chains – a global life cycle assessment. FAO, Rome
- Palmqvist P, Rodríguez-Gómez G, Bermúdez de Castro JM et al (2022) Insights on the early Pleistocene Hominin population of the Guadix-Baza depression (SE Spain) and a review on the ecology of the first peopling of Europe. *Front Ecol Evol* 10:297
- Pardo G, Casas R, del Prado A et al (2023) Carbon footprint of transhumant sheep farms: accounting for natural baseline emissions in Mediterranean systems. *Int J Life Cycle Assess*. <https://doi.org/10.1007/s11367-023-02135-3>
- Pauné, F (2021) Bases ecològiques per a una gestió pastoral (Ecological bases for rangeland management). PhD thesis, Universitat de Lleida, Lleida. <http://hdl.handle.net/10803/673004>
- Pausas JG, Bond WJ (2019) Humboldt and the reinvention of nature. *J Ecol* 107:1031–1037
- Pedersen RØ, Faurby S, Svenning J (2023) Late-Quaternary megafauna extinctions have strongly reduced mammalian vegetation consumption. *Glob Ecol Biogeogr*. <https://doi.org/10.1111/geb.13723>
- Perea R, Girardello M, San Miguel A (2014) Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. *Biodivers Conserv* 23:1303–1318
- Perea R, Perea-García-Calvo R, Díaz-Ambrona CG, San Miguel A (2015) The reintroduction of a flagship ungulate *Capra pyrenaica*: assessing sustainability by surveying woody vegetation. *Biol Conserv* 181:9–17
- Pérez-Barbería FJ (2017) Scaling methane emissions in ruminants and global estimates in wild populations. *Sci Total Environ* 579:1572–1580
- Pérez-Barbería FJ, García AJ, Cappelli J et al (2020) Heat stress reduces growth rate of red deer calf: climate warming implications. *PLoS ONE* 15:e0233809
- Rodríguez J, Blain H-A, Mateos A et al (2014) Ungulate carrying capacity in Pleistocene Mediterranean ecosystems: evidence from the Atapuerca sites. *Palaeogeogr Palaeoclimatol Palaeoecol* 393:122–134
- Running S, Zhao M (2021) MODIS/Terra Net Primary Production Gap-Filled Yearly L4 Global 500m SIN Grid V061. NASA EOSDIS Land Processes DAAC. <https://lpdaac.usgs.gov/products/mod17a3hgv061/>. Accessed: 30 Nov 2022
- San Miguel A, Roig S, Perea R (2017) The pastures of Spain. *Pastos* 46:6–39
- Scoones I (2022) Livestock, methane, and climate change: the politics of global assessments. *Wiley Interdiscip Rev Clim Change*. <https://doi.org/10.1002/wcc.790>
- Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator–prey system. *Nature* 425(6955):288–290
- Smith FA, Elliott SM, Lyons SK (2010) Methane emissions from extinct megafauna. *Nat Geosci* 3:374–375
- Smith FA, Lyons SK, Wagner PJ, Elliott SM (2015) The importance of considering animal body mass in IPCC greenhouse inventories and the underappreciated role of wild herbivores. *Glob Chang Biol* 21:3880–3888
- Smith FA, Hammond JI, Balk MA et al (2016) Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. *Proc Natl Acad Sci USA* 113:874–879
- Teitelbaum CS, Fagan WF, Fleming CH et al (2015) How far to go? Determinants of migration distance in land mammals. *Ecol Lett* 18:545–552
- Thompson L, Rowntree J, Windisch W et al (2023) Ecosystem management using livestock: embracing diversity and respecting ecological principles. *Anim Front* 13:28–34
- Tizzani P, Bessone M, Rossi L, Meneguz PG (2022) Does predation risk affect spatial use in an introduced ungulate species? The case of a Mediterranean mouflon alpine colony. *Eur J Wildl Res* 68:66
- Tucker MA, Böhning-Gaese K, Fagan WF et al (2018) Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science* (1979) 359:466–469
- USGS (2006) Landsat 7 image. <https://landsat-diss.eo.esa.int/socat/LandsatETM>. Accessed 25 Nov 2022
- Valente AM, Acevedo P, Figueiredo AM et al (2020) Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. *Mamm Rev* 50:353–366
- Varela E, Pulido F, Moreno G, Zavala M (2020) Targeted policy proposals for managing spontaneous forest expansion in the Mediterranean. *J Appl Ecol* 57:2373–2380
- Velamazán M, Sánchez-Zapata JA, Moral-Herrero R et al (2023) Contrasting effects of wild and domestic ungulates on fine-scale responses of vegetation to climate and herbivory. *Landscape Ecol*. <https://doi.org/10.1007/s10980-023-01676-0>
- Veldman JW, Buisson E, Durigan G et al (2015) Toward an old-growth concept for grasslands, savannas, and woodlands. *Front Ecol Environ* 13:154–162
- Vera FWM (2000) *Grazing ecology and forest history*. CABI, Wallingford
- Zhu D, Ciais P, Chang J et al (2018) The large mean body size of mammalian herbivores explains the productivity paradox during the last glacial maximum. *Nat Ecol Evol* 2:640–649

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