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10 **Three decades of research on Iberian wild ungulates: key insights and** 11 **promising research avenues**

12

13 **ABSTRACT**

14 1. The Iberian Peninsula is witnessing ever-faster environmental changes, and new
15 challenges for wild ungulates are continuously emerging as they become more
16 abundant and widespread.

17 2. We conducted a systematic review to analyse the knowledge on wild ungulates
18 inhabiting the Iberian Peninsula. We used Web of Science and Scopus search
19 engines, complemented by searches in non-indexed journals, to examine peer-
20 reviewed articles published between January 1990 and July 2023.

21 3. The annual average growth rate in the number of publications was 17%. Most
22 studies focused on diseases and pathogens (36%), physiology, endocrinology and
23 reproduction (19%), and behaviour, population and community ecology (17%).

24 Red deer and wild boar are the most targeted species in scientific literature,
25 followed by the Iberian wild goat, roe deer, fallow deer, Southern chamois,
26 mouflon and aoudad.

27 4. We identify key knowledge gaps that deserve further attention such as the
28 ecological and social impacts of (re)introductions, the effects of increasing
29 ungulate densities on ecosystem integrity, and the impact of different hunting and

30 management techniques (some unique to the Iberian Peninsula) on population
31 dynamics. We also highlight the need to stimulate Iberian collaboration and
32 extend the discussion to a wider range of stakeholders to integrate different
33 perspectives on the research agenda for Iberian wild ungulates.

34 **KEYWORDS**

35 Conservation, ecosystem engineers, human-wildlife conflicts, population monitoring,
36 wildlife management

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38 **RUNNING TITLE**

39 Three decades of research on Iberian wild ungulates

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76 INTRODUCTION

77 European wild ungulates are experiencing an increase in number and geographical
78 distribution, mainly due to land abandonment, re-naturalisation of habitats, wild ungulate
79 translocations, and a decrease in hunting activities (**Valente et al. 2020; Carpio et al.**
80 **2021a**). This trend can have positive effects on ecosystem functioning due to the
81 restoration of trophic networks (**Foster et al. 2020**) and may increase hunting revenues
82 and/or ecotourism opportunities (**Margaryan & Wall-Reinius 2017**). However, high
83 ungulate densities might also cause damage to forestry and agriculture, posing a risk to
84 human safety due to their increasing involvement in vehicle collisions (**Torres et al.**
85 **2023**). The negative impacts of high ungulate densities on biodiversity and ecosystems
86 can also be noticeable. For instance, large herbivores impact plants' growth, survival and
87 reproduction, affecting the structure of plant communities and forest succession. At high
88 densities, this impact may trigger direct or indirect effects on ecosystem properties (e.g.,
89 nutrient cycling) and cascade down to other trophic levels, from small mammals to
90 invertebrates (**Côté et al. 2004; Ramirez et al. 2021**). The situation escalates when
91 considering the role of wild ungulates as reservoirs of relevant shared diseases (**European**
92 **Food Safety Authority (EFSA) 2022**), tick-borne pathogens, protozoan infections
93 (**Pereira et al. 2016**), and bacteria with antibiotic resistance (**Torres et al. 2020**). These
94 issues have intensified conflicts with humans and are increasingly relevant as social
95 attitudes and competing interests among stakeholders may shape conservation and
96 management decisions (**Martínez-Jauregui et al. 2020**). However, the analysis of the

97 services and disservices that wild ungulates provide clearly shows that human-wild
98 ungulate conflicts are context-dependent (**Linnell et al. 2020**). Based on this assumption,
99 our review is an important supplement focused on the Iberian Peninsula (i.e., Portuguese
100 and Spanish territories), where the burgeoning of wild ungulates is also noticeable.

101 The Iberian Peninsula acted as a refuge during the glacial advances of the Late
102 Pleistocene, which directly impacted the ecology and diversity of wild ungulates
103 (**Drucker et al. 2014**). Characterised by an interrupted human presence, the Iberian
104 Peninsula experiences contrasting environments and houses different wild ungulate
105 communities. Here, climate, land use dynamics, management practices and
106 epidemiological scenarios differ significantly from those observed in central and northern
107 Europe. Wild ungulate management in Europe is ruled by different objectives resulting
108 from species distribution, local densities and cultural history. In central Europe, for
109 instance, management aims to control crop damage and forest production caused by high
110 population densities (**Morellet et al. 2011**). Ungulate-vehicle collisions are also an issue
111 for several European countries. In other countries (e.g., Hungary), damage control is a
112 priority, but the implementation of management measures aimed at increasing trophy
113 quality are also mentioned (**Morellet et al. 2011**). Hunting is a deeply rooted tradition in
114 Portugal and Spain. Still, management practices are variable across the Iberian Peninsula,
115 with goals varying within a species. For instance, the Iberian wild goat *Capra pyrenaica*,
116 an Iberian endemism, is protected in Portugal; however, in Spain, it has been the most
117 valuable trophy among all game species (**Carvalho 2019**). In some areas (centre and
118 northern Portugal), deer management serves conservation purposes, especially as an
119 important prey for the endangered Iberian wolf *Canis lupus signatus*, while in others
120 (southern Iberia), deer are managed for trophy and venison production. Recently, in
121 Spain, the prohibition of recreational hunting within Spanish National Parks (Law

122 30/2014 BOE-A-2014-12588) has resulted in negative ecological impacts (**Carpio et al.**
123 **2024**). In the Iberian Peninsula, the effects of wild ungulates have been particularly
124 pronounced across various domains, ranging from ecosystems to animal health. This
125 phenomenon aligns with a concurrent increase in aridity conditions throughout the
126 territory (**Andrade et al. 2021**).

127 Here, we synthesise the current knowledge and highlight promising research
128 avenues aimed at helping the development of strategies for enhanced research and
129 practical outcomes related to Iberian wild ungulates. Through a systematic review, we
130 provide the necessary information to meet a set of common research goals to ensure the
131 balance between the conservation and management of wild ungulates.

132

133 **SYSTEMATIC REVIEW**

134 Our review is focused on eight species of wild-ranging ungulates inhabiting the
135 Iberian Peninsula – five native species, red deer *Cervus elaphus*, roe deer *Capreolus*
136 *capreolus*, Iberian wild goat *Capra pyrenaica*, Southern chamois *Rupicapra pyrenaica*
137 and wild boar *Sus scrofa*; and three non-native species – fallow deer *Dama dama*,
138 mouflon *Ovis aries* and aoudad *Ammotragus lervia* (**Figure 1**). We used Web of Science
139 (WoS) and Scopus search engines to access peer-reviewed articles published in English
140 over the last three decades (1st January 1990 to 31st July 2023). Our search included two
141 Boolean search statements referring to the geographic area of interest (Iberia* OR
142 Portugal OR Spain), the target species (Ungulate* OR Wild ungulate* OR Large
143 herbivore* OR Red deer OR Roe deer OR Fallow deer OR Iberian ibex OR Iberian wild
144 goat OR Spanish ibex OR Spanish wild goat OR Wild boar OR Chamois OR Pyrenean
145 chamois OR Mouflon OR Barbary sheep OR Aoudad), and the intersection of both. We
146 also screened non-indexed journals published in the Iberian Peninsula (*Lucanus – Revista*

147 *de Ambiente e Sociedade, Silva Lusitana, Galemys* – Spanish Journal of Mammalogy,
148 *Quaderns Agraris*) and written in Portuguese, Spanish or English. Our analysis did not
149 include grey literature (*e.g.*, research and government reports, conference papers) and
150 academic works (MSc and PhD theses). We recognise that these sources of information
151 may contribute to reducing thematic and geographic bias and increasing the effectiveness
152 of communication between scientists, the general public and policy makers. However, we
153 are also aware that the results of official reports and theses are often translated into
154 scientific publications. Moreover, compiling grey literature remains challenging, posing
155 several constraints to the systematic search for evidence.

156

157 **RESULTS AND DISCUSSION**

158 **Overall trends**

159 Our search resulted in 1,863 articles that were individually screened (PRISMA
160 flow diagram, **Appendix S1**). The articles analysed were grouped into ten research areas,
161 listed in alphabetical order: i) behaviour, population and community ecology (BePCE),
162 ii) biology of introductions and reintroductions (BIR), iii) disease and pathogens (DP),
163 iv) ecosystem engineering and services (EEES), v) genetics, phylogeography and
164 evolution (GPE), vi) hunting (H), vii) human-wild ungulate conflicts (HWC), viii)
165 methods and techniques for population monitoring (MTPM), ix) physiology,
166 endocrinology and reproduction (PER), and x) wild ungulates in the food web (WUFW).
167 We observed an expected increase in the number of publications (overall annual average
168 growth rate (AAGR) = 17%), particularly evident between 2000 and 2011 (AAGR =
169 21%). The greater awareness of wild ungulate positive and negative impacts, along with
170 the availability of research funds and accessibility to methodologies that were once more

171 expensive (*e.g.*, molecular genetic tools), have contributed to data collection, analysis,
172 and publication.

173 Red deer was the most targeted species (29%, AAGR = 51%), followed by wild
174 boar (26%, AAGR = 71%), Iberian wild goat (12%, AAGR = 33%), roe deer (11%,
175 AAGR = 21%), fallow deer (8%, AAGR = 27%), Southern chamois (7%, AAGR = 77%),
176 mouflon (5%, AAGR = 45%) and aoudad (3%, AAGR = 24%) (**Figure 2** and **Figure 3**).

177 The number of studies focused on feral ungulates is also increasing. Feral cattle *Bos*
178 *taurus*, horses *Equus caballus* and goats *Capra hircus* have been studied in research areas
179 ranging from behavioural ecology and genetics (feral cattle and horses) to feeding
180 ecology and ecosystem impacts (feral goats). Domestic and semi-domestic ungulates
181 have been used by managers and conservationists as part of rewilding initiatives (**Gordon**
182 **et al. 2021**). Therefore, understanding, anticipating and managing the impacts of feral
183 populations on native biodiversity and ecosystems must be a priority. The number of free-
184 living Vietnamese pot-bellied pigs is also increasing; however, the number of studies is
185 still limited, despite the expected impacts of Vietnamese pig populations (*e.g.*,
186 hybridisation with wild boar, crop damage, disease spread, **Delibes–Mateos & Delibes**
187 **2013**). The accidental or deliberate release of domestic ungulates should be monitored
188 and prevented.

189 Regarding wild ungulates, most of the studies focused on DP (36%), which has
190 experienced growing interest throughout the years (AAGR = 30%). The PER (19%)
191 experienced growth in the number of studies until 2006 (AAGR = 39%) before stabilising
192 (AAGR = 4%), and BePCE studies (17%) have been decreasing since 2011 (AAGER = -
193 2%). Studies addressing ecosystem engineering and services (EEES) also represent a
194 significant proportion of the scientific literature (10%) and have been increasing
195 consistently since 1996 (AAGR = 16%). Although less representative, a recent upward

196 trend has been observed for HWC (3%, $AAGR_{\text{since2002}} = 54\%$), MTPM (4%,
197 $AAGR_{\text{since2006}} = 40\%$) and WUFW (3%, $AAGR_{\text{since2016}} = 16\%$). This fact mirrors the
198 burgeoning of Iberian wild ungulate populations and the consequent demand for
199 monitoring methods, as well as new approaches to mitigate conflicts and foster
200 coexistence. The number of studies on GPE (6%) of wild ungulates reached its highest
201 level between 2009 and 2011 and has decreased since then. The BIR (1%) has been less
202 explored, which may be related to many of these initiatives being private and/or poorly
203 documented through scientific forums. The number of studies on the effects of hunting
204 (H, 2%) on wild ungulate populations is still limited, even considering the ecological,
205 evolutionary and socioeconomic relevance of this activity. Studies including both Iberian
206 countries are scarce; however, they are gradually increasing, demonstrating a growing
207 awareness of the need to improve the effectiveness of conservation and management of
208 transboundary populations.

209

210 **Behaviour, population and community ecology**

211 In the Iberian Peninsula, most studies have focused on the mating system of red
212 deer, which is based on the defence of mating territories (**Carranza et al. 1990**). Females
213 usually visit particular sites for feeding, making them worthy of being defended by males
214 during the rutting season (**Carranza et al. 1996**). However, changes in weather
215 conditions over the years produce variations in the spatial distribution of females (**Pérez-**
216 **González & Carranza 2011**) and in the opportunities for sexual selection (**Millán et al.**
217 **2021**).

218 Management options also influence population productivity, composition (*e.g.*,
219 the proportion of adult males), and structure (*e.g.*, sex ratio), affecting male-male
220 competition (**Pérez-González et al. 2009**). Male competition for mates is weak in areas

221 characterised by many females and few mature males, which limits the transmission of
222 genetic diversity via paternal lineage (**Pérez-González et al. 2009**). The weak
223 competition between males also compromises the development of signals they use to
224 convey information about their willingness to compete (**de la Peña et al. 2020**).
225 Moreover, males inhabiting areas of low competition tend to develop smaller antlers than
226 those inhabiting areas with more equilibrated sex-ratios and a higher proportion of adult
227 males (**Carranza et al. 2020**).

228 Few studies have addressed the interactive effects of increasing wild ungulate
229 densities and aridity on ecological and behavioural traits. For instance, these concurrent
230 phenomena may delay conception dates (**Peláez et al. 2017**), which have marked and
231 long-lasting effects on population demography (**Peláez et al. 2021**). Population density
232 of wild ungulates affects nutritional condition, one of the most important determinants of
233 individual fitness. Despite the small number of studies in the Iberian Peninsula, it has
234 already been demonstrated in other environmental contexts that nutritional constraints
235 impact several life-history traits, causing a decrease in neonates' survival (**Monteith et**
236 **al. 2014**), an increase in the age of primiparity (**Festa-Bianchet et al. 1995**), a reduction
237 in the pregnancy rate (**Hamel et al. 2010**), and also influence the development of
238 phenotypic traits, such as the horn growth of the Iberian wild goat (**Carvalho et al. 2020**).
239 Understanding how density-dependence and intra and interspecific interactions in areas
240 explored by several ungulate species and populations (wild and feral) may exacerbate the
241 pressures induced by increasing aridity is pivotal to anticipating the impacts of ungulate
242 sympatry on life-history traits (e.g. pregnancy rate, age at first reproduction, litter size,
243 size at birth), sex- and age-related differences, space use, habitat selection, foraging
244 decisions and social organisation of wild Iberian populations. This is an essential step
245 towards adaptative management.

246

247

248 **Biology of introductions and reintroductions**

249 Species introductions and reintroductions are described as the deliberate release
250 of individuals to establish new, viable wild populations. In the Iberian Peninsula, four
251 ungulate species have been the focus of most reintroduction programmes – red deer, roe
252 deer, Iberian wild goat, and the Southern chamois. Different motivations drove
253 translocation initiatives, such as the demand for roe and red deer hunting, the increase in
254 prey density for the Iberian wolf *Canis lupus signatus* in Portugal, or the re-establishment
255 of species to increase local biodiversity and promote ecosystem functioning restoration
256 (**Valente et al. 2017, Fonseca et al. 2017**). Monitoring the reintroduced populations after
257 their release, and specifically understanding how different factors affect reintroductions,
258 is vital to shed light on the success of the reintroductions and maximise the effectiveness
259 of future interventions. Although limited in number, there are some good examples where
260 the status of the recently reintroduced populations has been monitored (**Perea et al. 2015;**
261 **Torres et al. 2016**). A key driver for the reintroduction's success is site fidelity.
262 Successful translocations should aim to achieve high site fidelity, since those sites are
263 often identified as having high habitat quality and reduced anthropogenic disturbance –
264 factors that would presumably increase survival (**Yott et al. 2011**). This is particularly
265 relevant during the initial period of animal release, as it will allow for the establishment
266 of a new population and the consequent colonisation of new areas due to natural dispersal.

267 We acknowledge the difficulty of classifying reintroductions as a success or a
268 failure, as some species might take a long period to form a self-sustainable population,
269 and failed initiatives are not usually reported. Releasing species to the wild without a
270 clearly defined programme based on the International Union for Conservation of Nature

271 (IUCN) guidelines (IUCN/SSC 2013, Torres et al., 2018) will probably lead to
272 unwanted consequences, with deleterious ecological, genetic, and socioeconomic
273 impacts. We suggest some factors to consider when designing and implementing a
274 reintroduction project: i) environmental – the identification of suitable habitat is crucial;
275 ii) biological – the assessment of the dynamics and genetics of the source population, as
276 reintroductions can cause population bottlenecks, leading to a decrease in genetic
277 diversity and/or inbreeding depression, iii) ecological – the study of species interactions,
278 including those with domestic relatives, and the effects on soil and vegetation (García-
279 Rodríguez et al. 2021), iv) socio-economic – the assessment of attitudes, tolerance, and
280 the willingness of local communities to support the reintroduction, and v) financial – the
281 estimation of the reintroduction and monitoring costs. It is crucial to document the results
282 of introduction and reintroduction initiatives, including unintentional releases (Moço et
283 al. 2006; Herrero et al. 2013), raise awareness among private entities about the
284 importance of animals' origins and monitoring, including non-native species, and
285 establish adequate and reliable indicators based on ecological changes (e.g., ecosystem
286 functioning, conservation of threatened flora, wildlife, or soil properties, among others)
287 to assess the long-term sustainability of a particular area to new introductions,
288 reintroductions, or population reinforcements (Refoyo et al. 2022).

289

290 **Disease and pathogens**

291 Wild ungulates are interesting models for disease research due to their diversity,
292 broad geographic distribution and close relationships with humans and livestock. Most
293 studies in Iberia have focused on pathogens of i) economic importance for livestock
294 husbandry, such as *Mycobacterium tuberculosis* complex (Santos et al. 2022),
295 gastrointestinal and respiratory parasites (Fontoura-Gonçalves et al. 2023), and

296 emerging viruses (*e.g.*, bluetongue, **Jiménez-Ruiz et al. 2022**), ii) conservation
297 relevance, in special sarcoptic mange *Sarcoptes scabiei* (**Pérez et al. 2021**) and
298 pestiviruses (**Jiménez-Ruiz et al. 2021**), particularly in the Iberian wild goat and
299 Southern chamois, respectively, and iii) zoonotic pathogens, such as tick-borne (**Díaz-
300 Cao et al. 2022**), *Toxoplasma gondii* (**Barroso et al. 2020**), and *Trichinella* spp
301 (**Boadella et al. 2012**). Case reports, descriptive pathology, and the development and
302 validation of diagnostic methods were common, reflecting the continuous emergence of
303 pathogens and the need to evaluate the performance of the diagnostic tools (**Michel et al.
304 2021**). While some studies were cross-sectional, allowing for the estimation
305 (sero)prevalences and the identification of risk factors, others focus on an eco-
306 epidemiological perspective, highlighting that many pathogens are maintained by multi-
307 host communities (**Santos et al. 2022**). Interestingly, some studies have investigated the
308 cross-species transmission of pathogens at the wildlife-livestock-human interfaces, in line
309 with the increasing recognition of the importance of spill-over from wildlife in disease
310 emergence (**Barroso et al. 2021**). Epidemiological studies characterising pathogens using
311 genetic tools were also common (**Dashti et al. 2022**), and antibiotic resistance in wild
312 ungulates has also been the subject of increasing attention in the last decade (**Torres et
313 al. 2020**).

314 The continuous emergence of pathogens in ungulates warrants further disease
315 surveillance and monitoring in wild populations and extensive farming (**Jiménez-Ruiz et
316 al. 2022**). This is particularly relevant as the Iberian Peninsula is geographically close to
317 Africa, where many pathogens absent in Europe circulate among domestic and wild
318 ungulates (**García-Bocanegra et al. 2016**). Disease surveillance should be performed by
319 integrating information on pathogen prevalence, risk factors, host abundance, and
320 behaviour (**Cardoso et al. 2021**). The build-up of wild ungulate biobanks will support

321 the trend for long-term epidemiological monitoring. The use of phylodynamic tools for
322 reconstructing transmission pathways from genomic data and dynamic epidemiological
323 models should become more frequent in the coming years to deepen knowledge of
324 pathogen transmission and potential management actions. The Iberian Peninsula has
325 pioneered the integrated monitoring of ungulate populations and pathogens at the
326 wildlife-livestock interface, as well as the assessment of alternative disease control
327 methods (**Gortázar et al. 2015**). However, as changes in land use and human interests
328 continuously disrupt and reshape the interface between wild ungulates, domestic animals,
329 and humans, experimental studies should continue to test the effectiveness of disease
330 control actions (e.g., vaccination, vector control, selective culling, zonation) *in situ*. This
331 is the most welcome step towards the implementation of proper management programmes
332 directed at controlling pathogens relevant to human and animal health.

333

334 **Ecosystem engineering and services**

335 Ecosystem services linked to wild ungulates include supporting (e.g., biodiversity,
336 seed dispersal), provisioning (e.g., meat, antlers), regulating (e.g., carbon stocks, nutrient
337 cycling) and cultural (e.g., landscape, tourism) services (**Appendix S2, Velamazán et al.**
338 **2020**). Supporting services are probably the most studied. The activity of wild ungulates
339 can define both ecosystem composition and structure in the long-term. Through grazing,
340 wallowing, excreting, and trampling, wild ungulates can alter plant diversity and
341 physiology, influence habitat characteristics and, ultimately, drive the dynamics of
342 vertebrate and invertebrate populations (**Bugalho et al. 2011**). Wild ungulate-plant
343 interactions have been extensively studied, showing that the effects of wild ungulates on
344 primary production are modulated by the seasonal and spatial oscillations of species'
345 feeding behaviour (**Muñoz-Reinoso 2017**) and habitat carrying capacity (**Paton et al.**

346 **1999**). Wild ungulates can alter plant recruitment through selective feeding and even
347 modify plant growth and physiology (**Perea et al. 2020**). Intense grazing, for instance,
348 affects vegetation's reproductive structures and cycles, thus impacting seed production
349 (**Lecomte et al. 2017**). This favours earlier successional stages of the vegetation,
350 maintaining small plants and open areas, while participating in the maintenance of
351 habitats such as the *dehesas* or *montados*, a cultural landscape characterised by a
352 multifunctional agro-silvo-pastoral system (**López-Sánchez et al. 2016**). By fostering
353 landscape heterogeneity and limiting shrub encroachment, wild ungulates may indirectly
354 contribute to increasing the resilience and stability of ecosystem properties and processes
355 under environmental change (**Barbosa et al. 2020**). Although several lines of evidence
356 reveal a decrease in most biodiversity components when wild ungulate populations
357 become overabundant (**Bugalho et al. 2011; Carpio et al. 2015; Velamazán et al. 2017**),
358 it remains unclear how and in which direction wild ungulates affect soil properties, as
359 both positive and negative responses have been reported. For instance, wild ungulates can
360 negatively impact terrestrial arthropods by decreasing food availability and suitable
361 places for egg production, laying and incubation (**Carpio et al. 2014**). In contrast, by
362 promoting soil disturbance and landscape heterogeneity, wild ungulates can positively
363 affect soil fauna diversity and abundance (**González-Megías et al. 2004**). Wild ungulates
364 also modify rodent behaviour (i.e., spatial distribution and space use), and thus their
365 foraging decisions and, ultimately, seed dispersal dynamics (**Sunyer et al. 2016**).

366 Although wild ungulate impacts are particularly noticeable when populations
367 reach high densities, the density thresholds beyond which ungulates have a negative effect
368 on ecosystem properties (e.g., forest regeneration, structure and functioning) are strongly
369 context-dependent (**Carpio et al. 2021**). A semi-quantitative review showed that a roe
370 deer density of 10-23 animals/km² reaches a tipping point where ungulates have a

371 negative effect on forest regeneration (**Ramirez et al. 2018**). In Iberian Mediterranean
372 landscapes, it has been demonstrated that red deer densities above 30 animals/km² are
373 clearly incompatible with the conservation and regeneration of vegetation (**Perea et al.**
374 **2014**). Using ecological indicators to monitor wild ungulate populations could be a step
375 towards sustainable wildlife communities (**Perea et al. 2015**). The management of wild
376 ungulates, oriented to partially take up the role of livestock in Mediterranean abandoned
377 landscapes, could ensure the conservation of high nature value systems or EU-protected
378 habitats included in the Natura 2000 network (supporting and cultural services, **San**
379 **Miguel et al. 2010**). The conversion of heterogeneous Iberian landscapes into simplified
380 and intensified systems has resulted in the loss or gain of important ecosystem services
381 provided by Iberian wild ungulate populations (**López-Sánchez et al. 2016**). Complex
382 multi-trophic networks, such as wild ungulate-plant-small mammal-arthropod
383 interactions represent a promising research avenue that could provide relevant
384 information on the effects of wild ungulates on pest control and ecosystem functioning.
385 Cross-scale wild ungulate-plant-soil interactions would also offer new insights into
386 supporting and regulating services such as water quality, carbon and water storage, and
387 wildfire prevention (**Lecomte et al. 2019**; **Barbero-Palacios et al. 2020**). Finally, the
388 cumulative effects of sympatric domestic and wild ungulates on ecosystem properties and
389 functioning should be evaluated.

390

391 **Genetics, phylogeography and evolution**

392 The first accounts on the genetics of Iberian wild ungulates – Cantabrian chamois,
393 fallow deer and roe deer (*e.g.* **Pérez-Barbería et al. 1996**) – date back to the late 90's.
394 Since then, the phylogeography, genetic structure and diversity of native Iberian ungulate
395 populations have been thoroughly studied, particularly for native species such as the

396 chamois (**Rodríguez et al. 2010**), Iberian wild goat (**Angelone-Alaasad et al. 2017**), red
397 deer (**Sommer et al. 2008**), roe deer (**Royo et al. 2007**) and wild boar (**Ferreira et al.**
398 **2009**). Knowledge concerning the genetics of introduced species remains limited despite
399 recent contributions on fallow deer (**Baker et al. 2017**) and aoudad (**Stipoljev et al.**
400 **2021**). Patterns of genetic structure and diversity of native Iberian ungulates primarily
401 reflect the natural dynamics caused by the climatic fluctuations of the Quaternary –
402 namely, the last glacial maximum (LGM) – in Iberia and Europe (**Sommer et al. 2008**),
403 with a minor influence from human-mediated translocations and reintroductions. Whether
404 Iberian ungulate populations played a substantial role in Europe’s post-LGM
405 recolonisation (**Velickovic et al. 2015**) or had a minor contribution is still debatable. Still,
406 recent evidence assigns a major role to populations located in southern France, as in the
407 case of red deer or wild boar (**Queirós et al. 2019, de Jong et al. 2023**). In either case,
408 Iberia was a faunal refugium during the Quaternary glaciations, resulting in the high
409 diversity and singularity of most of the Iberian ungulate populations (**Carranza et al.**
410 **2016, 2024**).

411 The impact of human-mediated translocations or reintroductions on the patterns
412 of genetic diversity and structure of Iberian ungulate populations has been shown to be
413 relevant in more local contexts and for highly managed species such as the Iberian wild
414 goat (**Barros et al. 2022**), red deer (**Queirós et al. 2019**), and roe deer (**Barros et al.**
415 **2020**). Hybridisation is likely to be relevant in local contexts and has been detected in the
416 cases of wild boar and domestic pig (**de Jong et al. 2023**), Iberian wild goat and domestic
417 goat (**Cardoso et al. 2021**), or even among native and introduced red deer populations
418 (**Queirós et al. 2020**). Wild ungulates are important game species, and the impacts of
419 management and hunting practices on the genetic diversity, structure, or fitness of Iberian
420 populations have been reported, mainly on red deer (**Martínez et al. 2002**). Investigation

421 into quantitative trait loci, adaptative traits and polymorphisms relevant to fitness or
422 development is still scarce and biased towards economically relevant species.

423

424 **Hunting**

425 Hunting is considered an effective measure to control overabundant wild ungulate
426 populations (**Quirós-Fernández et al. 2017**). Yet, when unrestricted and directed at
427 specific individual characteristics, hunting can have significant impacts on population
428 size and structure (**Pérez-González et al. 2012**) and can lead to evolutionary and/or
429 phenotypic changes in the life-history traits of wild ungulates (**Festa-Bianchet 2016**). In
430 the Iberian Peninsula, the number of well-replicated studies assessing the long-term
431 consequences of hunting at individual and population levels is scarce. By analysing the
432 temporal trends in horn size of the Iberian wild goat and aoudad, **Pérez et al. (2011)**
433 observed that horn length in harvested males decreased, suggesting that the selective
434 removal of large-horned animals contributed to this decline. Recently, it was
435 demonstrated that removing small-horned male individuals increased horn growth in male
436 wild goats, probably because it reduced the influence of density-dependent factors and
437 prevented smaller males from breeding (**Carvalho et al. 2020**). Regarding environmental
438 conditions, horn growth in Cantabrian chamois was positively correlated with annual
439 precipitation (**Pérez-Barbería et al. 1996**), and drought negatively influenced the body
440 and antler size of red deer males (**Peláez et al. 2018**). Antler size was also negatively
441 related to population density and hunting pressure but positively associated with acorn
442 yield in oak-dominated systems of Iberia (**Peláez et al. 2018**). It is therefore imperative
443 to understand how different hunting modalities, environmental variation and diseases
444 interact and drive the life-history traits and, ultimately, the dynamics of Iberian wild
445 ungulate populations. This data-dependent question requires a serious, long-term

446 commitment from game managers, hunters and wildlife researchers. This will help to
447 unravel research areas related to fundamental ecology but also focus on management and
448 potential threats (genetic (**Martínez et al. 2002**), demographic (**Carpio et al. 2021**) and
449 phenotypic (**Carvalho et al. 2018**)) that emerge from poorly regulated hunting, different
450 hunting strategies (e.g., trophy hunting, *montería*) and regimes (e.g., supplementary
451 feeding, restocking, fencing, mating arrangements), as well as environmental changes.

452

453 **Human-wild ungulate conflicts**

454 Conflicts between humans and wild ungulates are old, deeply rooted and have
455 long been recorded in the Iberian Peninsula. In rural regions, the damage to crops and
456 forests can incur significant costs for farmers, while pathogens transmission and disease
457 emergence are the main concerns in rural livestock areas (**Barasona et al. 2017**).
458 Although the adoption of preventive measures is underway (**Gortázar et al. 2015**,
459 **Laguna et al. 2022**), these conflicts are still current in the Iberian Peninsula and remain
460 an important issue for wildlife managers. Recently, these conflicts have also occurred in
461 urban and peri-urban areas due to the expansion of wild ungulates and urban sprawl. This
462 pose renewed management challenges that have been addressed in some recent scientific
463 literature. The main Iberian wild ungulates reported in urban and peri-urban areas are the
464 wild boar and roe deer (**Carpio et al. 2021a**). The availability of food, water, and
465 vegetation patches, the lack of hunting and predators, and the existence of landscape
466 features that promote movement, such as streams, rivers and urban parks, seem to be the
467 leading causes of wild boar presence in urban environments (**Castillo-Contreras et al.**
468 **2018**). Besides the well-known human-ungulate conflicts (**Castillo-Contreras et al.**
469 **2022**), urban life may present risks for urban ungulates, such as exposure to poison or
470 pollutants, injuries or death following vehicle collisions or dog attacks, and lethal control

471 (Conejero et al. 2020). Moreover, in response to urban selection pressures, wild
472 ungulates, particularly the wild boar, can experience changes in their behaviour (e.g.,
473 altered feeding behaviour), morphology (e.g., larger size), physiology (e.g., altered
474 metabolites), or genetics (e.g., differentiated genetic structure) (Castillo-Contreras et al.
475 2021). Recommended management measures aimed at mitigating human-wild ungulate
476 conflicts include the reduction of the attractiveness of the urban and peri-urban areas (e.g.,
477 food availability) and removing urban individuals (Torres-Blas et al. 2020). As lethal
478 control is not generally approved by the public (Martínez-Jauregui et al. 2020),
479 management strategies should also include awareness campaigns to inform people about
480 the causes and consequences of maintaining large wild ungulates in urban and peri-urban
481 areas (Howe et al. 2012). The capture and translocation of individuals are not advised
482 since translocated animals can resume their problematic behaviour in the new location
483 (Massei et al. 2010). Female fertility control is probably not feasible or efficient in free-
484 living populations (González-Crespo et al. 2018).

485 Increasing populations of wild ungulates will likely lead to more frequent
486 conflicts in the future. The opportunities and risks of human-wild ungulate coexistence
487 are well-known (Linnell et al. 2020). Here, we focused on the human-wild ungulate
488 conflicts in urban and peri-urban settings; however, the conflicts in rural areas are
489 persistent and widespread. Different social perceptions regarding wild ungulates demand
490 context-specific management approaches aimed at limiting risks (e.g., crop damage,
491 pathogen transmission, vehicle collisions) and boosting opportunities (e.g., ecological
492 restoration, hunting and touristic revenues).

493

494 **Methods and techniques for population monitoring**

495 The estimation of population metrics related to Iberian wild ungulates is required
496 from a management perspective to adjust extraction quotas (**Carpio et al. 2021b**) and,
497 from an ecological perspective, to describe the key traits that drive population dynamics
498 (**Carranza et al. 2020**). Earlier studies on Iberian wild ungulates were based on
499 abundance indices (i.e., proxies for population size), such as hunting yields and the
500 kilometric abundance index (**Vicente et al. 2006**). Although these methods are currently
501 deprecated, they remain useful for producing and comparing population trends at large
502 spatial and temporal scales (**Acevedo et al. 2014**). Since the early 1990s, the distance
503 sampling approach based on direct observations has been recognised as the gold standard
504 and has been widely used to estimate wild ungulate density and abundance (**Prada et al.**
505 **2019**), even in large-scale and long-term monitoring programmes (**Granados et al. 2020**).
506 Comparative studies have been carried out to develop and validate feasible and cost-
507 effective methods (i.e., direct observations require significant sampling efforts that are
508 not always feasible due to financial and human constraints), mostly based on different
509 approaches to pellet counts, also including the theoretical framework of distance sampling
510 (**Torres et al. 2015**). However, the behaviour of wild boar (e.g., vigilance, natural anti-
511 predatory strategies such as fleeing and hiding behaviour, **Morelle et al. 2014**), the most
512 abundant and widespread Iberian ungulate, strongly limits the capability of both direct
513 and indirect methods to estimate the density and abundance of its populations (but see
514 **Acevedo et al. 2007**). In this context, the use of camera traps, mainly coupled with models
515 that do not require individual recognition (e.g., random encounter models - REM,
516 **Rowcliffe et al. 2008**), has recently emerged as a promising approach to estimating the
517 density and abundance of elusive species (**Palencia et al. 2019**). Large-scale studies using
518 REM are currently being conducted to optimise and standardise the method
519 (**ENETWILD Consortium et al. 2019**). There are other models, also independent of

520 individual recognition, that are being tested (**Palencia et al. 2021**), such as the random
521 encounter and staying-time model (**Nakashima et al. 2018**) and the distance sampling
522 with camera traps (**Howe et al. 2017**). The study of disease dynamics and the prevention
523 of wildlife and livestock contacts has also fostered methodological progress. For instance,
524 the use of unmanned aircraft systems has been employed to study the spatial
525 epidemiology of tuberculosis (**Barasona et al. 2014**); the development of proximity
526 loggers and GPS tracking devices has enabled the study of transmission risks and allowed
527 the description of different transmission dynamics using movement-based models
528 (**Herraiz et al. 2024**). Moreover, tools and apps have been improved to standardise data
529 collection and reporting (**ENETWILD Consortium et al. 2022**). A notable example of
530 the long-term monitoring of a wild ungulate comes from the Sierra Nevada (southeastern
531 Spain), where data on the abundance and demographic structure of the Iberian wild goat
532 population have been systematically collected over the last three decades (**Granados et**
533 **al. 2020**). Population density and abundance should be one of the bases for population
534 monitoring, but not the only one. As overabundance (i.e., the population density threshold
535 beyond which socioeconomic, ecological and/or health negative impacts are recorded)
536 relies on the environmental and social context, developing indicators of change provides
537 a robust and complementary framework for scientifically based monitoring programmes
538 of both free-living and confined populations.

539 **Physiology, endocrinology and reproduction**

540 Wild ungulates health and survival are compromised when a stressor agent is very
541 intense or perpetuated over time (**Boyle et al. 2021**). In the Iberian Peninsula, studies
542 have primarily focused on the physiological stress responses of red and roe deer, usually
543 by quantifying the concentration of metabolised glucocorticoids in faeces. High
544 population densities and mass hunting, for instance, have been associated with higher

545 long-term faecal glucocorticoid metabolite (FGM) levels in red deer (**Santos et al. 2018**).
546 The same authors also reported variations in FGM levels due to local climate conditions
547 and individual traits in distinct Iberian red deer populations. Recently, a positive
548 correlation was reported between endoparasite load, faecal testosterone metabolites, and
549 the size of the dark ventral patch (an indicator of male reproductive effort) when male-
550 male competition is particularly intense (**de la Peña et al. 2020**). Regarding roe deer, a
551 negative impact of traffic volume and livestock presence on the FGM levels was
552 documented (**Iglesias-Merchan et al. 2018**). FGM levels are lower when roe deer body
553 condition increases in the non-breeding season. Yet, these levels are positively correlated
554 with the reproductive condition of roe deer, which is higher where food resources are
555 abundant (**Escribano-Ávila et al. 2013**). Methodologically, it is worth highlighting
556 enzyme immunoassays and radioimmunoassays to extract glucocorticoids or their
557 metabolites present in biological samples (**Barja 2015**), as well as the validation
558 (viability, reliability and prediction) of near-infrared spectroscopy to quantify
559 glucocorticoids in wild ungulate faeces (**Santos et al. 2016**).

560 The physiology and endocrinology of Iberian wild ungulates are poorly explored.
561 Future lines of research should focus on a multi-species approach, including the stressors
562 that generally induce physiological stress responses, such as individual (e.g., sex and age),
563 population (e.g., density and population structure), ethological (e.g., social status,
564 intraspecific interactions and the presence of predators), environmental (e.g., climate and
565 resource availability) and human-induced (e.g., hunting and infrastructures) factors.

566

567 **Wild ungulates in the food web**

568 Wild ungulates are key elements in the food web. They are the main prey of the
569 Iberian wolf, progressively replacing the role of domestic livestock in some regions of

570 their distribution area (**Figueiredo et al. 2020**). Their role as wolves' prey has been
571 associated with a positive perception of wild ungulates by shepherds (**Pascual-Rico et al.**
572 **2020**). There are other mammals, such as the brown bear *Ursus arctos*, the Iberian lynx
573 *Lynx pardinus*, the red fox *Vulpes vulpes*, and birds of prey, such as the golden eagle
574 *Aquila chrysaetos*, that also sporadically prey on wild ungulates, mainly offspring or
575 weakened individuals (**Sánchez-Zapata et al. 2010**). Nevertheless, the main input of wild
576 ungulates to the food chain is mediated by the consumption of carrion. Most species listed
577 above as predators of wild ungulates are also facultative scavengers. To these should be
578 added the four species of obligate scavengers: the griffon *Gyps fulvus*, the cinereous
579 vulture *Aegypius monachus*, the Egyptian vulture *Neophron percnopterus* and the
580 bearded vulture *Gypaetus barbatus*, as well as other facultative scavengers including
581 mesocarnivores, corvids, raptors, and the wild boar. In fact, up to 31 species of terrestrial
582 vertebrates have been documented consuming carrion from Iberian wild ungulates
583 (**Appendix S3, Mateo-Tomás et al. 2015**). The availability of wild ungulate carcasses is
584 linked to human activities, such as hunting and vehicle collisions, and natural phenomena,
585 such as predation or diseases (**Morant et al. 2022**). The seasonality and predictability of
586 massive hunting events seem to favour consumption by obligate scavengers such as large
587 vultures. In contrast, stalking would offer more opportunities to facultative scavengers
588 (**Carrasco-García et al. 2018**). However, the consumption of hunting remains could
589 have negative effects associated with lead consumption from hunting ammunition, which
590 may be a relevant cause of intoxication for scavengers (**Arrondo et al. 2020**). The
591 consumption of carrion from other causes of mortality, such as diseases, has been less
592 studied but could have a very relevant effect in the context of the progressive expansion
593 and growth of wild ungulate populations.

594 Wild ungulates and their consumers are regaining ground after centuries of human
595 persecution. The increasing availability of wild ungulate carcasses and the decline in
596 extensive livestock farming result in highly heterogeneous spatio-temporal patterns of
597 carrion availability, which have scarcely been studied yet are of great relevance to the
598 functioning of ecosystems and the structure of scavenger communities.

599

600 **SYNTHESIS AND WAY FORWARD**

601 The paradigm that drives the management of Iberian wild ungulates has changed
602 in less than three decades. Previously focused on fostering wild ungulates, the aim in
603 some Iberian regions is now to mitigate the impacts of overabundant populations.
604 Balancing the conservation of wild ungulates while mitigating their impacts remains a
605 challenging endeavour. Scientific evidence, transparency, social involvement, and
606 improved communication across borders are key to tackling this challenge and improving
607 coexistence between humans and wild ungulates. The Iberian Peninsula has been an
608 important region where the impact of wild ungulates on the social and health settings has
609 been studied in unprecedented detail. Still, as new methods are readily available and new
610 challenges for wild ungulates are emerging as they become more abundant and
611 widespread, the time is right to generate fundamental and new applied knowledge in
612 different research areas. Our systematic review represents an important summary of
613 scientific evidence and will assist in the strategic application of resources to tackle a set
614 of open questions (**Appendix S4**).

615 The combination of natural, field and laboratory experiments has been envisaged
616 as the best way to assess the ecological effects of large herbivores (**Côte et al. 2004**). By
617 coupling natural and field experiments with remote sensing technologies (e.g., multi- and
618 hyperspectral sensors), we will be able to estimate the carrying capacity of ecosystems,

619 clarify the role of wild ungulates as ecosystem engineers, and shed light on the ecosystem
620 services they provide. This is important for predicting how an ecosystem will respond to
621 the reintroduction, reinforcement, or control of wild ungulate populations. The Iberian
622 Peninsula is experiencing increasing aridity and land abandonment, which impact land
623 configuration and promote shrub encroachment (**Peñuelas et al., 2017**). How and in what
624 densities wild ungulates contribute to the reverse shrubification of Iberian landscapes and
625 slow down the intensity of wildfires is key to adjusting land and population management
626 measures.

627 By increasing the reliability of population estimates, we will be able to assess the
628 impacts of intra- and interspecific interactions on the behaviour and physiological
629 responses of populations under environmental changes. The knowledge of wild ungulate
630 distribution, abundance and behaviour will also allow for anticipating the emergence and
631 spread of zoonotic and multi-host pathogens, as well as understanding how land use
632 changes drive the risk of spillover to livestock and humans. This is particularly relevant
633 in the Iberian Peninsula, where the ongoing land use changes, motivated by land
634 abandonment, intensive agriculture, urban sprawl and wildfires, continuously reshape the
635 interface between wild ungulates, domestic animals and humans.

636 By harnessing the synergies between natural and social sciences, we will gain
637 access to a wide range of complementary methods that will aid in tailored land-sharing
638 strategies, define control measures in human-modified regions and propose innovative
639 participatory methods to reconcile opposing stakeholder views. This is an important step
640 as recent evidence suggests that the coexistence between large mammals, including wild
641 ungulates, and humans is mainly driven by the human willingness to share the landscape
642 with wildlife (**Cretois et al. 2020**).

643 Hunters and researchers have been cooperating for years. The information
644 collected from hunted wild ungulates (*e.g.*, hunting bags, sex-ratios, body measurements,
645 body samples) is relevant and should be carefully standardised to make it available over
646 time and comparable across space (**ENETWILD et al. 2019; Carvalho et al. 2024**). This
647 will help to increase the understanding of several research areas related to fundamental
648 ecology, diseases and management, such as the effects of human-induced and/or
649 environmental changes on phenotypic trait variation and the reproductive performance of
650 wild populations. We will gain a more comprehensive and mechanistic understanding of
651 wild ungulate ecology and management if we look at how the different research areas fit
652 together. Overabundance, for instance, cannot be defined rigorously unless it is placed in
653 a specific context and supported by tangible social, economic, ecological and health
654 indicators. The resulting information from the different research areas would allow for
655 the identification of density thresholds aimed at limiting the negative effects of wild
656 ungulates and will provide the necessary support to shift from population-based to
657 ecosystem-based management. The multidisciplinary and multi-sectorial collaboration is
658 needed to evaluate the contexts (*e.g.*, socioeconomic, environmental) and situations (*e.g.*,
659 fenced or free-ranging populations) upon which wild ungulates can be considered
660 overabundant (see also **Caughley (1981)** and **Côte et al. (2004)**): i) are wild ungulates
661 threatening human activities and health? ii) are they jeopardising their own body
662 condition and individual performance? iii) are wild ungulates negatively impacting the
663 conservation and subsistence of other species? and/or iv) are they disrupting ecosystem
664 functionality? Here, we incorporated the contributions of wildlife researchers. Still, future
665 assessments should rely on a wider range of perspectives, including different
666 stakeholders, as their opinions and knowledge are pivotal, and the success of evidence-

667 based measures relies on their prior acceptance. We hope our approach stimulates Iberian
668 collaboration and an extended discussion in empirical, theoretical and applied work.

669

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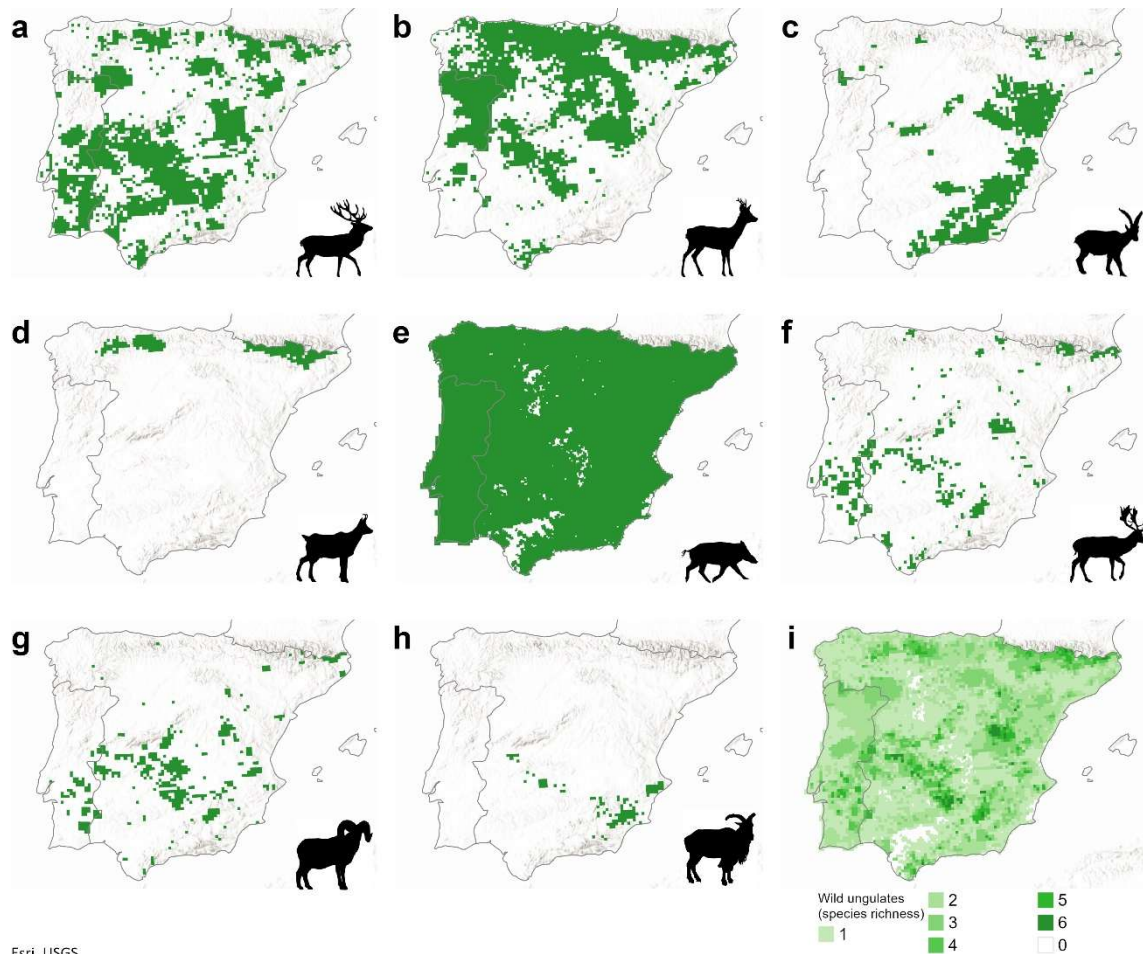
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1275 Esri, USGS

1276 **Figure 1** – Distribution of Iberian wild ungulates: (a) red deer (currently present in 34%
 1277 of the Iberian territory), (b) roe deer (39%), (c) Iberian wild goat (16%), (d) Pyrenean
 1278 chamois (3%), (e) wild boar (80%), (f) fallow deer (8%), (g) mouflon (8%), (h) Aoudad
 1279 (2%) and (i) diversity of wild ungulates (species richness) in the Iberian Peninsula. We
 1280 refer to **Vingada et al. (2010)**, **Fonseca et al. (2019)** and **Palomo et al. (2007)** for further
 1281 insights into the historical distribution and abundance of these species in Portugal and
 1282 Spain. The wild boar distribution was updated using presence data from **Illanas et al.**
 1283 **(submitted)**.

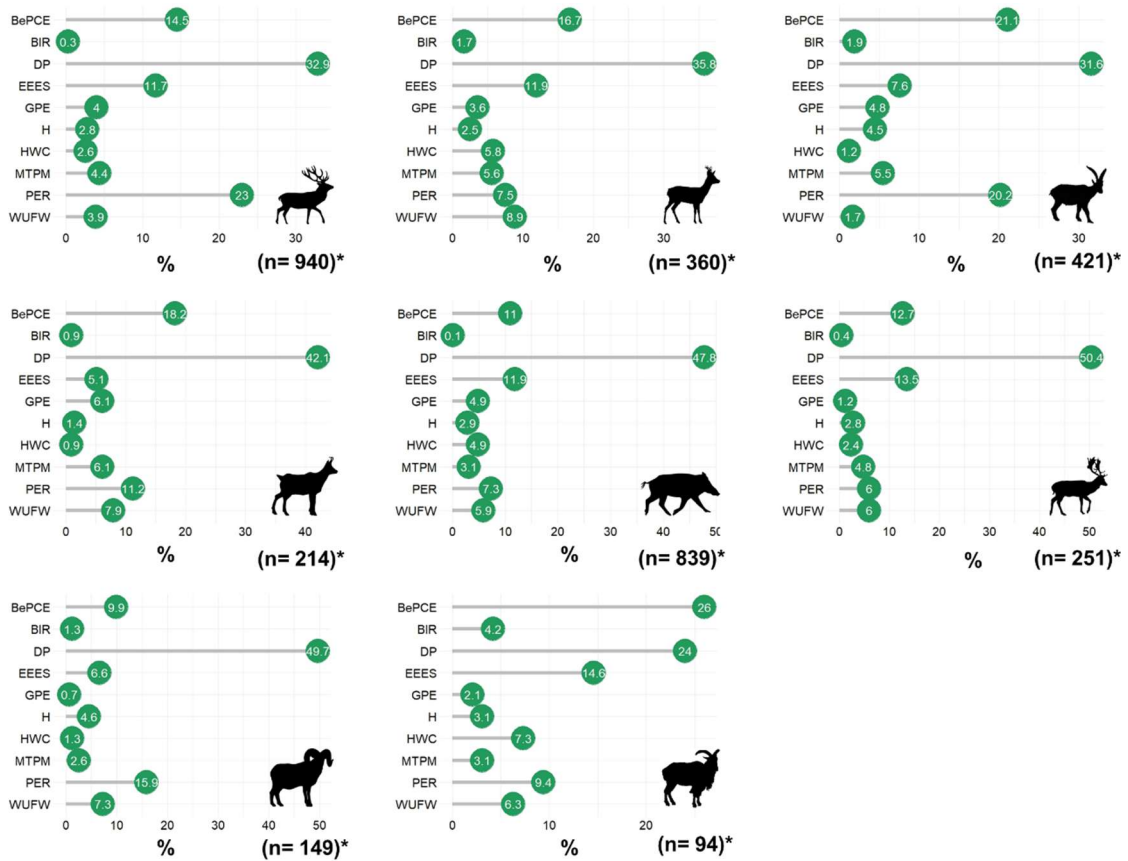
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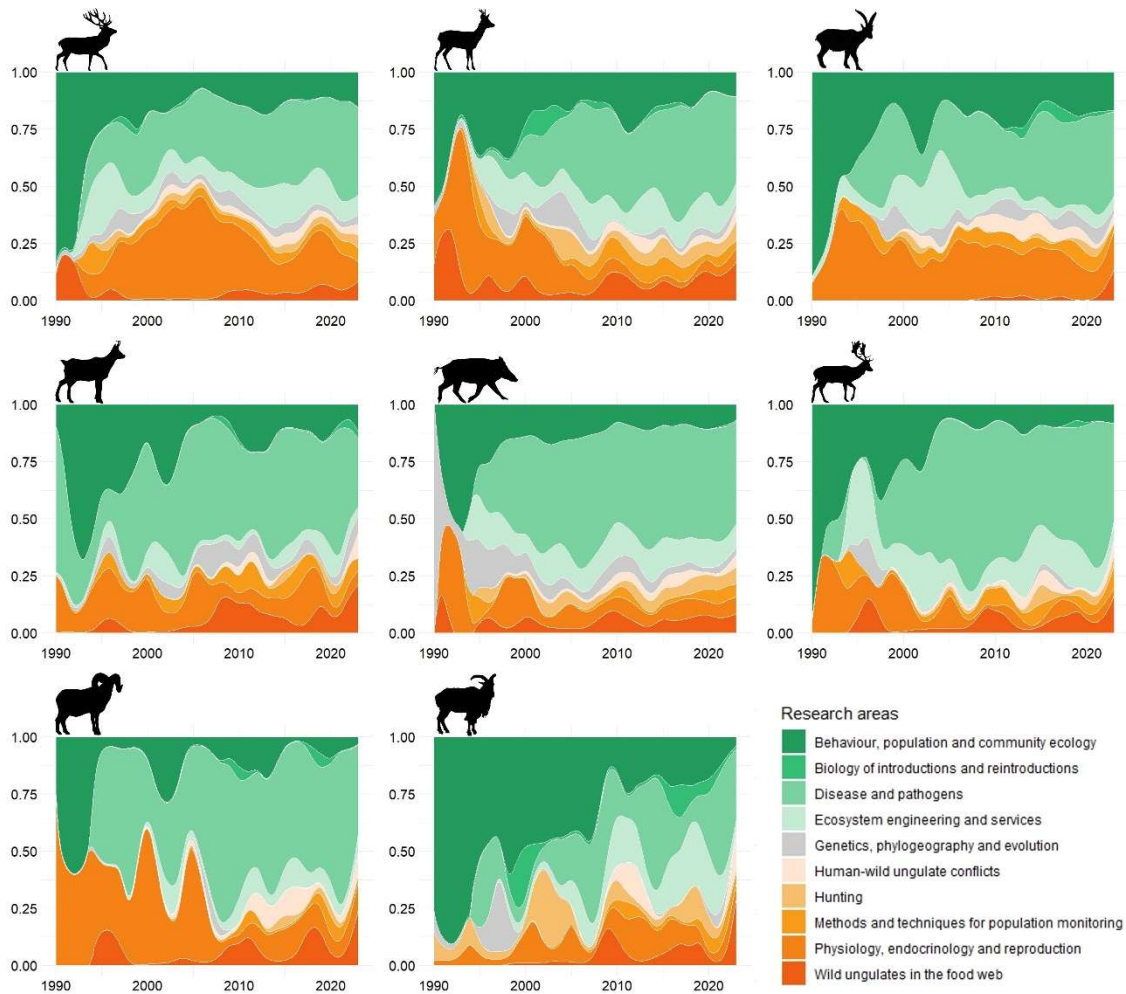
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1290 **Figure 2** – Percentage of published articles *per* species (red deer, roe deer, Iberian wild
 1291 goat, Southern chamois, wild boar, fallow deer, mouflon and aoudad) and research area
 1292 between January 1990 and July 2023: i) behaviour, population and community ecology
 1293 (BePCE), ii) biology of introductions and reintroductions (BIR), iii) disease and
 1294 pathogens (DP), iv) ecosystem engineering and services (EEES), v) genetics,
 1295 phylogeography and evolution (GPE), vi) hunting (H), vii) human-wild ungulate conflicts
 1296 (HWC), viii) methods and techniques for population monitoring (MTPM), ix)
 1297 physiology, endocrinology and reproduction (PER), x) wild ungulates in the food web
 1298 (WUFW). (*) depicts the absolute number of studies per species. Note that each study
 1299 analysed may refer to one or more wild ungulate species.

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1304 **Figure 3** – Trends in the proportion of published articles *per species* (red deer, roe deer,
 1305 Iberian wild goat, Southern chamois, wild boar, fallow deer, mouflon and aoudad) and
 1306 research area between January 1990 and July 2023.