



Large-Scale Quantification and Correlates of Ungulate Carrion Production in the Anthropocene

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ABSTRACT

Carrion production is one of the most crucial yet neglected and understudied processes in food webs and ecosystems. In this study, we performed a large-scale estimation of the maximum potential production and spatial distribution of ungulate carrion biomass from five major sources in peninsular Spain, both anthropogenic (livestock, big game hunting, roadkills) and natural (predation, natural mortality). Using standardized ungulate carrion biomass (kg/year/100km²) estimates, we evaluated the relationship between ungulate carrion production and two ecosystem-level factors:

global human modification (GHM) and primary productivity (NDVI). We found that anthropogenic carrion sources supplied about 60 times more ungulate carrion biomass than natural sources (mean = 90,172 vs. 1533 kg/year/100km², respectively). Within anthropogenic carrion sources, livestock was by far the major carrion provider (91.1% of the annual production), followed by big game hunting (7.86%) and roadkills (0.05%). Within natural carrion sources, predation of ungulates provided more carrion (0.81%) than natural mortality (0.13%). Likewise, we found that the spatial distribution of carrion differed among carrion sources, with anthropogenic carrion being more aggregated in space than natural carrion. Our models showed that GHM was positively related to carrion production from livestock and roadkills, and that wild ungulate carrion supplied by natural sources and big game hunting was more frequently generated in more productive areas (higher NDVI). These findings indicate a disconnection between the main ungulate carrion source (livestock) and primary productivity. Ongoing socio-economic changes in developed countries (for example in-

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crease of intensive livestock husbandry and rewinding processes) could lead to additional alteration of carrion production processes, with potential negative impacts at the community and ecosystem levels. Overall, we highlight that carrion biomass quantification should be considered a crucial tool in evaluating ecosystem health and delineating efficient ecosystem management guidelines in the Anthropocene.

Key words: big game hunting; carrion biomass quantification; global human modification; livestock; primary productivity; roadkill; terrestrial ecosystems; ungulates.

HIGHLIGHTS

- Anthropogenic ungulate carrion sources exceeded natural carrion production in terrestrial ecosystems
- Overall, anthropogenic carrion depended mainly on human activities, while wild ungulate carrion was linked to ecosystem productivity
- Thus, the supply of the main ungulate carrion sources was largely disconnected from ecosystem processes

INTRODUCTION

Understanding detritus production and energy transfer across food webs has concerned ecologists for decades, as it is necessary to explain ecological complexity (that is, community structure) and ecosystem functioning (Moore and others 2004). Full recognition of the eco-evolutionary and applied implications of decomposition and nutrient cycling among trophic levels within and across ecosystems requires quantifying the fundamental ecological processes involved (Rooney and others 2006; Philippe and others 2012). Nevertheless, major gaps exist in the quantification of detritus biomass. Importantly, most studies to date have focused on estimating dead plant biomass (for example, Shuring and others 2006; Zhou and others 2018; Veen and others 2019; Pausas and Bond 2020 and references therein). Although plants contribute the most to global detritus biomass (Bar-On and others 2018), animal carcasses (that is, carrion) are comparatively higher-quality detritus that exerts disproportionate effects on ecosystem energetics, structure, and function (Swift and others

1979; DeVault and others 2003; Payne and Moore 2006; Wilson and Wolkovich 2011; Beasley and others 2012; Barton and others 2013; Moleón and others 2014). Carrion is rapidly consumed, in both terrestrial and aquatic systems, by a plethora of scavengers and decomposers (DeVault and others 2003; Wilson and Wolkovich 2011; Beasley and others 2012; Barton and others 2013). However, it is precisely this ephemeral nature of carrion that has probably contributed to its historical underestimation in food webs (DeVault and others 2003; Moleón and Sánchez-Zapata 2015), and also complicates its quantification. Therefore, more detailed assessments of carrion biomass and its spatial distribution are needed to model carrion as a distinct detrital pool, and to acknowledge its manifold ecological and anthropogenic ramifications (Benbow and others 2015; Barton and others 2019; Moleón and others 2019).

When quantifying carrion biomass in ecosystems, a distinction should be made between carrion production, which is the focus of this study, and carrion availability, which is the result of how the carrion produced is partitioned among different consumers and the environment (Moleón and others 2020). The quantity and quality of carcasses supplied in a given area and period of time are strongly dependent on factors such as species identity and mortality cause (Selva and others 2005; Moleón and others 2019). Two main sources of carrion can be distinguished depending on whether it comes from natural processes (for example, predation, disease, and senescence) or anthropogenic activities (for example, livestock husbandry, game hunting, and roadkills; Selva and others 2005; Moreno-Opo and Margalida 2019; Moleón and others 2019). In general, naturally produced carrion is supplied more unpredictably (that is, sometimes in the form of “pulses”; Pereira and others 2014; Cortés-Avizanda and others 2009, 2012, 2016), and is of higher quality than carrion from human-caused mortality, which is supplied in a more regular fashion but may contain toxics such as lead bullets (in the case of game species, Arrondo and others 2020) and veterinary drugs (in the case of livestock; Newsome and others 2015; Cortés-Avizanda and others 2016; Blanco and others 2019).

The contribution of naturally and artificially produced carcasses to the overall carrion pool may vary widely in different areas and seasons. For instance, in some protected and relatively natural areas, natural mortality causes are predominant (Wilmers and others 2003; Selva and others 2004), while the opposite may be true in more anthro-

pized areas (Margalida and others 2011). In addition, the provision of carrion from anthropogenic sources is heavily dependent on livestock and game management techniques (Olea and Mateo-Tomás 2009) and environmental and sanitary policies that regulate waste disposal (Donázar and others 2009). In contrast, natural mortality may depend on bottom-up effects such as primary productivity, which is usually linked to wild ungulate abundance (Barbosa and others 2020). Similarly, top-down forces such as diseases and predation also provide carrion to ecosystems (Wilson and Wolkovich 2011). In turn, disentangling the factors associated with ungulate carrion production is essential to understand the role of carrion in food webs.

Carrion production is increasingly linked to the main human-related forces of global environmental change. Humans have modified almost all ecosystems worldwide in a very short period (Watson and others 2018; Kennedy and others 2019). The increase in the demand for resources and/or socio-economic changes have facilitated the introduction, removal or increase of certain forms of matter in ecosystems (for example, anthropogenic food subsidies; Oro and others 2013). In Spain, such changes have involved a large increase in reactive nitrogen inputs, which has been largely associated with growing livestock production (Lassaletta and others 2013). Socio-economic changes have also led to the abandonment of rural areas and the urbanization and agricultural intensification in others, especially in developed countries (Westhoek and others 2006), causing the colonization of abandoned areas by wild ungulates and a progressive land-use change in a process known as “passive rewilding” (Navarro and Pereira 2015). Similarly, some historical activities have largely been replaced by more productive techniques; for example, the traditional agro-pastoral practices such as extensive livestock husbandry are progressively being substituted by intensive farming (Olea and Mateo-Tomás 2009; Perino and others 2019). Far beyond the positive and negative effects that these changes may have on biodiversity, these processes also affect the supply and cycle of nutrients (for example, carrion) that shape the productivity, composition, and diversity of terrestrial ecosystems (Oro and others 2013; Newsome and others 2021). Thus, estimating the distribution and abundance of carrion could help to understand the extent to which humans are impacting crucial ecosystem-level processes under a global change scenario.

The goal of this study is twofold. First, we aim to quantify the amount and spatial distribution of

ungulate carrion from different natural and anthropogenic sources that is annually produced throughout peninsular Spain, a hotspot for the conservation of vertebrate scavengers (Margalida and others 2010). Second, we aim to explore the relationship between the amount of ungulate carrion supplied from different sources and two factors operating at the ecosystem level: human pressure and primary productivity. We hypothesize that, in a developed country such as Spain, the biomass of anthropogenic ungulate carrion will exceed the biomass of naturally produced carrion, and that human pressure and primary productivity will affect anthropogenic and natural ungulate carrion production processes differently. In particular, we expect that the relationship between human pressure and ungulate carrion biomass will be determined by the degree of dependence of each particular carrion source on human activities, and that greater carrion biomass will be found in highly productive areas (Barton and others 2019). We discuss how carrion production processes have been altered in the Anthropocene in the context of global change and rewilding scenarios, emphasizing the effects at the ecosystem level and for communities depending on this trophic resource. Finally, based on this experience, we offer a set of recommendations towards obtaining more accurate carrion biomass estimates at the ecosystem level.

MATERIALS AND METHODS

Data Collection

We focused on five major *sources* of ungulate carrion, from both domestic (1. carcasses not used for commercial purposes) and wild ungulates (2. big game hunting, 3. roadkills, 4. predation, and 5. other causes of natural mortality; see Moleón and others 2019). For some purposes, these sources were further grouped into two main *types*: A. anthropogenic (that is, livestock, big game hunting, and roadkills) and B. natural (that is, predation and other natural mortality). For each ungulate carrion source, we studied the species that are known to supply most of the carrion biomass in peninsular Spain. In relation to livestock, we selected the most abundant species (cattle, pigs, and goats/sheep) (Morales-Reyes and others 2015). Regarding wild ungulates, we chose the species most frequently hunted (namely wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, barbary sheep *Ammotragus lervia*, chamois *Rupicapra pyrenaica*, fallow deer *Dama dama*, iberian ibex *Capra pyrenaica* and mouflon *Ovis orientalis*; Mateo-Tomás

and others 2015; MAGRAMA 2020) and road-killed (namely wild boar, roe deer and red deer; Zuberogoitia and others 2014; Sáenz-de-Santa-María and Tellería 2015). In the case of predation and other causes of mortality, we focused on the wild boar, given that it is a main prey species for wolves *Canis lupus* (see Blanco and others 1992; Barja 2009; Lagos and Bárcena 2018) and the most abundant wild ungulate species in the Iberian Peninsula (Acevedo and others 2014; Valente and others 2020).

For each carrion source, we estimated the maximum annual biomass of carrion (kg/year) produced in peninsular Spain, and represented it using the UTM 10×10 km grid. Details on carrion biomass estimation are provided in Supp Mat Appendix S1. In short, carrion biomass from livestock was obtained by multiplying the number of censused individuals at the municipality level in 2018 by the mortality rate and average weight for each species (Supp Mat Table S1). To estimate carrion from big game hunting, we gathered data of the average number of hunted ungulate species between 2005–2016 at the province level (MAGRAMA 2020; Supp Mat Table S2) and multiplied them by the average weight of each species (Table S3). In the case of roadkills, we multiplied the number of road-killed individuals for each of the three selected species between 2006 and 2012 at each municipality (obtained from Sáenz-de-Santa-María and Tellería 2015; Supp Mat Table S4) by their average weight (Supp Mat Table S3). Carrion from predation was calculated by using wolf presence data from the Spanish national census of 2014 and applying killing rates (Vucetich and others 2002; Supp Mat Table S6) for each wild boar abundance grid cell overlapping the wolf distribution area (Acevedo and others 2014; MITECO, 2014) and the average weight of wild boar (Supp Mat Table S3). Finally, carrion biomass from natural mortality of wild boars was estimated from spatial data of abundance (from Acevedo and others 2014), mortality rate and average weight of this species in peninsular Spain (Supp Mat Table S3; Table S5).

Statistical Analyses

We first assessed the spatial distribution of each ungulate carrion source (according to the UTM 10×10 km grid) by developing a global Moran's I test accounting for spatial autocorrelation by using "Moran" function implemented in the "raster" package in R (Hijmans 2020). Global Moran's I test ranges from -1 to +1, indicating dispersed (values towards -1), random (values around 0) or clustered

(values towards +1) resources. Furthermore, to check how the correlation varies in relation to distance, we plotted the results of the Moran's test by using "correlogram" function implemented in the "ELSA" package in R (Naimi and others 2019).

Then, we evaluated the relationship between ungulate carrion biomass production and a) human pressures, represented by the Global Human Modification Index (hereafter GHM) (Kennedy and others 2018), and b) primary productivity, indicated by the Normalized Difference Vegetation Index (hereafter NDVI) (Pettorelli and others 2011). The GHM map measures the spatial extent of 13 anthropogenic stressors and their estimated intensities of influence, producing a continuous 0–1 metric of the ecological condition of the landscape at a resolution of 1 km (Kennedy and others 2018). It accounts for the proportion of each grid cell covered by the stressor and multiplies it by an intensity value based on 'emergy' measures of human-induced impacts on biological, chemical, and physical processes of lands (see Kennedy and others 2019 for more details). NDVI is a proxy of primary productivity and resource distribution and dynamics across different ecological levels (from population to entire ecosystems) (see Pettorelli and others 2006, 2011), being closely linked to the population dynamics of ungulate species (Hurley and others 2014). NDVI layer is on 1 km resolution with values ranging from -1 (lowest productivity) to +1 (highest productivity; Copernicus Global Land Service 2020). We used the mean NDVI monthly values for peninsular Spain between 1997 and 2017. For each carrion source raster dataset, grid cells were converted into points to match covariate values to each 1 km pixel at which both GHM and NDVI were recorded. For each point, the mean value of GHM and NDVI was calculated.

We performed Generalized Linear Models (GLM, McCullag and Nelder 1989) with a Gaussian distribution and identity link function, separately for each carrion source. Prior to modelling, we ensured that each carrion biomass source was independent of each other by performing a matrix correlation test (see Supp Mat Table S7). Carrion biomass (kg/year/100km²) was the response variable, while GHM and NDVI were the explanatory variables. We used every 1×1 km square with data for carrion biomass, GHM and NDVI as the sample unit ($n = 4979$ squares). The two variables were included in the models, as they were uncorrelated (Spearman correlation: -0.15). Model selection was based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We considered models within two AICc units of the best model

(that is, the model with lowest AIC) as having similar support (Burnham and Anderson 2002). To assess the overall explanatory power of the selected models for each carrion source, we computed their deviance (D^2 ; Burnham and Anderson 2002) using the “modEvA” package in R (Barbosa and others 2015). Finally, we visually checked the homogeneity of variance and normality of residuals by using residpanel() function implemented in the “ggresidpanel” package in R (Goode and Rey 2019).

Spatial and statistical analyses were done, respectively, in ArcGIS 10.5 (ESRI, 2016) and R version 3.5.1 (R Core Team 2020).

RESULTS

Considering all carrion sources together, we estimated a mean potential annual production of ungulate carrion in peninsular Spain of c. 31 tonnes/100km² (Table 1). Ungulate carrion came mostly from anthropogenic sources (c. 99% of the total carrion biomass estimated; Table 1; Figure 1A). Carrion from livestock (c. 91%) represented the majority of total carrion biomass, compared to wild ungulates (c. 9%; Table 1; Figure 1B). Within wild ungulates, carrion was mainly supplied by big game hunting (c. 97% of total wild ungulate carrion; Table 1). These carrion resources were unevenly distributed throughout peninsular Spain (Figure 2A–E), with livestock carrion being the most widely distributed resource (Figure 2A) and carrion from predation showing the most restricted distribution (Figure 2C). Overall, the highest amount of carrion biomass was located in the central-west part of peninsular Spain, which is mainly dominated by “dehesas” (that is, savannah-like Mediterranean landscapes; Figure 2F) rich in livestock exploitations and big game

hunting activity. When analysed in detail, the Moran’s I test values showed that, in general, carrion from natural processes exhibited lower auto-correlation values, thus occurring in a more random and dispersed way (Moran’s I: 0.20 and 0.66 for carrion biomass from predation and natural mortality, respectively; Supp Mat Figure S1) compared to anthropogenic carrion sources, which appeared more spatially clustered (Moran’s I: 0.63, 0.73 and 0.74 for carrion from roadkills, big game hunting and livestock, respectively; Supp Mat Figure S1).

Our models showed that both GHM and NDVI were associated with carrion production in peninsular Spain, with the best model including both variables. In addition, the model including GHM only was also selected in the case of carrion from livestock, and the model including NDVI only was ranked first in the case of carrion from predation (Table 2 and Supp Mat Table S8). As expected, GHM was especially relevant to explain anthropogenic sources of carrion, showing a positive but weak relationship with carrion from livestock and roadkills (Figures 3A and C) and a clear negative association otherwise (Figures 3B, D and E). NDVI showed a more pronounced positive association with carrion produced from natural sources and big game hunting (Figures 3D and E) than with carrion supplied by livestock and roadkills (Figures 3A and C).

DISCUSSION

In this study, we quantified ungulate carrion potential production in terrestrial ecosystems of mainland Spain and showed that, nowadays, anthropogenic carrion sources (livestock mortality, big game hunting and roadkills) clearly exceed those from natural processes, such as natural

Table 1. Ungulate Carrion Biomass (kg/year/100 km²) Supplied by Different Carrion Sources in Peninsular Spain, and Their Relative Contribution (%)

Category	Details	Mean ± SD	Range	Contribution
Type	Anthropogenic	90,172 ± 144,765	0–1,783,270	99.1
	Natural	1533 ± 763	0–1660	0.865
Wild vs. domestic	Livestock	82,796 ± 140,581	0–1,783,270	91.1
	Wild ungulates	8909 ± 5225	0–20,466	8.895
Source	Livestock	82,796 ± 140,303	0–1,783,270	91.1
	Big game hunting	7264 ± 4208	0–20,466	7.91
	Roadkills	112 ± 254	0–3451	0.053
	Predation	854 ± 394	0–1660	0.812
	Natural mortality	679 ± 369	0–1354	0.125

SD = Standard Deviation.

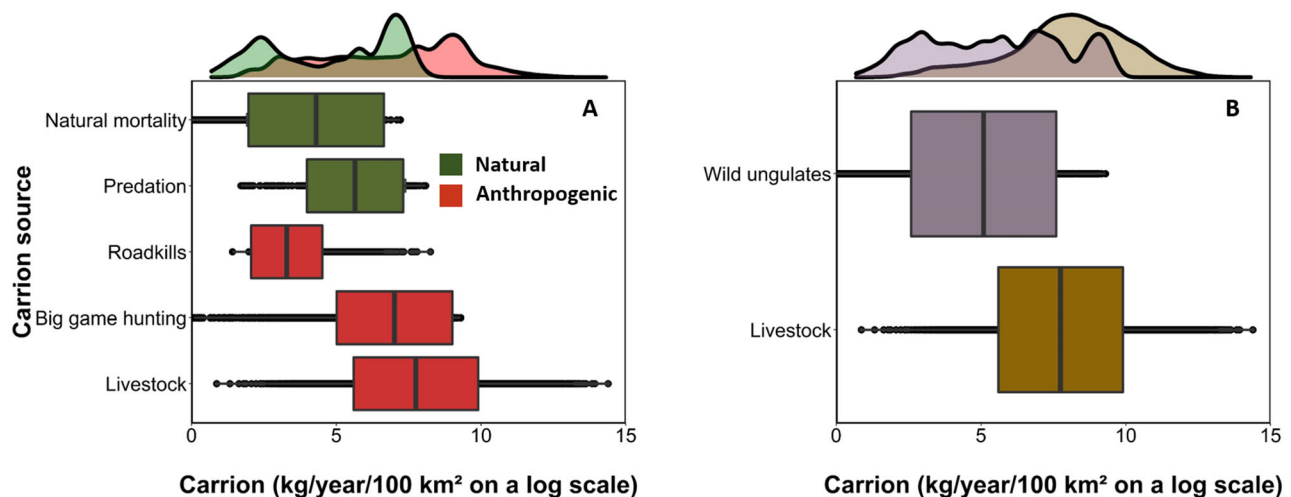


Figure 1. Estimated ungulate carrion biomass (in a natural log scale) in peninsular Spain, according to (A) carrion *type* (natural or anthropogenic) and (B) wild vs. domestic species. Density plots show the distribution of values of each carrion *source*.

mortality and predation. Not surprisingly, livestock stood out as the major source of ungulate carrion. The increasing demands for meat and derivatives from a growing human population worldwide (Oro and others 2013) have led to an exponential rise in global livestock biomass in recent decades (c. 0.1 Gt of livestock, mainly cattle and pigs, vs c. 0.007 Gt of wild mammals; Bar-On and others 2018). For example, in Spain, pig numbers have increased from 6 to more than 30 million heads since the 1960s, becoming the main pig producer in Europe (Lassaletta and others 2014). This, together with the fact that big game hunting is a common practice in many regions of the world (Mateo-Tomás and others 2015; Benítez-López and others 2019) and that the road networks are increasing globally (Ibisch and others 2016), suggests that humans are currently the major providers of carrion biomass, especially in developed countries. Overall, our findings contribute to the increasing perception that food subsidies from humans are greatly reshaping natural communities and ecosystems at a global scale (Oro and others 2013).

Our results showed that, in general, the most productive areas (that is, highest NDVI) were associated with the highest wild and domestic ungulate carrion supply, though the models explaining livestock carrion biomass had very low explanatory capacity (see Table 1). This may be due to the contrasting environments that are occupied by extensive and intensive livestock, with the latter inhabiting areas of higher human influence than the former. In relation to human pressure (GHM), the generally positive association found with

anthropogenic carrion sources indicates a strong disconnection of livestock mortality and roadkills from primary productivity (Naylor and others 2005), which still positively correlates with ungulate carrion production from natural sources and big game hunting in Spain. Traditional livestock husbandry has been largely reduced over the last twenty years in Europe, as opposed to intensive farming (Food and Agriculture Organisation of the United Nations; available at <http://faostat.fao.org/>). Intensive farming production often relies on feed produced far away from the farms, which requires large-scale transportation (McAuliffe and others 2016). Importantly, these changes in livestock production systems also mean a redistribution and homogenization of the carrion supplied by domestic ungulates. The large-scale input of nutrients derived from livestock carcass consumption might contribute to anthropogenic nitrogen enrichment of terrestrial ecosystems potentially affecting biogenic GHGs (Liu and Greaver 2009). This fact might be particularly relevant in Spain where the main scavenger (griffon vulture) is a highly mobile species breeding in natural areas but foraging in anthropogenic ecosystems and such mobile links have a relevant role in ecosystem functioning (Lundberg and Moberg 2003; Gutiérrez-Cánovas and others 2020). Thus, anthropogenic nitrogen from carcasses mediated by vulture scavenging might have a key role on nutrient cycling potentially influencing food webs at the landscape level (Polis and others 2004).

Our results showing the important role of anthropogenic sources of ungulate carrion pro-

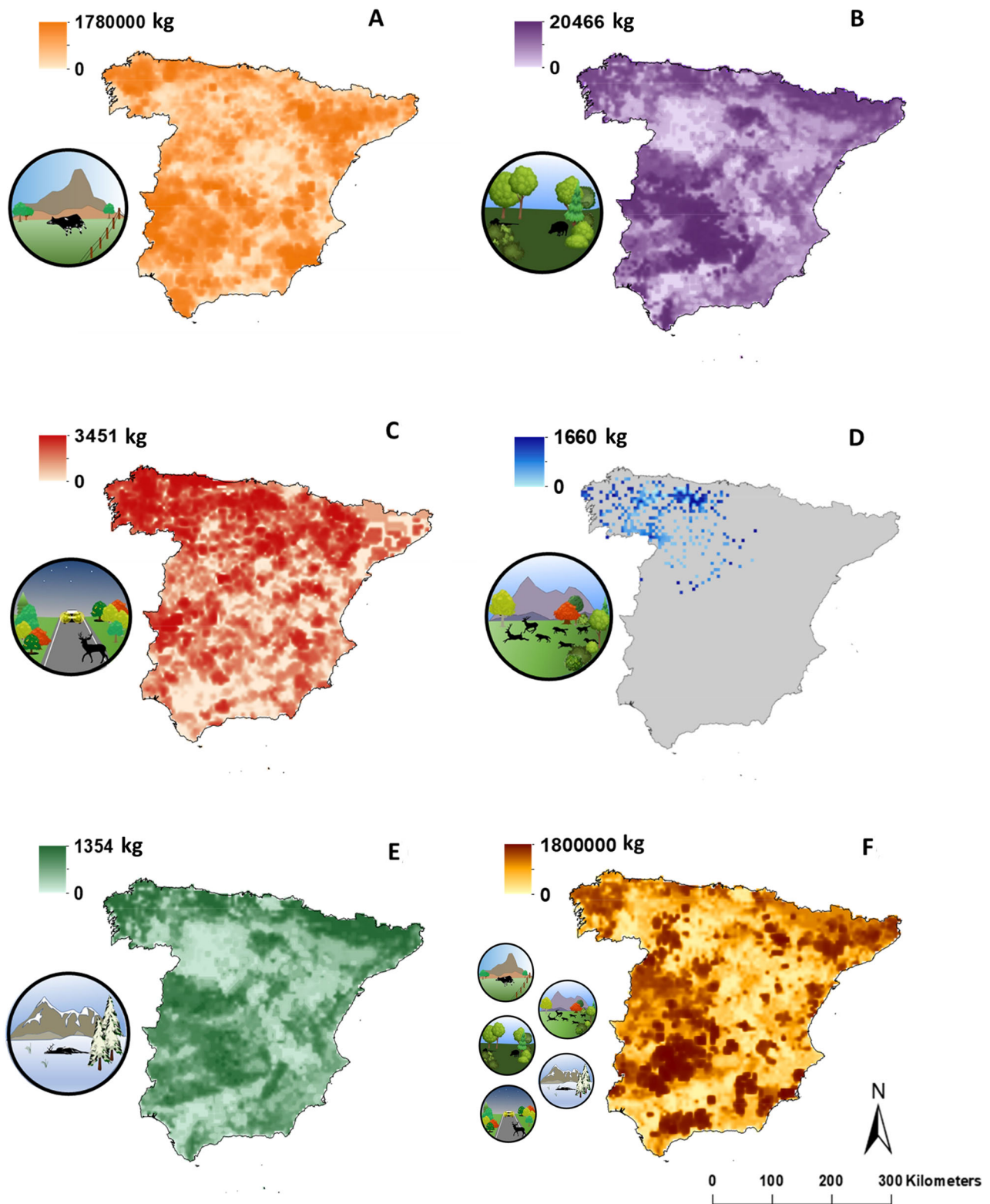


Figure 2. Spatial distribution of ungulate carrion biomass production ($\text{kg/year}/100 \text{ km}^2$) for (A) livestock, (B) big game hunting, (C) roadkills, (D) predation, (E) natural mortality and (F) total carrion in peninsular Spain.

duction could be extrapolated to many other regions of the world. Areas devoted to livestock

currently account for up to 26% of the Earth's surface (Foley and others 2011). This means that

Table 2. Results of the Generalized Linear Models to Assess the Relationship Between Ungulate Carrion Biomass Supplied by Different Sources and a) Human Pressure (GHM) and b) Primary Productivity (NDVI) in Peninsular Spain

Carrion source	Ranking	k	Model	AIC	Δ AIC	D ²
Livestock	1	3	GHM + NDVI	132,141.5	0.00	0.31
	2	2	GHM	132,143.0	1.46	0.20
	3	1	Null	132,151.6	10.10	
	4	2	NDVI	132,151.8	10.26	
Big game hunting	1	3	GHM + NDVI	94,975.2	0.00	22.01
	2	2	NDVI	95,414.2	438.97	
	3	2	GHM	95,656.8	681.59	
	4	1	Null	96,196.0	1220.72	
Roadkills	1	3	GHM + NDVI	67,454.1	0.00	10.53
	2	2	NDVI	67,486.3	32.17	
	3	2	GHM	67,990.3	536.22	
	4	1	Null	67,993.3	539.17	
Predation	1	2	NDVI	4064.7	0.00	29.10
	2	3	GHM + NDVI	4066.2	1.44	28.95
	3	1	GHM	4156.8	92.10	
	4	2	Null	4158.7	94.01	
Natural mortality	1	3	GHM + NDVI	70,601	0.00	28.31
	2	2	NDVI	70,951.5	350.51	
	3	2	GHM	71,771.6	1170.61	
	4	1	Null	72,237	1636.06	

Model AICc values, the relative difference in AIC units compared with the top-ranked model (Δ AIC), and the variability of the models explained by the predictors (percentage of explained deviance, D²) are shown. Selected models are highlighted in bold.

livestock carrion is available in most terrestrial ecosystems. Similarly, big game hunting also subsidizes ecosystems with large amounts of carrion (Mateo-Tomás and others 2015). In Europe and the USA, game hunting generates about $1.0 \cdot 10^8$ and about $6.9 \cdot 10^5$ tonnes of carrion every year (Vicente and others 2011; Oro and others 2013). The relatively high predictability of these carrion resources, from local (Cortés-Avizanda and others 2016) to large scales (this study), facilitates their consumption by scavengers (Cortés-Avizanda and others 2012; Mateo-Tomás and others 2015). Moreover, livestock mainly graze in open areas, which facilitates carrion detection, especially to vultures and other avian scavengers (Arrondo and others 2019). Roadkills also provide important inputs to ecosystems in certain areas. Grilo and others (2020) estimated that about 194 million birds and about 29 million mammals might be killed every year on European roads. This represents a huge reward of highly detectable carcasses to opportunistic scavengers (Lambertucci and others 2009).

Nevertheless, anthropogenic carrion poses several risks for scavenger communities. For instance, Gangoso and others (2021) showed that exploiting anthropogenic-derived carrion could entail physiological costs in vultures. Also, anti-inflammatory

drugs used for livestock, such as diclofenac, pose deadly risks for scavengers (see Herrero-Villar and others 2021; Margalida and others 2021). Another potential threat for scavengers is the lead from rifle bullets found in tissues of hunted ungulate carcasses (Hunt and others 2006). Lead contamination could have both subclinical and lethal effects on vultures that regularly feed in areas with frequent hunting activity (for example, Monclús and others 2020; Arrondo and others 2020). Roadkills may also pose a threat for avian scavengers due to their risk of collision with vehicles (De Vault and others 2015). Finally, the predictable nature of anthropogenic carrion sources makes scavengers particularly sensitive to changes in their availability (López-López and others 2013, 2014), alters evolutionary pressures that shaped specialist scavengers' life history (Oro and others 2013; Cortés-Avizanda and others 2016), and compromises species diversity and coexistence in scavenging guilds (Cortés-Avizanda and others 2012).

Despite the huge quantity of ungulate carrion annually produced in mainland Spain, not all becomes available to scavengers, decomposers, and the environment. For example, the disposal in the field of livestock carrion in Europe was subject to regulation (EC 1774/2002) after the mad cow

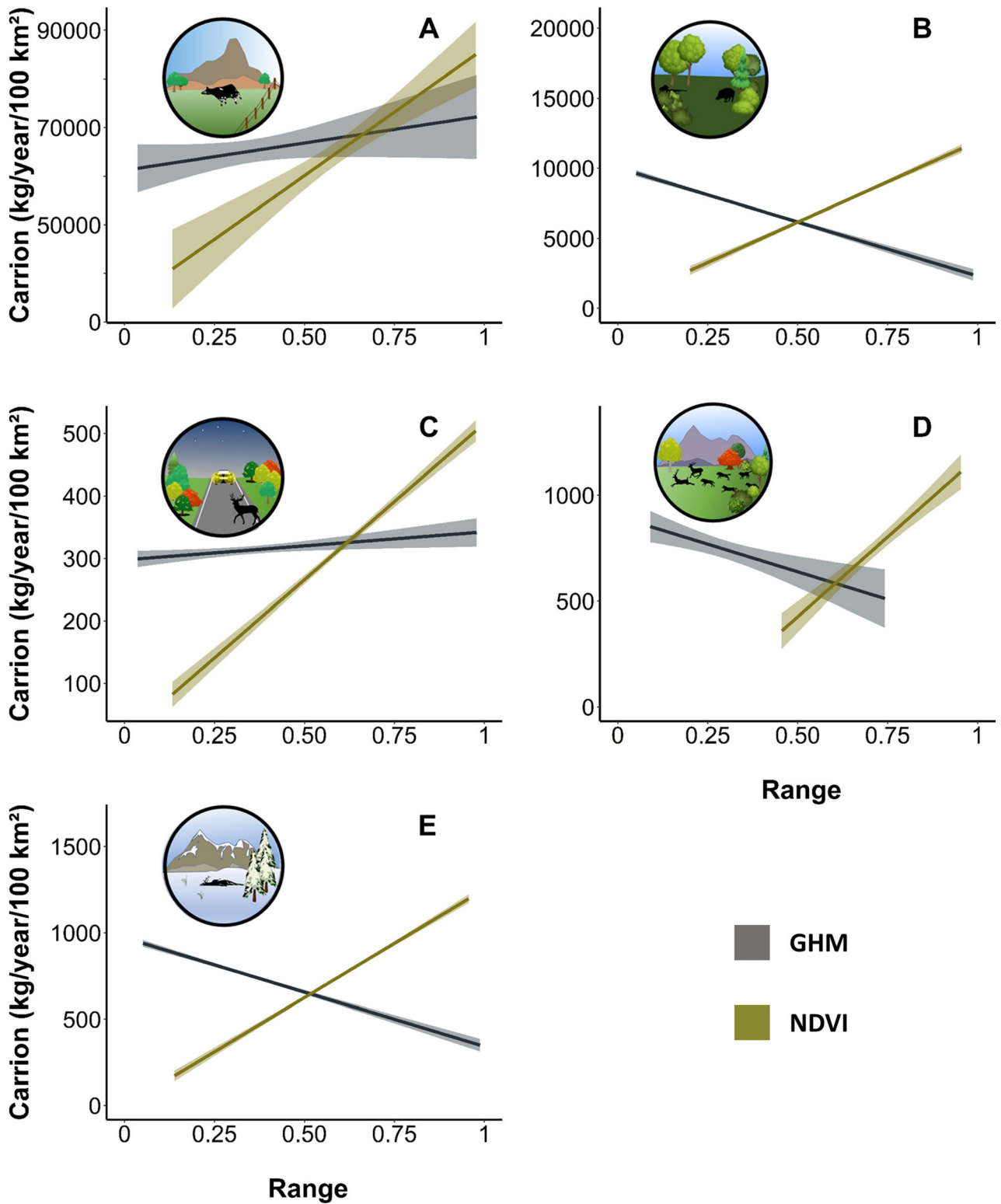


Figure 3. Modelled relationship between ungulate carrion biomass production (kg/year/100 km²) and the selected covariates GHM and NDVI. Results are shown separately for carrion from livestock (A), big game hunting (B), roadkills (C), predation (D) and natural mortality (E). Range represents the values (0–1) that covariates GHM and NDVI could take. Shaded areas represent the 95% confidence intervals.

outbreak in 2001. This led to the obligation of removing livestock carrion for many areas until 2012, when a new regulation (EC 142/2011; Spanish RD 1632/2011) allowed leaving extensive livestock carcasses in the field in certain areas which are especially important for the feeding of necrophagous species. These areas represent a large part of mainland Spain (> 60%; Morales-Reyes and others 2017). Moreover, the implementation of such measures in the Spanish autonomous communities has been highly uneven (Morales-Reyes and others 2017; Mateo-Tomás and others 2019). This has led to wide availability of extensive livestock carcasses, even in the period with most restrictive regulations. Intensive livestock carcasses are sometimes removed to be transformed or destroyed in authorized plants (Morales-Reyes and others 2015), though others are made available, either intentionally or due to ineffective collection systems, in landfills (Fernández-Gómez and others 2022). Regarding carrion from big game hunting, gut piles are often abandoned in the field, plus whole carcasses that are unrecovered by hunters (Mateo-Tomás and Olea 2010; Vicente and others 2011). Road-killed ungulates are usually removed by road services (sometimes after the arrival of scavengers), but their effectiveness depends on factors such as the size of the animal or the road type (pers. observ.; Putman and others 2011). However, many carcasses are just moved some meters away (pers. observ.). As opposed to anthropogenic carrion, carcasses from natural mortality and predation are readily available in the landscape (Wilmers and others 2003).

CAVEATS AND FUTURE DIRECTIONS

We identified some potential caveats in the quantitative assessment of carrion biomass production that should be considered when interpreting our results (see Table S9). First, the official data on livestock numbers that we assessed do not separate between extensive and intensive livestock systems. This prevents quantifying their separate contribution to the total supply of livestock carrion biomass and identifying potential differences in their correlates. In addition, a high variability exists in the extensive/intensive livestock farming spectrum, which includes semi-intensive or semi-extensive forms. Second, there were no detailed spatial data (that is, at 10×10 km grid or municipality scale) in the case of big game hunting, which probably obscured the relationship between carrion from this source and GHM and NDVI. Third, the lack of accurate data on the density/abundance of wild

ungulates prevented us from obtaining predation- and natural mortality-related carrion biomass estimates for other ungulate species. Fourth, the available data did not allow us to quantify to which extent predation and big game were additive or compensatory to other mortality causes in wild ungulates (see Sandercock and others 2011). Although improving the abovementioned points would have allowed us to get more accurate calculations, we think our main conclusions on the relative carrion biomass supplied by each source are robust. This is mainly due to the substantial differences obtained for each carrion source. For instance, carrion biomass from livestock and big game hunting was, respectively, about 97 and 9 times higher compared to carrion supplied by predation. Also, many of the abovementioned constraints are shared across different areas, which allows for spatial comparisons, especially considering the 10×10 km grid scale.

We estimated the maximum ungulate carrion quantity potentially produced by different sources. Apart from increasing the accuracy of carrion biomass production, the main challenge for future research is estimating the proportion of the carrion produced that enters the ecosystems and is available to scavengers, decomposers and the environment. For instance, it is important to account for how many livestock carcasses are removed from the field to be transformed or incinerated in authorized processing plants (Morales-Reyes and others 2015) and to estimate the proportion of hunted wild ungulates that is destroyed or used for human consumption (Sevillano-Morales and others 2011; Margalida and Moleón 2016; Sevillano-Morales and others 2018). In this sense, differences in sanitary and environmental policies delineation and implementation among different supra- and infra-national administrative units should also be integrated when accounting for spatial availability of carrion (for example, Morales-Reyes and others 2017). Moreover, estimates of carrion biomass in ecosystems should integrate the seasonality in carrion production (Pereira and others 2014; Barton and others 2019). Future studies should also recognize the differential ecological roles of different types of carrion, in relation to not only mortality cause, but also carcass type and species (Moleón and others 2020). In this regard, estimates of carrion biomass from non-ungulate vertebrates (including herbivorous and carnivorous species) and invertebrates, which may represent an important part of the total carrion biomass in an ecosystem (Barton and others 2019), would be highly welcome. Finally, further research on car-

tion biomass quantification should acknowledge the ongoing global changes in the socioecological context. For instance, the current scenario of abandonment of rural areas and traditional practices in developed countries (Perino and others 2019) is leading to a rewilding process that includes the drastic reduction of free grazing herds and increased niche availability for wild ungulates (Apollonio and others 2010; Acevedo and others 2011), with the subsequent expected increase in wild ungulate carrion biomass.

Addressing all these points could settle steps to follow in carrion production quantification research. This will undoubtedly improve carrion resource management, assessment of the risks linked to each resource, and accounting for ecosystem health state.

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DATA AVAILABILITY

The data that support the findings and scripts used to develop models embedded in this study are openly available in Zenodo; <https://zenodo.org/badge/DOI/10.5281/zenodo.5196414.svg>.

Declarations

Conflict of Interest The authors declare that they have no known competing financial interests or personal relationships that could have

appeared to influence the work reported in this research work

REFERENCES

- Acevedo P, Farfán MA, Márquez AL, Delibes-Mateos M, Real R, Vargas JM. 2011. Past, present and future of wild ungulates in relation to changes in land use. *Landscape Ecology* 26:19–31.
- Acevedo P, Quirós-Fernández F, Casal J, Vicente J. 2014. Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management. *Ecological Indicators* 36:594–600.
- Apollonio M, Andersen R, Putman R. (Eds.). 2010. *European ungulates and their management in the 21st century*. Cambridge University Press.
- Arrondo E, Morales-Reyes Z, Moleón M, Cortés-Avizanda A, Donázar JA, Sánchez-Zapata JA. 2019. Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns. *Basic and Applied Ecology* 41:56–66.
- Arrondo E, Navarro J, Perez-García JM, Mateo R, Camarero PR, Martín-Doimeadios RCR, Jiménez-Moreno M, Cortés-Avizanda A, Navas I, García-Fernández AJ, Sánchez-Zapata JA, Donázar JA. 2020. Dust and bullets: stable isotopes and GPS tracking disentangle lead sources for a large avian scavenger. *Environmental Pollution* 266:115022.
- Barbosa JM, Pascual-Rico R, Martínez SE, Sánchez-Zapata JA. 2020. Ungulates attenuate the response of Mediterranean mountain vegetation to climate oscillations. *Ecosystems* 23:957–972.
- Barbosa AM, Real R, Muñoz AR, Brown JA. 2015. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions* 19:1333–1338.
- Barja I. 2009. Prey and prey-age preference by the Iberian wolf *Canis lupus signatus* in a multiple-prey ecosystem. *Wildlife Biology* 15:147–154.
- Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences U.S.A* 115:6506–6511.
- Barton PS, Cunningham SA, Lindenmayer DB, Manning AD. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171:761–772.
- Barton PS, Evans MJ, Foster CN, Pechal JL, Bump JK, Quagiotto MM, Benbow ME. 2019. Towards quantifying carrion biomass in ecosystems. *Trends in Ecology & Evolution* 34:950–961.
- Beasley JC, Olson ZH, DeVault TL. 2012. Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos* 121:1021–1026.
- Benbow EM, Tomberlin JK, Tarone AM. 2015. *Carrion Ecology, Evolution, and Their Applications*. Boca Raton, Florida: CRC Press.
- Benítez-López A, Santini L, Schipper AM, Busana M, Huijbregts MA. 2019. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biology* 17:e3000247.
- Blanco G, Cortés-Avizanda A, Frías Ó, Arrondo E, Donázar JA. 2019. Livestock farming practices modulate vulture diet-disease interactions. *Global Ecology and Conservation* 17:e00518.

- Blanco JC, Reig S, de la Cuesta L. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation* 60:73–80.
- Burnham KP, Anderson DR. 2002. Model selection and multi-model inference: a practical information-theoretical approach. New York: Springer-Verlag.
- Copernicus Global Land Service 2020. <https://land.copernicus.eu/global/products/ndvi> (accessed July 2020).
- Cortés-Avizanda A, Selva N, Carrete M, Donazar JA. 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic and Applied Ecology* 10:265–272.
- Cortés-Avizanda A, Jovani R, Carrete M, Donazar JA. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93:2570–2579.
- Cortés-Avizanda A, Donazar JA, Pereira HM. 2015. Top scavengers in a wilder Europe. In: Pereira HM, Navarro LM, Eds. *Rewilding European landscapes*, . Cham: Springer International Publishing.
- Cortés-Avizanda A, Blanco G, DeVault TL, Markandya A, Virani MZ, Brandt J, Donazar JA. 2016. Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies. *Frontiers in Ecology and the Environment* 14:191–199.
- DeVault TL, Rhodes OE, Shivik JA. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.
- DeVault TL, Blackwell BF, Seamans TW, Lima SL, Fernández-Juricic E. 2015. Speed kills: ineffective avian escape responses to oncoming vehicles. *Proceedings of the Royal Society of London B: Biological Sciences* 282:20142188.
- Díaz M, Campos P, Pulido FJ. 1997. The Spanish dehesa: a diversity in land use and wildlife. In: Pain DJ, Pienkowski MW, Eds. *Farming and Birds in Europe*, . The Common Agricultural Policy and its Implications for Bird Conservation: Academic Press, London. pp 178–209.
- Donazar JA, Margalida A, Campión D. 2009. Vultures, feedings stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. *Munibe* 29 (Suppl). Spain: Sociedad de Ciencias Aranzadi San Sebastián.
- ESRI. 2016. ArcGIS Desktop: Release 10.5, Redlands, CA: Environmental Systems Research Institute.
- Fernández-Gómez L, Cortés-Avizanda A, Arrondo A, García-Alfonso M, Ceballos O, Montelío E, Donazar JA. 2022. Vultures feeding on the dark side: current sanitary regulations may not be enough. *Bird Conservation International*, in press.
- Foley J, Ramankutty N, Brauman K, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PC, Balzer C, Bennett EM, Carpenter SR, Hill J, Monfreda C, Polasky S, Rockström J, Sheehan J, Siebert S, Tilman D, Zaks DPM. 2011. Solutions for a cultivated planet. *Nature* 478:337–342.
- Gangoso L, Cortés-Avizanda A, Sergiel A, Pudifoot B, Miranda F, Muñoz J, Delgado-González A, Moleón M, Sánchez-Zapata JA, Arrondo E, Donazar JA. 2021. Avian scavengers living in anthropized landscapes have shorter telomeres and higher levels of glucocorticoid hormones. *Science of the Total Environment* 782:146920.
- Goode K, Rey K. 2019. ggResidpanel: Panels and Interactive Versions of Diagnostic Plots using 'ggplot2'. R package version 0.3.0. <https://CRAN.R-project.org/package=ggResidpanel>
- Grilo C, Koroleva E, Andrášik R, Bíl M, González-Suárez M. 2020. Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment* 18:323–328.
- Gutiérrez-Cánovas C, Moleón M, Mateo-Tomás P, Olea PP, Sebastián-González E, Sánchez-Zapata JA. 2020. Large home range scavengers support higher rates of carcass removal. *Functional Ecology* 34:1921–1932.
- Herrero-Villar M, Delepouille É, Suárez-Regalado L, Solano-Manrique C, Juan-Sallés C, Iglesias-Lebrija JJ, Camarero PR, González F, Álvarez E, Mateo R. 2021. First diclofenac intoxication in a wild avian scavenger in Europe. *Science of the Total Environment* 782:146890.
- Hijmans RJ. 2020. Raster: Geographic Data Analysis and Modelling. R package version 3.4–5. <https://CRAN.R-project.org/package=raster>
- Hunt WG, Burnham W, Parish CN, Burnham KK, Mutch B, Oaks JL. 2006. Bullet fragments in deer remains: Implications for lead exposure in avian scavengers. *Wildlife Society Bulletin* 34:167–170.
- Hurley MA, Hebblewhite M, Gaillard JM, Dray S, Taylor KA, Smith WK, Zager P, Bonenfant C. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369:20130196.
- Ibisch PL, Hoffmann MT, Kreft S, Pe'er G, Kati V, Biber-Freudenberger L, DellaSala DA, Vale MM, Hobson PR, Selva N. 2016. A global map of roadless areas and their conservation status. *Science* 354:1423–1427.
- Kennedy CM, Oakleaf JR, Theobald DM, Baruch-Mordo S, Kiesecker J. 2019. Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology* 25:811–826.
- Lagos L, Bárcena F. 2018. Spatial variability in wolf diet and prey selection in Galicia (NW Spain). *Mammal research* 63:125–139.
- Lambertucci SA, Speziale KL, Rogers TE, Morales JM. 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodiversity and Conservation* 18:2063–2074.
- Lessard JP, Belmaker J, Myers JA, Chase JM, Rahbek C. 2012. Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution* 27:600–607.
- Liu L, Greaver TL. 2009. A review of nitrogen enrichment effects on three biogenic GHGs: the CO2 sink may be largely offset by stimulated N2O and CH4 emission. *Ecology Letters* 12:1103–1117.
- López-López P, Benavent-Corai J, García-Ripollés C, Urios V. 2013. Scavengers on the move: behavioural changes in foraging search patterns during the annual cycle. *PloS One* 8:e54352.
- López-López P, García-Ripollés C, Urios V. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecological Applications* 24:938–949.
- Lundberg J, Moberg F. 2003. Mobile link organisms and ecosystem functioning: 710 Implications for ecosystem resilience and management. *Ecosystems* 6:87–98.

- MAGRAMA. 2020. Spanish Ministry of Agriculture, Food, and Environment. https://www.mapa.gob.es/es/desarrollo-rural/estadisticas/Est_Anual_Caza.aspx (accessed April 2020).
- Margalida A, Donázar JA, Carrete M, Sánchez-Zapata JA. 2010. Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47:931–935.
- Margalida A, Colomer MÀ, Sanuy D. 2011. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS One* 6:e20248.
- Margalida A, Moleón M. 2016. Toward carrion-free ecosystems? *Frontiers in Ecology and Environment* 14:183–184.
- Margalida A, Green RE, Hiraldo F, Blanco G, Sánchez-Zapata JA, Santangeli A, Duriez O, Donázar JA. 2021. Ban veterinary use of diclofenac in Europe. *Science* 372:694–695.
- Martin-Díaz P, Cortés-Avizanda A, Serrano D, Arrondo E, Sánchez-Zapata JA, Donázar JA. 2020. Rewilding processes shape the use of Mediterranean landscapes by an avian top scavenger. *Scientific Reports* 10:1–12.
- Mateo-Tomás P, Olea PP, Moleón M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JA. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions* 21:913–924.
- Mateo-Tomás P, Olea PP, López-Bao JV. 2019. Time to monitor livestock carcasses for biodiversity conservation and public health. *Journal of Applied Ecology* 56:1850–1855.
- McAuliffe GA, Chapman DV, Sage CL. 2016. A thematic review of life cycle assessment (LCA) applied to pig production. *Environmental Impact Assessment Review* 56:12–22.
- McCullagh P, Nelder JA. 1989. *Generalized Linear Models*. London: Chapman and Hall.
- MITECO. 2014. Ministry for Ecological Transition and Demographic Challenge. https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especiesrestr/es/ieet_mamiferos_censo_lobo.aspx (accessed April 2020).
- MNCN-CSIC. 2007. Virtual encyclopedia of the Spanish vertebrates. <http://www.vertebradosibericos.org/> (accessed April 2020).
- Moleón M, Sánchez-Zapata JA, Selva N, Donázar JA, Owen-Smith N. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* 89:1042–1054.
- Moleón M, Selva N, Sánchez-Zapata JA. 2020. The components and spatiotemporal dimension of carrion biomass quantification. *Trends in Ecology and Evolution* 35:91–92.
- Moleón M, Selva N, Quaggiotto MM, Bailey DM, Cortés-Avizanda A, DeVault TL. 2019. Carrion availability in space and time. *Carrion ecology and management*. Springer: Cham. pp 23–44.
- Moleón M, Sánchez-Zapata JA. 2015. The living dead: time to integrate scavenging into ecological teaching. *BioScience* 65:1003–1010.
- Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* 124:1391–1403.
- Monclús L, Shore RF, Krone O. 2020. Lead contamination in raptors in Europe: A systematic review and meta-analysis. *Science of the Total Environment* 748:141437.
- Moore JC, Berlow EL, Coleman DC, Ruitter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7:584–600.
- Morales-Reyes Z, Pérez-García JM, Moleón M, Botella F, Carrete M, Lazcano C, Moreno-Opo R, Margalida A, Donázar JA, Sánchez-Zapata JA. 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Scientific Reports* 5:7811.
- Morales-Reyes Z, Pérez-García JM, Moleón M, Botella F, Carrete M, Donázar JA, Cortés-Avizanda A, Arrondo E, Moreno-Opo R, Jiménez J, Margalida M. 2017. Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. *Journal of Applied Ecology* 54:1120–1129.
- Morales JS, Rojas RM, Perez-Rodriguez F, Casas AA, López MA. 2011. Risk assessment of the lead intake by consumption of red deer and wild boar meat in Southern Spain. *Food Additives and Contaminants: Part A* 28:1021–1033.
- Moreno-Opo R, Margalida A. 2019. Human-mediated carrion: effects on ecological processes. *Carrion Ecology and Management*. Springer: Cham. pp 183–211.
- Muñoz-Lozano C, Martín-Vega D, Martínez-Carrasco C, Sánchez-Zapata JA, Morales-Reyes Z, González M, Moleón M. 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. *PLoS One* 14:e0221890.
- Naimi B, Hamm NA, Groen TA, Skidmore AK, Toxopeus AG, Alibakhshi S. 2019. ELSA: Entropy-based local indicator of spatial association. *Spatial Statistics* 29:66–88.
- Naylor R, Steinfeld H, Falcon W, Galloway J, Smil V, Bradford E, Mooney H. 2005. Losing the links between livestock and land. *Science* 310:1621–1622.
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2015. The ecological effects of providing resource subsidies to predators: resource subsidies and predators. *Global Ecology and Biogeography* 24:1–11.
- Nyhus PJ. 2016. Human–wildlife conflict and coexistence. *Annual Review of Environment and Resources* 41:143–171.
- Olea PP, Mateo-Tomás P. 2009. The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. *Biological Conservation* 142:1844–1853.
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* 16:1501–1514.
- Pausas JG, Bond WJ. 2020. On the three major recycling pathways in terrestrial ecosystems. *Trends in Ecology & Evolution* 35:767–775.
- Payne LX, Moore JW. 2006. Mobile scavengers create hotspots of freshwater productivity. *Oikos* 115:69–80.
- Pereira LM, Owen-Smith N, Moleón M. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review* 44:44–55.
- Perino A, Pereira HM, Navarro LM, Fernández N, Bullock JM, Ceausu S, Cortés-Avizanda A, van Klink R, Kuemmerle T, Lomba A, Pe'er G, Plieninger T, Rey Benayas JM, Sandom CJ, Svenning JC, Wheeler HC. 2019. Rewilding complex ecosystems. *Science* 364:6438.
- Pettorelli N, Gaillard JM, Mysterud A, Duncan P, Chr. Stenseth N, Delorme D, Van Laere G, Toïgo C, Klein F. 2006. Using a

- proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* 112:565–572.
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K. 2011. The Normalised Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research* 46:15–27.
- Polis GA, Power ME, Huxel GR. 2004. Food webs at the landscape level. University of Chicago Press.
- Putman R, Apollonio M, Andersen R, Eds. 2011. Ungulate management in Europe: problems and practices. Cambridge University Press.
- R Development Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna: R
- Rooney N, McCann K, Gellner G, Moore JC. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269.
- Sáenz-de-Santa-María A, Tellería JL. 2015. Wildlife-vehicle collisions in Spain. *European Journal of Wildlife Research* 61:399–406.
- Sandercock BK, Nilsen EB, Brøseth H, Pedersen HC. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology* 80:244–258.
- Sebastián-González E, Morales-Reyes Z, Botella F, Naves-Alegre L, Pérez-García JM, Mateo-Tomás P, Olea PP, Moleón M, Barbosa JM, Hiraldo F, Arrondo E, Donázar JA, Cortés-Avizanda A, Selva N, Lambertucci SA, Bhattacharjee A, Brewer AL, Abernethy EF, Turner KL, Beasley JC, DeVault TL, Gerke HC, Rhodes OE, Ordiz A, Wikenros C, Zimmermann B, Wabakken P, Wilmers CC, Smith JA, Kendall CJ, Ogada D, Frehner E, Allen ML, Wittmer HU, Butler JRA, du Toit JT, Margalida A, Oliva-Vidal P, Wilson D, Jerina K, Krofel M, Kostecke R, Inger R, Per E, Ayhan Y, Ulusoy H, Vural D, Inagaki A, Koike S, Samson A, Perrig PL, Spencer E, Newsome TM, Heurich M, Anadón JD, Buechley ER, Sánchez-Zapata JA. 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. *Ecography* 43:1143–1155.
- Selva N, Jędrzejewska B, Jędrzejewski W. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology* 83:1590–1601.
- Sevillano Morales J, Moreno-Ortega A, Amaro Lopez MA, Arenas Casas A, Cámara-Martos F, Moreno-Rojas R. 2018. Game meat consumption by hunters and their relatives: a probabilistic approach. *Food Additives and Contaminants: Part A* 35:1739–1748.
- Shuring JB. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B* 273:1–9.
- Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in terrestrial ecosystems. Berkeley and Los Angeles, CA: University of California Press.
- Valente AM, Acevedo P, Figueiredo AM, Fonseca C, Torres RT. 2020. Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. *Mammal Review* 50:353–366.
- Veen C, Fry E, ten Hooven F, Kardol P, Morriën E, De Long JR. 2019. The role of plant litter in driving plant-soil feedbacks. *Frontiers in Environmental Science* 7:168.
- Vicente J, Carrasco R, Acevedo P, Montoro V, Gortazar C. 2011. Big game waste production: sanitary and ecological implications. integrated waste management – Volume II (ed. by S. Kumar), pp. 97–128. InTech, Rijeka, Croatia.
- Vucetich JA, Peterson RO, Schaefer CL. 2002. The effect of prey and predator densities on wolf predation. *Ecology* 83:3003–3013.
- Watson JE, Venter O, Lee J, Jones KR, Robinson JG, Possingham HP, Allan JR. 2018. Protect the last of the wild. *Nature* 563:27–30.
- Wilmers CC, Getz WM. 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. *Ecological Modelling* 177:193–208.
- Wilson EE, Wolkovich EM. 2011. Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26:129–135.
- Zhou X, He Z, Ding F, Li L, Stoffella PJ. 2018. Biomass decaying and elemental release of aquatic macrophyte detritus in waterways of the Indian River Lagoon basin, South Florida, USA. *Science of the Total Environment* 635:878–891.
- Zuberogoitia I, del Real J, Torres JJ, Rodríguez L, Alonso M, Zabala J. 2014. Ungulate vehicle collisions in a peri-urban environment: consequences of transportation infrastructures planned assuming the absence of Ungulates. *PLoS ONE* 9:e107713.