Science of the Total Environment 801 (2021) 149652

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Usually hated, sometimes loved: A review of wild ungulates' contributions to people

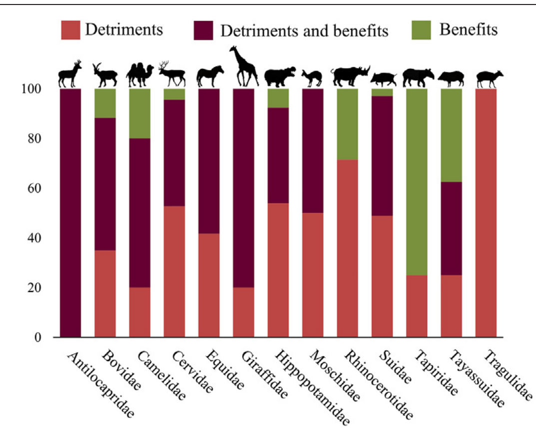
Roberto Pascual-Rico [a,b], Zebensui Morales-Reyes [b,c,*], Natividad Aguilera-Alcalá [b,c], Agnieszka Olszańska [d], Esther Sebastián-González [b,e], Robin Naidoo [f,g], Marcos Moleón [h], Jorge Lozano [i], Francisco Botella [b,c], Henrik von Wehrden [j], Berta Martín-López [j], José A. Sánchez-Zapata [b,c]

[a] Instituto de Investigación en Recursos Cinegéticos (IREC - CSIC, UCLM, JCCM), Ronda de Toledo, 12, 13071 Ciudad Real, Spain
[b] Department of Applied Biology, Miguel Hernández University of Elche, Avda. de la Universidad, s/n, 03202 Elche, Spain
[c] Centro de Investigación e Innovación Agroalimentaria y Agroambiental (CIAGRO-UMH), Universidad Miguel Hernández de Elche, Elche, Spain
[d] Institute of Nature Conservation Polish Academy of Sciences, Al. Adama Mickiewicza 33, 31-120 Krakow, Poland
[e] Department of Ecology, University of Alicante, Ctra San Vicente del Raspeig, s/n, 03690 San Vicente del Raspeig, Alicante, Spain.
[f] WWF-US, 1250 24th Street NW, Washington, DC 20037, USA
[g] Institute of Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC VfT 1Z4, Canada
[h] Department of Zoology, University of Granada, Av. de Fuentenueva, s/n, 18071 Granada, Spain
[i] Departamento de Biodiversidad, Ecología y Evolución, Universidad Complutense de Madrid, C/José Antonio Novais 12, 28040 Madrid, Spain.
[j] Faculty of Sustainability, Leuphana University of Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany

HIGHLIGHTS

- We systematically reviewed 20 years of human-ungulate interactions research.
- Research mostly focused on detrimental ungulates' contributions to people.
- Human-ungulate interactions research is taxonomically and geographically biased.
- Management tools to mitigate human-ungulate conflicts have rarely been evaluated.
- Studies on how ungulates may benefit human welfare are urgently needed.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 June 2021
Received in revised form 8 August 2021
Accepted 10 August 2021
Available online 14 August 2021

Editor: Rafael Mateo Soria

Keywords:
Artiodactyla

ABSTRACT

Nature's contributions to people (NCP) may be both beneficial and detrimental to humans' quality of life. Since our origins, humans have been closely related to wild ungulates, which have traditionally played an outstanding role as a source of food or raw materials. Currently, wild ungulates are declining in some regions, but recovering in others throughout passive rewilding processes. This is reshaping human-ungulate interactions. Thus, adequately understanding the benefits and detriments associated with wild ungulate populations is necessary to promote human-ungulate co-existence. Here, we reviewed 575 articles (2000-2019) on human-wild ungulate interactions to identify key knowledge gaps on NCP associated with wild ungulates. Wild ungulate research was mainly distributed into seven research clusters focussing on: (1) silvicultural damage in Eurasia; (2) herbivory and natural vegetation; (3) conflicts in urban areas of North America; (4) agricultural damage in Mediterranean agro-ecosystems; (5) social research in Africa and Asia; (6) agricultural damage in North America; (7) research in natural American Northwest

* Corresponding author at: Department of Applied Biology, Miguel Hernández University of Elche, Avda. de la Universidad, s/n, 03202 Elche, Spain.
E-mail address: zmorales@umh.es (Z. Morales-Reyes).

https://doi.org/10.1016/j.scitotenv.2021.149652

Ecological functions, herbivores
Human-wildlife relations
Mammal management
Perissodactyla

areas. Research mostly focused on detrimental NCP. However, the number of publications mentioning beneficial contributions increased after the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services conceptual framework was implemented. Human-ungulate interactions' research was biased towards the Global North and Cervidae, Suidae and Bovidae families. Regarding detrimental NCP, most publications referred to production damage (e.g. crops), followed by biodiversity damage, and material damage (e.g. traffic collisions). Regarding beneficial NCP, publications mainly highlighted non-material contributions (e.g. recreational hunting), followed by material NCP and regulating contributions (e.g. habitat creation). The main actions taken to manage wild ungulate populations were lethal control and using deterrents and barriers (e.g. fencing), which effectiveness was rarely assessed. Increasing research and awareness about beneficial NCP and effective management tools may help to improve the conservation of wild ungulates and the ecosystems they inhabit to facilitate people-ungulate co-existence in the Anthropocene.

Contents

1. Introduction

Nature's contributions to people (NCP) include all contributions of nature that are both beneficial (i.e. ecosystem services) and detrimental (i.e. disservices, damages or conflicts) to societies' quality of life (Díaz et al., 2018). The NCP concept builds on the Ecosystem Services framework and aims for a more inclusive approach to people and nature research (Kadykalo et al., 2019; Dean et al., 2021). Biodiversity contributes in many ways to societies' well-being (Brooks et al., 2006; Hevia et al., 2017) by, for instance, the provision of meat and recreational or cultural values via harvesting vertebrate animals (Alves, 2012). At the same time, nature can cause a reduction of human well-being, for instance via pest damages to agriculture, pollen allergens or snake bites (e.g. Lyytimäki, 2015; Shackleton et al., 2016). Depending on cultural and environmental contexts, different ecological processes or species can be conceived by society as providers of beneficial or detrimental NCP (Rasmussen et al., 2017; Morales-Reyes et al., 2018). In turn, human perceptions of NCP may impact biodiversity conservation (Bennett, 2016). Moreover, NCP are being altered by human impacts (e.g. Vanbergen, 2013; Johnson et al., 2017), which affect the structure and functioning of ecological communities (Schwartz et al., 2000; Mooney et al., 2009). Thus, studying NCP can be a useful tool to fully understand our relationship with nature and to improve the conservation of natural communities in a rapidly changing world.

Of all the animal groups that have historically benefitted humans, ungulates stand out. Ungulate species are distributed throughout Africa, America, Asia and Europe, and also appear in Australia as introduced species (Wilson and Mittermeier, 2011). The species belonging to this diverse group are typically herbivorous and inhabit a wide range of diverse habitats, including forests, steppes, mountains, and deserts. Perissodactyla (odd-toed) and Artiodactyla (even-toed) orders are the groups typically considered to be true ungulates. The Perissodactyla order includes three families with a total of 16 species. The Artiodactyla order is represented by 10 families and 380 species (Fennessy et al., 2016; Wilson and Mittermeier, 2011).

Humans around the world have historically interacted with wild ungulates since they were scavenged, hunted and later domesticated (see Moleón et al., 2014), and societies have benefited from them by the many NCP they provide (see e.g. Pascual-Rico et al., 2020; Velamazán et al., 2020). Besides being a source of food and materials, such as bushmeat, leather and bones, some human groups are linked with wild ungulates through cultural aspects; for instance, some

Sahelo-Saharan clans have totemic species like dama gazelle (*Nanger dama*), and Barbary sheep (*Ammotragus lervia*) (Tubiana, 2005). Ungulates are also key species in many ecosystems by, for example, conditioning nutrient cycles and influencing forest dynamics (Danell et al., 2006). Despite ungulates being a group closely linked to humans, we lack a global synthesis of the beneficial and detrimental NCP associated with them.

The way humans and wild ungulates interact varies vastly worldwide. In many African and Asian countries, most wild ungulate populations are declining because of changes in land use and direct persecution, to the extent that urgent conservation measures are needed (Havemann et al., 2016; Ghoddousi et al., 2017). However, in European and North American countries, the abundance and distribution of some ungulate populations have increased in recent times throughout a passive or unintentional rewilding process (Carpio et al., 2020; Valente et al., 2020a). In turn, passive rewilding has led to enhanced impacts (i.e. direct negative interactions; Redpath et al., 2013) of wild ungulates on human activities, such as damage to agriculture and forestry, and ungulate-vehicle collisions (Carpio et al., 2020; Linnell et al., 2020). Also, some wild ungulate populations are establishing around and inside cities, particularly in the Northern hemisphere. This promotes direct encounters with urban people, which may lead to damages to humans and their properties (e.g. Castillo-Contreras et al., 2018; McDonald et al., 2012).

Different management tools have been used to avoid or mitigate these emerging detrimental NCP related to wild ungulates. For example, increasing hunting, habitat fencing or supplementary feeding are popular management tools designed to alleviate detrimental NCP (e.g. Hildreth et al., 2012; Pascual-Rico et al., 2018; Walter et al., 2011). However, these management tools often prove ineffective for solving the problems associated with this animal group (Apollonio et al., 2010, 2017). These strategies might also have negative effects on wild ungulate populations, such as demographic imbalance, disease transmission, behavioural alterations, and limitation of their evolutionary potential (Geisser and Reyer, 2004; Hayward and Kerley, 2009).

Overall, there is a complex link between people and ungulates with both positive and negative interactions that results in different management measures to facilitate the co-existence of modern human societies and wild ungulate populations. Our aim is to synthesise and appraise scientific evidence on human-wild ungulate interactions, and to identify key knowledge gaps and future research priorities. We performed a systematic review to: (1) identify different research lines in human-ungulate interactions (i.e. thematic clusters); and (2) characterise the current scientific literature on human-ungulate interactions according to: (i) temporal and geographical distribution (i.e. continents; biomes); (ii) biological components (i.e. taxonomy); (iii) nature of the interactions (beneficial vs. detrimental NCP); (iv) ungulate management strategies mentioned, recommended and evaluated.

2. Material and methods

2.1. Literature review

We reviewed scientific articles that characterised detrimental and beneficial interactions between humans and wild ungulates (i.e. Perissodactyla and Artiodactyla orders; Table S1) following the guidelines for systematic reviews by Pullin and Knight (2009). The protocol followed a strict method to guarantee transparency and to minimise sources of bias. We searched the Scopus database by using a search string that combined different terms related to detrimental NCP, beneficial NCP, human-ungulate interactions and ungulates (see Appendix S1 for the full search string). The search was made in titles, abstracts and keywords in English-written articles published from 2000 to 2019 in the Scopus database. We found 995 articles of potential relevance, which were restricted to 575 articles after excluding book chapters or conference papers (see Appendix S2 for the list of articles). We screened the articles to ensure that they reported empirical studies (i.e. we excluded reviews or theoretical papers), and analysed human-ungulate detrimental and beneficial contributions provided by wild ungulates (i.e. if the article studied or mentioned detrimental NCP or beneficial NCP).

From each publication, we extracted information about: (1) its general description (year of publication, journal, and ungulate species examined); (2) any detrimental contribution (i.e. conflict, damage, disservice) of wild ungulates to humans' well-being (detrimental NCP mentioned and studied); (3) any beneficial contribution (i.e. ecosystem services) of wild ungulates to humans' well-being (beneficial NCP mentioned and studied); and (4) type of management strategy mentioned, recommended or evaluated (based on Lozano et al., 2019). We associated the species included in each study with the beneficial and detrimental NCP mentioned or studied in the publication.

The classification of detrimental NCP was based on Pascual-Rico et al. (2020) (Table 1). Beneficial NCP were categorised according to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) classification, including regulating, material and non-material NCP (Díaz et al., 2018; Table 2).

2.2. Clusters of human-ungulate interactions research

We used the words taken from the entire text of the reviewed articles to identify different research lines that studied human-ungulate interactions. Once the words from articles had been extracted, we excluded meaningless words, such as prepositions and articles. Then, we conducted a cluster analysis of the meaningful words' dataset (i.e. terms related to ungulates and research) to classify articles into groups (i.e. thematic clusters) based on a permutation test, in which significantly higher word co-occurrences were compared among clusters. Afterwards, these word groups were graphed and analysed by a detrended correspondence analysis (DCA; Hill and Gauch, 1980). Closer words in the two-dimensional space performed by the DCA co-occurred together in articles (for more details, see Dufrene and Legendre, 1997; Paterlow et al., 2017; Lozano et al., 2019). This analysis allowed us to identify research clusters on human-ungulate interactions research. A DCA analysis was conducted using R (http://www.r-project.org/R) with these packages: 'tm' for text mining, 'plyr' for data sorting, 'vegan' for the DCA analysis, 'cluster' for cluster analyses and 'labdsv' to estimate the importance of the words for each cluster (see Roberts (2016) for more details).

2.3. Statistical analyses

We used Chi-square contingency tables and Fisher's exact tests ($\alpha = 0.05$) to test whether there were any significant associations between the identified clusters and the detrimental and beneficial NCP included in the scientific literature. We also conducted Kruskal-Wallis tests ($\alpha = 0.05$) and *posteriori* multiple comparison Tukey's post hoc contrast to determine any differences among the obtained clusters as regards the quantitative variables for the number of: (1) detrimental and beneficial NCP mentioned or studied; and (2) management tools mentioned, recommended or evaluated.

We also ran a unpaired two-samples Wilcoxon test to compare the number of publications per year that mentioned beneficial NCP during three time periods by pairs: (1) 1st period from 2000 to 2004 (before the ecosystem services framework formalised in the Millennium Ecosystem Assessment; MEA (Millennium Ecosystem Assessment), 2005) vs. (2) 2nd period from 2005 to 2015 (between the ecosystem services and the IPBES framework Díaz et al., 2015); and (2) vs. (3) 3rd period from 2016 to 2019 (after the IPBES framework). Here, the aim was to assess if the conclusions and

Table 1
Categories of detrimental NCP related to wild ungulates taken from the literature review. The classification of detrimental NCP is based on Pascual-Rico et al. (2020).

Categories of detrimental NCP		Description	References
Damage to biodiversity	Vegetation damage	Negative effects on vegetation, including rooting (i.e. foraging activity within surface soil layers).	Bueno and Jiménez, 2014.
	Animal biodiversity damage	Negative effects on wild animal species with no direct economic interest.	Carpio et al., 2014; Bernes et al., 2018
	Soil alteration	For instance, negative effects of wild ungulates on soil properties.	Martínez-Jauregui and Soliño, 2021; Pascual-Rico et al., 2018, 2021
Damage to production	Grazing competition	Wild ungulates consume pasture and other natural resources that could be used by livestock. For example, the European bison (*Bison bonasus*) competes directly with livestock.	Kuemmerle et al., 2011
	Disease to livestock	Risk of disease transmission from wild ungulates to livestock.	Acevedo et al., 2014
	Silvicultural damage	Impairment of natural forests or plantations intended for forestry.	Charco et al., 2016
	Crop damage	Direct physical impairment of croplands and orchards.	Giménez-Anaya et al., 2016
	Damage to animals	Direct physical damage caused by ungulates to livestock, and big and small game species. For example, the wild boar as the main nest predator of the common pheasant (*Phasianus colchicus*).	Senserini and Santilli, 2016; Haule et al., 2002
Damage to human safety		Ungulates causing injuries, frightening and/or transmitting infectious agents to humans.	García-Bocanegra et al., 2016
Material damage	Property damage	Ungulates damaging human properties, particularly buildings and/or physical structures, such as fences.	Duarte et al., 2015
	Traffic collisions	Ungulates damaging vehicles by ungulate-vehicle collisions and/or causing traffic accidents.	Colino-Arrabal et al., 2018
Human-human conflict		Conflict related to human disagreements about management decisions of wild ungulates or deriving from distinct opinions and interests by different social actors.	Gerhardt et al., 2013; Valente et al., 2020b

Bold signifies damage or changes in physical, chemical or biological soil properties.

recommendations of those seminal publications influenced subsequent scientific literature.

Finally, we also explored whether some ungulate families were associated with certain detrimental and beneficial NCP, using Chi-square contingency tables and Fisher's exact tests.

3. Results

3.1. Clusters of studies on human-ungulate interactions

The DCA identified seven research clusters (Silvicultural damage in Eurasia; Herbivory and natural vegetation; Conflicts in urban areas of North America; Agricultural damage in Mediterranean agro-ecosystems; Social research in Africa and Asia; Agricultural damage in North America; Research in natural American Northwest areas; Fig. 1) distributed along two axes. Each cluster represented research on human-ungulate interactions in different ways and focused mainly on diverse detrimental NCP and associated species (see Table 3). The words characterising each cluster according to the DCA are shown in Fig. S2.

3.1.1. Detrimental and beneficial NCP

We found positive associations between some clusters and several detrimental NCP ($\chi^2 = 125.9$, df $= 78$, $p < 0.001$; see Table S2). The clusters did not show any significant association with the identified beneficial NCP ($\chi^2 = 35.5$, df $= 72$, $p = 1.0$). We found differences

Table 2
Categories of beneficial NCP provided by wild ungulates taken from the literature review. Classification of beneficial NCP based on Díaz et al. (2018) and Pascual-Rico et al. (2020).

Categories of beneficial NCP		Description	References
Regulating	Habitat maintenance	The formation and continued production by ungulates of ecological conditions necessary or favourable for important organisms to humans, e.g. to contribute to maintain semiopen habitats and nutrient cycling.	Díaz et al., 2018; Danell et al., 2006
	Dispersal of seeds	Facilitation by ungulates of seed dispersion of important species to humans. For example, grass or small herbs species via coats, hoofs or faeces.	Gill and Beardall, 2001
	Maintenance of soils	Maintenance of soil structure (e.g. aeration or contribution with nutrients).	Asner et al., 2004
	Regulation of organisms	Removal of animal carcasses by wild boars, i.e. acting as a scavenger and/or reducing attacks on livestock due to the presence of alternative prey.	Sebastián-González et al., 2020; Sidorovich et al., 2003
Material	Food	Production of food from wild ungulates, such as meat from red deer.	Milner et al., 2006
	Materials and assistance	Production of materials deriving from organisms in wild ecosystems, clothing, ornamental purposes (e.g. skin, horns, antlers).	MacMillan and Phillip, 2008
	Medicinal, biochemical and genetic resources	Production of materials deriving from ungulates used for medicinal, veterinary and pharmacological purposes.	Haule et al., 2002
Non-material	Supporting identities	Source of satisfaction deriving from knowing that a particular ungulate exists in the present. This is also referred to as existence value.	Pascual-Rico et al., 2020
	Learning and inspiration	Provision of opportunities for developing capabilities that allow humans to prosper through education, knowledge acquisition and skills for well-being, information, and inspiration for art and technological design.	Pascual-Rico et al., 2020; García-Llorente et al., 2012
	Physical and psychological experiences	Extractive experiences: provision by ungulates of opportunities for physically beneficial leisure activities that are extracted from nature, such as recreational hunting.	Gamborg et al., 2017; Naidoo et al., 2011, 2016
		Non-extractive experiences: provision by ungulates of beneficial opportunities related to being in close contact with nature, such as the aesthetic value that derives from species.	Naidoo et al., 2011, 2016
	Maintenance of options	Species' capacity to keep human options open to support subsequent good quality of life.	Fernández-Olalla et al., 2016

Bold signifies ungulates influence and condition ecological processes that affect habitats, structuring plant composition or how nutrients flow through the ecosystem.

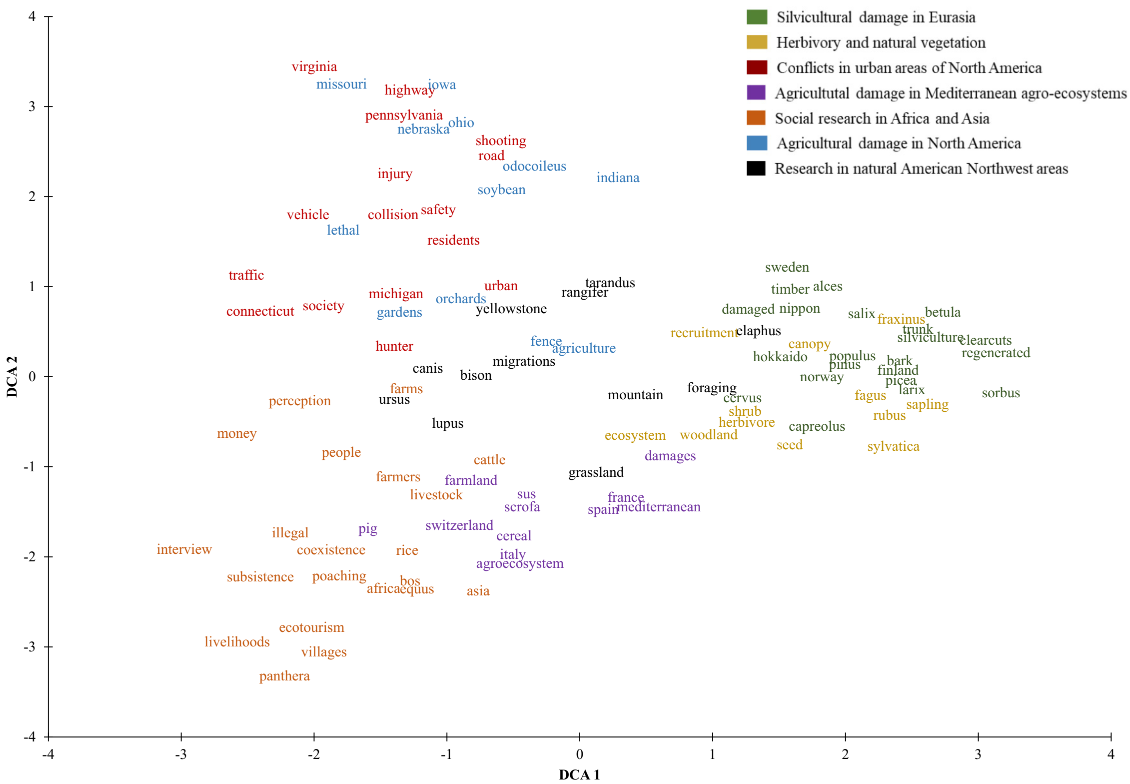


Fig. 1. Results of the detrended correspondence analysis showing the seven research clusters on human-ungulate interactions (differentiated by colour), and their relation in the space shaped by both axes.

among clusters regarding the number of detrimental ($\chi^2 = 41.5$, df = 6, $p < 0.001$) and beneficial ($\chi^2 = 54.1$, df = 6, $p < 0.001$) NCP mentioned (see Fig. S1A and B).

3.1.2. Management tools

We did not find any relationship between the clusters and the mentioned, recommended or evaluated management tools ($\chi^2 = 44.9$; 47.7; 17.6, all df = 90, all $p = 1.00$). However, we found differences when comparing the number of mentioned, recommended and evaluated management tools ($\chi^2 = 48.2$; 37.9; 36.2, all df = 6, all $p < 0.001$; Fig. S1C-E). Clusters "*Conflicts in urban areas of North America*", and "*Social research in Africa and Asia*" included the most management tools mentioned and recommended, while the cluster "*Agricultural damage in Mediterranean agro-ecosystems*" was the one that included more evaluated management tools.

3.2. Temporal and geographical distribution

The number of published studies on human-ungulate interactions has increased since 2000 (Fig. 2), with 2018 being the year with the highest number of publications ($n = 66$). Publications mentioning beneficial NCP increased significantly from first to second period (W = 59, $p = 0.002$) after the MEA conceptual framework (MEA (Millennium Ecosystem Assessment), 2005). Between period 2 and 3, publications mentioning beneficial NCP also increased, but not significantly (W = 31, $p = 0.14$).

Table 3
Clusters on human-ungulate interactions identified in the detrended correspondence analysis, the main characteristics of each one, and the number of papers included in each cluster (N).

Cluster	Description	Area/biome	Family	NCP	Social actors	Management tools	N
1	Silvicultural damage in Eurasia	Eurasia	Cervidae	Silvicultural damage	Foresters	–	96
2	Herbivory and natural vegetation	Temperate forest	Cervidae	Habitat maintenance, seed dispersal, extractive experiences/forest damage	Foresters, environmental managers, hunters	Deterrents and barriers; lethal control	87
3	Conflicts in urban areas of North America	Urban	Cervidae	Traffic collisions	Residents, hunters	Deterrents and barriers; lethal control	100
4	Agricultural damage in Mediterranean agro-ecosystems	Mediterranean	Suidae	Crop damage	Farmers, hunters	Deterrents and barriers; lethal control	87
5	Social research in Africa and Asia	Temperate & tropical forest/grassland	Bovidae, Equidae, Suidae	Crop damage, livestock competition	Farmers, local communities, hunters	Deterrents and barriers; livestock/crop guardians; lethal control	87
6	Agricultural damage in North America	Agrosystem	Cervidae	Crop damage	Farmers	Deterrents and barriers	28
7	Research in natural American Northwest areas	Temperate forest/grassland	Bovidae, Cervidae	Habitat maintenance; extractive experiences	–	–	90

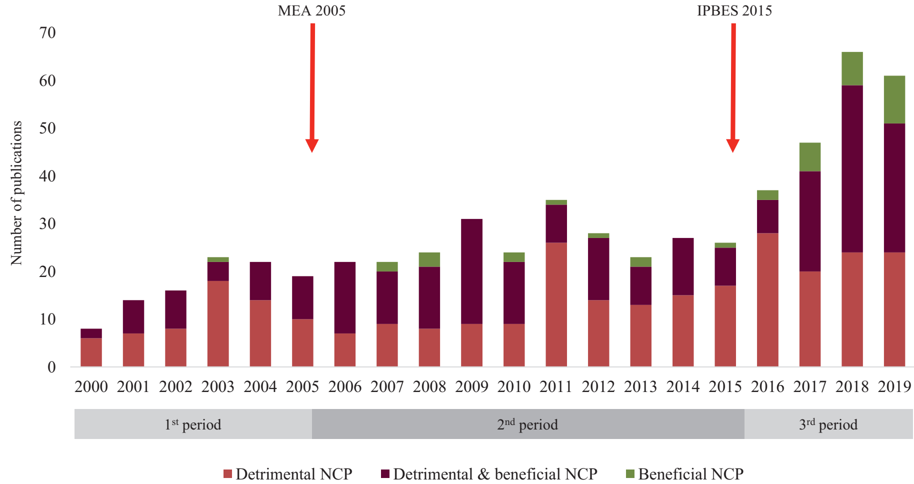


Fig. 2. Number of publications per year during three relevant periods according to the way in which NCP were conceived and approached. Bars indicate the total number of papers that focused on each NCP type.

The largest proportion of research, according to the number of papers reviewed, was performed in Europe (37.9%) and North America (32.3%). In contrast, Asia (15.6%), Africa (7.3%), Central and South America (5.2%) and Oceania (1.7%) received less scientific attention (Fig. 3A; Table S3). Regarding the biomes, most studies were performed in temperate forests (52.7%) and agro-ecosystems (23.0%). At the other

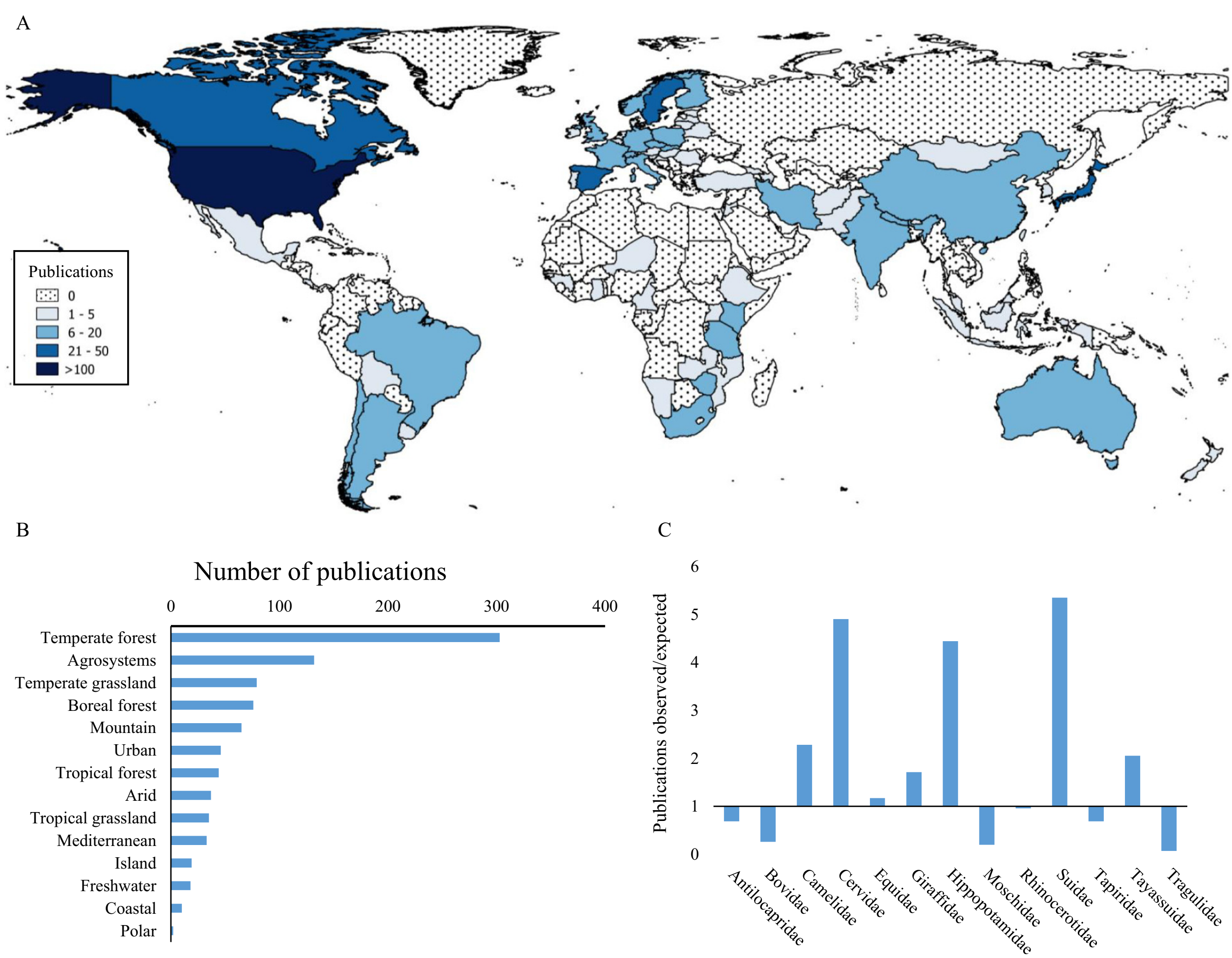


Fig. 3. (A) World map showing the number of publications on human-ungulate interactions per country between 2000 and 2019 ($n = 575$). (B) Distribution of the reviewed studies according to biome type. (C) Distribution of the reviewed publications according to the taxonomic family of artiodactyls and perissodactyls. The ratio of studies observed/expected in B represents the number of articles found in the review for each taxonomic group (i.e. studies observed), divided by the number of expected articles given a proportional distribution based on the number of species belonging to each taxonomic group (i.e. studies expected).

extreme, islands (3.3%), freshwater (3.1%), coastal (1.7%) and polar (0.3%) ecosystems were poorly represented. Urban environments were studied in 8.0% of articles (Fig. 3B).

3.3. Biological components

The most studied ungulate families were Cervidae (deer; 65.9% of the publications), Suidae (pigs; 23.1%) and Bovidae (bovines, ibexes and sheep; 17.9%). When evaluating the number of publications in relation to the proportion of species in each family, we found that scientific attention was taxonomically biased, with families Antilocapridae, Bovidae, Moschidae, Rhinocerotidae, Tapiridae and Tragulidae being underrepresented (Fig. 3C).

Most studies focused on a single species (77.9% of the publications), with the most studied species being red deer (*Cervus elaphus*; 21.2%), wild boar (*Sus scrofa*; 21.0%), white-tailed deer (*Odocoileus virginianus;* 18.1%), moose (12.0%), roe deer (*Capreolus capreolus*; 9.6%) and sika deer (*Cervus nippon*; 7.8%). Furthermore, 11.0% of the publications addressed exotic species like red deer, wild boar, aoudad (*Ammotragus lervia*) or cheetah deer (*Axis axis*), introduced into non-native environments (Table S3).

3.4. Detrimental and beneficial contributions of ungulates

Publications focused mostly on detrimental NCP alone (49.7%), and on both detrimental and beneficial NCP (44.0%). The articles that mentioned only beneficial NCP represented 6.3% of the publications. Regarding families, most publications addressed both kinds of NCP, except for a single publication on Tragulidae, which focused only on detrimental NCP (see details per families in Fig. S3).

3.4.1. Detrimental NCP

Among the publications that focused on detrimental NCP ($n = 539$), 71.8% referred to production damage (studied: 25.0% of articles; only mentioned: 46.8% of articles), particularly crop damage (37.9% of the publications), silvicultural damage (26.3%) and disease transmission to livestock (13.4%). Biodiversity damage, the second most important detrimental NCP, was referred to in 41.6% of the publications (studied: 17.4%; only mentioned: 24.1%), mainly about vegetation damage (33.4%). Material damage was included in 23.0% of the publications (studied: 3.3%; only mentioned: 19.7%), including traffic collisions (16.7%) and property damage (11.1%). Other detrimental NCP (i.e. damage to human safety and human-human conflicts) were included in less than 10% of the publications (Table 1; Fig. 4). We found no associations between particular detrimental NCP and the ungulate families mentioned as a cause of damage ($\chi^2 = 66.3$, df = 156, $p = 1.00$).

3.4.2. Beneficial NCP

Regarding the publications about beneficial NCP ($n = 289$), 80.6% referred to non-material contributions (studied: 2.4%; only mentioned: 78.2%), mainly extractive experiences (recreational hunting; 33.6% of the publications), followed by non-extractive experiences (e.g. aesthetic value of wild ungulates; 10.1%); only 6.1% of the publications mentioned supporting identities and 1.0% referred to learning and inspiration. The second most important beneficial NCP was material contributions, which was included in 29.4% of the publications (studied: 8.7%; only mentioned: 20.8%), and particularly considered wild ungulates to be a food resource (12.0%). Finally, regulating contributions appeared in 24.9% of the publications (studied: 1.7%; only mentioned: 23.2%; Table 2; Fig. 5). We did not find associations between beneficial NCP and the ungulates providing them ($\chi^2 = 27.3$, df = 132, $p = 1.00$).

3.5. Management actions

Authors frequently mentioned (63.7% of articles) or recommended (57.2%) some management tools to mitigate human-ungulate conflicts, but these were evaluated only in 19.3% of the reviewed publications. Firstly, among the publications that mentioned management tools ($n = 366$), the most widely mentioned were lethal control (44.0% of the publications) and deterrents and barriers (e.g. fencing; 38.3%), regulation of local hunting (20.8%) and economic compensation (12.6%). Supplementary feeding, zoning, aversive conditioning, co-management, education and awareness raising, translocation of animals, and livestock/crops guarding were mentioned to a lesser extent (≤ 9.3%; Table S4). Secondly, among the publications that recommended management tools ($n = 329$), the authors referred to lethal control (28.3% of the publications), deterrents and barriers (25.8%), habitat management strategies (17.9%), regulate local hunting (16.4%), co-management (14.9%), education and awareness raising (11.9%) and zoning (10.3%). Other recommended tools were less frequently recommended (≤ 7.6%; Table S4). Finally, among the publications that included evaluations of management tools ($n = 110$), deterrents and

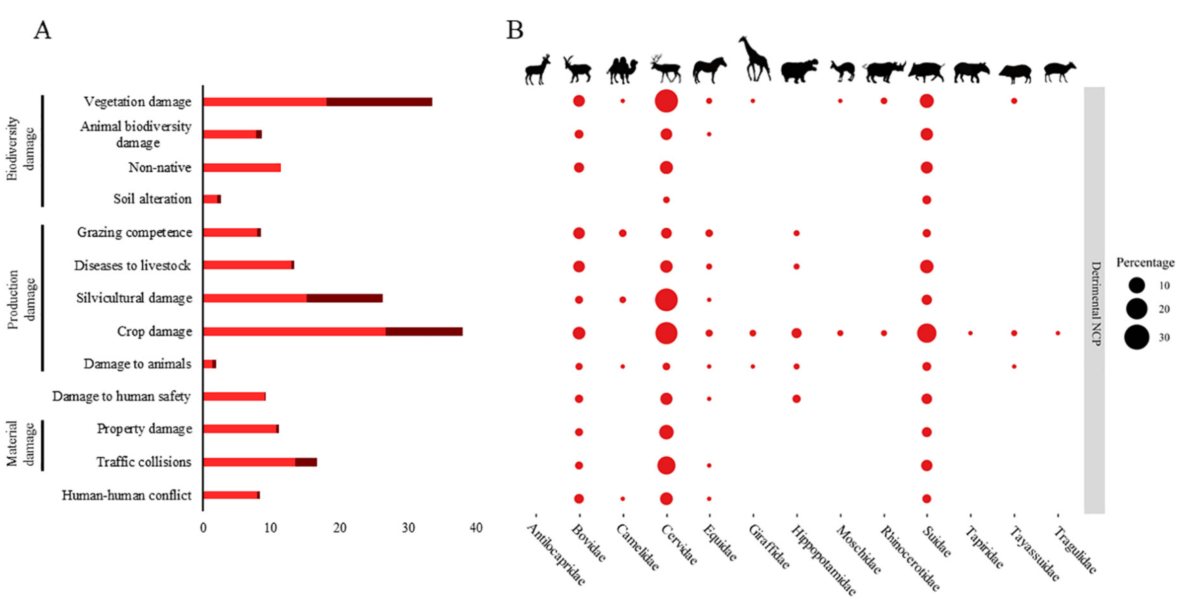


Fig. 4. (A) Percentage of publications that included specific detrimental NCP (red bars. Full colour: studied; light colour: mentioned). (B) Percentages of publications that included each detrimental NCP (red circles) per ungulate family.

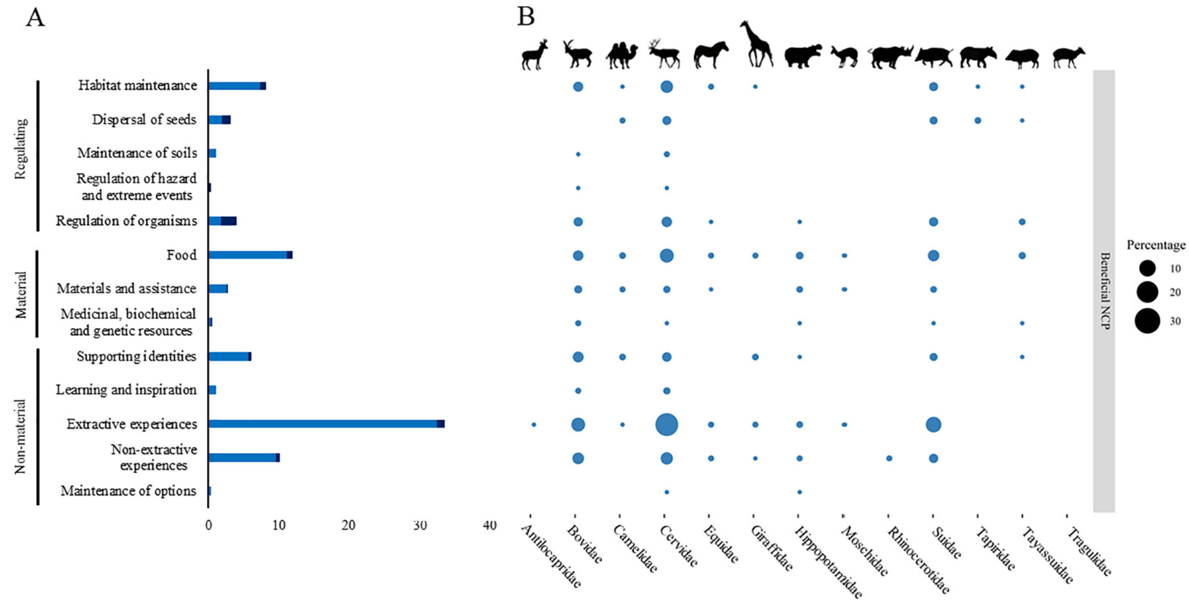


Fig. 5. (A) Percentage of publications that included specific beneficial NCP (blue bars. Full colour: studied; light colour: mentioned). (B) Percentages of publications that included each beneficial NCP (blue circles) per ungulate family.

barriers (32.4% of the publications), lethal control (25.2%) and aversive conditioning (13.5%) were the most evaluated tools. The remaining management tools were less evaluated (≤ 11.7%; Table S4). In general, the evaluated management tools were partially (31.8% of 110 papers) or totally effective (49.1%). Among the most effective evaluated management tools were lethal control (totally effective in the 60.7% of 28 papers where were evaluated), the use of deterrents and barriers (55.6% of 36 papers), and aversive conditioning (partially effective 60.0% of 15 papers; Table S5).

4. Discussion

4.1. Towards a more positive vision of ungulates?

In accordance with previous reviews that evaluated both the beneficial and detrimental NCP of different wildlife groups (see e.g. Kansky and Knight, 2014; Lozano et al., 2019; Methorst et al., 2020), our findings revealed that human-ungulate interactions research is clearly biased towards detrimental NCP, as evidenced by the DCA. Some thematic clusters (usually linked to the Bovidae, Cervidae and Suidae families) were related to several detrimental NCP, but none was associated with beneficial NCP. However, we observed that after the implementation of the ecosystem services framework (MEA (Millennium Ecosystem Assessment), 2005) and, especially, the IPBES conceptual framework (Díaz et al., 2015), the number of publications that focused on beneficial NCP have increased. This trend could help to raise increasing awareness about the numerous positive contributions that ungulates can provide to societies' quality of life, which could favour human co-existence with wild ungulates, particularly in human-dominated landscapes subject to rewilding (Pascual-Rico et al., 2020).

4.2. Global trends in human-ungulate interactions research

4.2.1. The Global North bias

Despite the recent increase in published studies on human-ungulate interactions, we found a global geographical bias in research effort, as most studies were conducted in Europe and North America. This contrasts with the fact that these regions only include c. 7% of the existing ungulate species (Wilson and Mittermeier, 2011). Only the thematic cluster “*Social research in Africa and Asia*” was specific of the Global South, whereas Central and South America were not included in any cluster. This geographical pattern, which has been previously described for other faunal groups (e.g. Lozano et al., 2019; Martin et al., 2012), likely led to the overrepresentation in the reviewed literature of some ungulate families that are frequent in the Global North (e.g. Cervidae, Suidae, Bovidae), as well as the underrepresentation of ungulates that inhabit other regions. Interestingly, studies conducted in the Global South, particularly in Africa, highlighted proportionally more beneficial NCP compared to the Global North (see Table S3), which could be related to the local importance of ecotourism and big game hunting industries (Naidoo et al., 2011, 2016). In Oceania, represented in our review by Australia and New Zealand (Global North countries), all ungulate species were exotic and produced negative ecological impacts on native ecosystems. This very likely determined the preponderance of detrimental NCP in this continent (e.g. Bee et al., 2007; Natusch et al., 2017). In fact, exotic species are generally associated with more detriments than benefits, being the latter normally related to hunting (e.g. Kerr, 2019).

The geographical bias was also related to the investigated biomes, so that temperate forests, which occupy one quarter of the Earth's terrestrial surface (Ashton et al., 2012), was represented in more than half of the publications. In contrast, tropical grassland covers one fifth of the Earth's land surface (Sankaran et al., 2005), but this biome was very poorly studied (c. 5% of the publications). The fact that we considered only English-written articles for our systematic review may have reinforced this bias, at least partially. This may be related to the higher resource capacity of European and North American countries to face publication in international journals (e.g. Martin et al., 2012), but also with the fact that studies of more local scope are frequently written in the local language.

4.2.2. Management tools: frequently mentioned, but rarely evaluated

Management actions were neither highlighted in the cluster analysis nor associated with any specific cluster, despite they are essential to facilitate human-wildlife co-existence in areas where a rewilding process is ongoing (Apollonio et al., 2010) and where human activities are spreading (e.g. Kurten, 2013). We found that 64% of the reviewed publications mentioned management tools, but only a few publications evaluated them (21%; e.g. Gilsdorf et al., 2004; Perea and Gil, 2014; Jenkins et al., 2002). Most articles mentioned lethal control, and deterrents and barriers. However, lethal control is sometimes limited or avoided because of public opinion (see Walter et al., 2011). Moreover, compensatory reproductive success in response to increased mortality of species such as the wild boar could compromise the effectiveness of lethal control (see Boadella et al., 2012. Fencing is a common strategy to manage human-ungulate conflicts (e.g. Hildreth et al., 2012; Honda et al., 2009), often applied on a large scale. Some paradigmatic examples of this are veterinary cordon fences around many African protected areas (Osofsky, 2019), and wild boar fences along borders of European countries to mitigate African swine fever spread (Mysterud and Rolandsen, 2019). However, this management tool can cause undesired effects on wild species ecology and conservation (Gadd, 2012). Moreover, fence installation and maintenance involves high economic costs (Ferguson and Hanks, 2012). Despite its effectiveness being questioned, fences are usually recommended in combination with other management tools (e.g. Geisser and Reyer, 2004; Martínez-Pastur et al., 2016).

In relation to the studies that evaluated management techniques, the most frequently evaluated tool were deterrents and barriers, and lethal control. In general, these studies found that the evaluated measures were effective (76.6% of the publications that included evaluations of management tools), at least partially. Apart from evaluating the effectiveness of these tools, wild ungulate management should consider biological aspects of the targeted species, and assess potential effects on the ecosystem to avoid undesirable ecological cascade effects (e.g. Barbosa et al., 2019; Teichman et al., 2013).

4.2.3. From ecosystem functioning to nature's contributions to people

The studies of ungulate ecology published in the second half of the 20th century generally addressed topics from a purely ecological perspective, such as regulation of vegetation and primary productivity (e.g. Hobbs, 1996), and competitive interactions (e.g. Lamprey, 1936; Leuthold, 1978). Much of this early research aimed to understand the role of ungulates in ecosystem functioning in relatively natural landscapes. By then, very few studies were primarily approached from a socio-ecological perspective. Currently, much of the scientific literature explicitly considers that ecological systems interact positively and negatively with humans (Díaz et al., 2018), as revealed by our literature review. We recognise that our systematic review was focused on human-wildlife interactions, and we did not consider studies beyond our search criteria, which could limit our framework. However, given the widespread occupation of ecosystems by humans (Goudie, 2013), today it is difficult to find unaltered areas in which wildlife is unconnected to human activities (Di Marco et al., 2019).

4.3. Biodiversity conservation and future perspectives

Wild herbivores, such as ungulates, especially those with body weights exceeding 1000 kg (i.e. megaherbivores; Owen-Smith, 1989), have been important ecological engineers globally until the rise of agriculture some 12,000 years ago, when humans triggered their extinction outside of Africa (Bocherens, 2018). This megafaunal extinction led to profound ecological and evolutionary impacts (Galetti et al., 2018). Interestingly, extant megaherbivores are able to reverse negative impacts of livestock on ecological processes such as nutrient cycling (Sitters et al., 2020). Currently, ungulates, especially the largest species, are at the forefront of conservation and management strategies for contrasting reasons. On the one hand, wild ungulates are recolonising large areas of Europe and North America (Apollonio et al., 2010; Valente et al., 2020a). On the other hand, some species and populations continue to decline and face extinction in other world regions, e.g. in Africa, where wild ungulates are suffering a general decline (e.g. Durant et al., 2014; Rduch and Jentke, 2021). However, in some regions of Africa there are emerging new forms of conservation and maintenance of ecosystem functioning, such as wildlife ranching (Cousins et al., 2008; Taylor et al., 2020). This activity allows financial self-sustaining of private lands with conservation interests, and profits generation to landowners from biodiversity resources through tourism and hunting (i.e. beneficial NCP) (Naidoo et al., 2011, 2016).

Despite these attempts, introduction of non-native species and predators removal still continue in some regions, which strongly affects ungulate population dynamics and ecosystem functioning (e.g. Gass and Binkley, 2011; Nuñez et al., 2010). Moreover, anthropogenic activities often occur close to the habitat (or even constitute the habitat itself) of some ungulate species (e.g. Boan et al., 2011; Hegel et al., 2009). All these disturbing factors can increase conflicts between wild ungulates and human activities. In addition, strategies to mitigate human-wildlife conflicts that propose the recovery of natural ecosystem functioning are still scarce (e.g. Beschta et al., 2013; Licht et al., 2010).

5. Conclusions

Despite the negative aspects traditionally associated with wild ungulates, it has been increasingly demonstrated that they may also provide benefits to socio-ecological systems by providing numerous material, regulating and non-material NCP, such as tourism, hunting, and habitat maintenance, thus generating economic benefits and promoting conservation and awareness raising. The future management of wild ungulates, especially the largest species, will require co-operation between different social actors to apply the most appropriate management measures that favour the co-existence between humans and wildlife. Increasing conservation concern about wild ungulate populations in some world regions is being voiced, while important management problems and dilemmas arise in those regions undertaking passive rewilding processes. We argue that more studies dealing with the full role (i.e. including both detrimental and beneficial, NCP) of ungulates in the ecological functioning of human-dominated ecosystems are urgently needed. In addition, further research is needed to evaluate the effectiveness of the management tools aimed to reduce human-ungulate conflict. This will facilitate people-ungulate co-existence in an increasingly anthropized planet.

Declaration of competing 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 paper.

Acknowledgements

Z.M.-R. was supported by a postdoctoral contract (APOSTD/2019/016) cofunded by the Generalitat Valenciana and the European Social Fund (ESF), N.A.-A. by a pre-doctoral grant (BES-2016-077351) from the Spanish Ministry of Economy and Competitiveness (MINECO) and the ESF, E.S.-G. by the Generalitat Valenciana (SEJI/2018/024) and with a Ramón y Cajal research contract (RYC-2019-027216I) from the Spanish Ministry of Science and Innovation (MICINN). M.M. was supported by a Ramón y Cajal research contract (RYC-2015-19231) from the MINECO. The study was partially supported by the Spanish Ministry of Science, Innovation and Universities and the European Regional Development Fund (ERDF) (Project “TRASCAR” RTI2018-099609-B-C21).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.149652.

References

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. Ecol. Indic. 36, 594–600.

Alves, R.R.N., 2012. Relationships between fauna and people and the role of ethnozoology in animal conservation. Ethnobiol. Conserv. 1, 1–69.

Apollonio, M., Andersen, R., Putman, R. (Eds.), 2010. European ungulates and their management in the 21st century. Cambridge Univ. Press, Cambridge.

Apollonio, M., Belkin, V.V., Borkowski, J., Borodin, O.I., Borowik, T., Cagnacci, F., Danilkin, A.A., Danilov, P.I., Faybich, A., Ferretti, F., Gaillard, J.M., Hayward, M., Heshtaut, P., Heurich, M., Hurynovich, A., et al., 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. Mammal Res. 62, 209–217.

Ashton, M.S., Tyrrel, M.L., Spalding, D., Gentry, B. (Eds.), 2012. Managing forest carbon in a changing climate. Springer Science & Business Media.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T., 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environmental Resources 29, 261–299.

Barbosa, J.M., Pascual-Rico, R., Martinez, S.E., Sánchez-Zapata, J.A., 2019. Ungulates attenuate the response of mediterranean mountain vegetation to climate oscillations. Ecosystems 23, 957–972.

Bee, J.N., Kunstler, G., Coomes, D.A., 2007. Resistance and resilience of New Zealand tree species to browsing. J. Ecol. 95, 1014–1026.

Bennett, N.J., 2016. Using perceptions as evidence to improve conservation and environmental management. Conserv. Biol. 30, 582–592.

Bernes, C., Macura, B., Jonsson, B.G., Junnien, K., Müller, J., Sandström, J., Lõhmus, A., Macdonald, E., 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates A systematic review. 7, 1–32.

Beschta, R.L., Donahue, D.L., DellaSala, D.A., Rhodes, J.J., Karr, J.R., O'Brien, M.H., Fleischner, T.L., Williams, C.D., 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environ. Manag. 51, 474–491.

Boadella, M., Vicente, J., Ruiz-Fons, F., De la Fuente, J., Gortázar, C., 2012. Effects of culling Eurasian wild boar on the prevalence of Mycobacterium bovis and Aujeszky's disease virus. Prev. Vet. Med. 107, 214–221.

Boan, J.J., McLaren, B.E., Malcolm, J.R., 2011. Influence of post-harvest silviculture on understory vegetation: implications for forage in a multi-ungulate system. For. Ecol. Manag. 262, 1704–1712.

Bocherens, H., 2018. The rise of the anthroposphere since 50,000 years: an ecological replacement of megaherbivores by humans in terrestrial ecosystems? Front. Ecol. Evol. 6, 3.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. Science 313, 58–61.

Bueno, C.G., Jiménez, J.J., 2014. Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain). Appl. Soil Ecol. 83, 71–78.

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S., 2014. The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit? Wildl. Biol. 20, 161–166.

Carpio, A.J., Apollonio, M., Acevedo, P., 2020. Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. Mammal Rev. 51, 95–108.

Castillo-Contreras, R., Carvalho, J., Serrano, E., Mentaberre, G., Fernández-Aguilar, X., Colom, A., González-Crespo, C., Lavín, S., López-Olvera, J.R., 2018. Urban wild boars prefer fragmented areas with food resources near natural corridors. Sci. Total Environ. 615, 282–288.

Charco, J., Perea, R., Gil, L., Nanos, N., 2016. Impact of deer rubbing on pine forest: implications for conservation and management of Pinus pinaster populations. Eur. J. For. Res. 135, 719–729.

Colino-Arrabal, V., Langen, T.A., Peris, S.J., Lizana, M., 2018. Ungulate: vehicle collision rates are associated with the phase of the moon. Biodivers. Conserv. 27, 681–694.

Cousins, J.A., Sadler, J.P., Evans, J., 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: stakeholder perspectives. Ecol. Soc. 13, 43.

Danell, K., Bergström, R., Duncan, P., Pastor, J. (Eds.), 2006. Large herbivore ecology, ecosystem dynamics and conservation (Conservation Biology). Cambridge University Press, Cambridge.

Dean, G., Rivera-Ferre, M.G., Rosas-Casals, M., Lopez-i-Gelats, F., 2021. Nature`s contribution to people as a framework for examining socioecological systems: the case of pastoral systems. Ecosyst. Serv. 49, 101265.

Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J., Watson, J.E.M., 2019. Wilderness areas halve the extinction risk of terrestrial biodiversity. Nature 573, 582–585.

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Báldi, A., Bartuska, A., Baste, I.A., Bilgin, A., Brondizio, E., Chan, K.M.A., et al., 2015. The IPBES conceptual framework — connecting nature and people. Curr. Opin. Environ. Sustain. 14, 1–16.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., et al., 2018. Assessing nature's contributions to people. Science 359, 270–272.

Duarte, J., Farfán, M.A., Fa, J.E., Vargas, J.M., 2015. Deer populations inhabiting urban areas in the south of Spain: habitats and conflicts. Eur. J. Wildl. Res. 61, 365–377.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqamy, H., Baillie, J., Beddiaf, M., Belbachir, F., Belbachir-Bazi, A., Berbash, et al., 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Divers. Distrib. 20, 114–122.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M.A., Vamberger, M., Fritz, U., Janke, A., 2016. Multi-locus analyses reveal four giraffe species instead of one. Curr. Biol. 26, 2543–2549.

Ferguson, K., Hanks, J., 2012. The effects of protected area and veterinary fencing on wildlife conservation in southern Africa. Parks 18, 49–60.

Fernández-Olalla, M., Martínez-Jauregui, M., Perea, R., Velamazán, M., San Miguel, A., 2016. Threat or opportunity? Browsing preferences and potential impact of Ammotragus lervia on woody plants of a Mediterranean protected area. J. Arid Environ. 129, 9–15.

Gadd, M.E., 2012. Barriers, the beef industry and unnatural selection: a review of the impact of veterinary fencing on mammals in southern Africa. In: Somers, M., Hayward, M. (Eds.), Fencing for Conservation. Springer, New York.

Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimaraes Jr., P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., de Mattos, J.S., Schweiger, A.H., Owen-Smith, N., Johnson, C.N., et al., 2018. Ecological and evolutionary legacy of megafauna extinctions. Biol. Rev. 93, 845–862.

Gamborg, C., Jensen, F.S., Sandøe, P., 2017. Killing animals for recreation? A quantitative study of hunters' motives and their perceived moral relevance. Soc. Nat. Resour. 31, 489–502.

García-Bocanegra, I., Paniagua, J., Gutiérrez-Guzmán, A.V., Lecollinet, S., Boadella, M., Arnas-Montes, A., Cano-Terrizo, D., Lowenski, S., Gortázar, C., Höfle, U., 2016. Spatio-temporal trends and risk factors affecting West Nilus virus and related flavivirus exposure in Spanish wild ruminants. BMC Vet. Res. 12, 249.

García-Llorente, M., Martín-López, B., Iniesta-Arandia, I., López-Santiago, C.A., Aguilera, P.A., Montes, C., 2012. The role of multi-functionality in social preferences toward semi-arid rural landscapes: an ecosystem service approach. Environ. Sci. Pol. 19, 136–146.

Gass, T.M., Binkley, D., 2011. Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. J. Appl. Ecol. 48, 952–960.

Geisser, H., Reyer, H.U., 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J. Wildl. Manag. 68, 939–946.

Gerhardt, P., Arnold, J.M., Hackländer, K., Hochbichler, E., 2013. Determinants of deer impact in european forests – a systematic literature analysis. For. Ecol. Manag. 310, 173–186.

Ghoddousi, A., Soofi, M., Kamidi, A.K., Ashayeri, S., Egli, L., Ghoddousi, S., Speicher, J., Khorozyan, I., Kiabi, B.H., Waltert, M., 2017. The decline of ungulate populations in iranian protected areas calls for urgent action against poaching. Oryx 53, 151–158.

Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218.

Gilsdorf, J.M., Hygnstrom, S.E., VerCauteren, K.C., Clements, G.M., Blankenship, E.E., Engeman, R.M., 2004. Evaluation of a deer-activated bio-acoustic frightening device for reducing deer damage in cornfields. Wildl. Soc. Bull. 32, 515–523.

Giménez-Anaya, A., Herrero, J., García-Serrano, A., García-González, R., Prada, C., 2016. Wild boar battues reduce crop damage in a protected area. Foila Zool. 65, 214–220.

Goudie, A.S., 2013. Human impact on the natural environment: past, present and future. Seventh edition. John Wiley & Sons, Oxford.

Haule, K.S., Johnsen, F.H., Maganga, S.L.S., 2002. Striving for sustainable wildlife management: the case of kilombero game controlled area, Tanzania. J. Environ. Manag. 66, 31–42.

Havemann, C.P., Retief, T.A., Tosh, C.A., de Bruyn, P.J.N., 2016. Roan antelope Hippotragus equinus in Africa: a review of abundance, threats and ecology. Mammal Rev. 46, 144–158.

Hayward, M.W., Kerley, G.I.H., 2009. Fencing for conservation: restriction of evolutionary potentialor a riposte to threatening processes? Biol. Conserv. 142, 1–13.

Hegel, T.M., Gates, C.C., Eslinger, D., 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. J. Environ. Manag. 90, 222–235.

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., González, J.A., 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: synthesizing existing evidence and future challenges. Ecol. Evol. 7, 831–844.

Hildreth, A.M., Hygnstrom, S.E., Blankenship, E.E., VerCauteren, K.C., 2012. Use of partially fenced fields to reduce deer damage to corn. Wildl. Soc. Bull. 36, 199–203.

Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 47–58.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. J. Wildl. Manag. 60, 695–713.

Honda, T., Miyagawa, Y., Ueda, H., Inoue, M., 2009. Effectiveness of newly-designed electric fences in reducing crop damage by medium and large mammals. Mammal Study 34, 13–17.

Jenkins, R.K.B., Corti, G.R., Fanning, E., Roettcher, K., 2002. Management implications of antelope habitat use in the Kilombero Valley, Tanzania. Oryx 36, 161–169.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–275.

Kadykalo, A.N., López-Rodriguez, M.D., Ainscough, J., Droste, N., Ryu, H., Le Clec'h, S., Ávila-Flores, G., Muñoz, M.C., Nilsson, L., Rana, S., Sarkar, P., Sevecke, K.J., Harmácková, Z.V., 2019. Disentangling 'ecosystem services' and 'nature's contributions to people'. Ecosyst. People 15, 269–287.

Kansky, R., Knight, A.T., 2014. Key factors driving attitudes towards large mammals in conflict with humans. Biol. Conserv. 179, 93–105.

Kerr, G., 2019. Himalayan tahr (Hemitragus jemlahicus) recreational hunting values. Wildl. Res. 46, 114–126.

Kuemmerle, T., Radeloff, V.C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Bashta, A.T., Chikurova, E., Parkinoza, I., Baskin, L., Angelstam, P., Waller, D.M., 2011. Predicting potential European bison habitat across its former range. Ecol. Appl. 21, 830–843.

Kurten, E.L., 2013. Cascading effects of contemporaneous defaunation on tropical forest communities. Biol. Conserv. 163, 22–32.

Lamprey, H.F., 1936. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. Afr. J. Ecol. 1, 63–92.

Leuthold, W., 1978. Ecological separation among browsing ungulates in Tsavo East National Park. Kenya. Oecol. 35, 241.

Licht, D.S., Millspaugh, J.J., Kunkel, K.E., Kochanny, C.O., Peterson, R.O., 2010. Using small populations of wolves for ecosystem restoration and stewardship. Bioscience 60, 147–153.

Linnell, J.D.C., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G.R., Kaltenborn, B., 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's anthropocene. Biol. Conserv. 244, 108500.

Lozano, J., Olszanska, A., Morales-Reyes, Z., Castro, A.A., Malo, A.F., Moleón, M., Sánchez-Zapata, J.A., Cortés-Avizanda, A., von Wehrden, H., Dorresteijn, I., Kansky, R., Fischer, J., Martín-López, B., 2019. Human-carnivore relations: a systematic review. Biol. Conserv. 237, 480–492.

Lyytimäki, J., 2015. Ecosystem disservices: embrace the catchword. Ecosyst. Serv. 12, 136.

MacMillan, D.C., Phillip, S., 2008. Consumptive and non-consumptive values of wild mammals in Britain. Mammal Rev. 38, 189–204.

Martin, L.J., Blossey, B., Ellis, E., 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Front. Ecol. Environ. 10, 195–201.

Martínez-Jauregui, M., Soliño, M., 2021. Society's preferences when ecological values and health risks are at stake: an application to the population control of a flagship ungulate (Iberian ibex) in Sierra de Guadarrama national park, Spain. Sci. Total Environ. 776, 146012.

Martínez-Pastur, G., Soler, R., Ivancich, H., Lencinas, M.V., Bahamonde, H., Peri, P.L., 2016. Effectiveness of fencing and hunting to control Lama guanicoe browsing damage: implications for Nothofagus pumilio regeneration in harvested forests. J. Environ. Manag. 168, 165–174.

McDonald, A.M.H., Rea, R.V., Hesse, G., 2012. Perceptions of moose-human conflicts in an urban environment. Alces: A Journal Devoted to the Biology and Management of Moose 48, 123–130.

MEA (Millennium Ecosystem Assessment), 2005. Ecosystems and human well-being: synthesis. Island Press, Washington DC.

Methorst, J., Arbieu, U., Bonn, A., Böhning-Gaese, K., Müller, T., 2020. Non-material contributions of wildlife to human well-being: a systematic review. Environ. Res. Lett. 15, 093005.

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Cdányi, S., Stenseth, N.C., 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. J. Appl. Ecol. 43, 721–734.

Moleón, M., Sanchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., Donázar, J.A., 2014. Humans and scavengers: the evolution of interactions and ecosystem services. Bioscience 64, 394–403.

Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., Mace, G.M., Palmer, M., Scholes, R., Yahara, T., 2009. Biodiversity, climate change, and ecosystem services. Curr. Opin. Environ. Sustain. 1, 46–54.

Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A., 2018. Farmer perceptions of the ecosystem services provided by scavengers: what, who, and to whom. Conserv. Lett. 11, e12392.

Mysterud, A., Rolandsen, C.M., 2019. Fencing for wildlife disease control. J. Appl. Ecol. 56, 519–525.

Naidoo, R., Weaver, L.C., Stuart-Hill, G., Tagg, J., 2011. Effect of biodiversity on economic benefits from communal lands in Namibia. J. Appl. Ecol. 48, 310–316.

Naidoo, R., Weaver, L.C., Diggle, R.W., Matongo, G., Stuart-Hill, G., Thouless, C., 2016. Complementary benefits of tourism and hunting to communal conservancies in Namibia. Conserv. Biol. 30, 628–638.

Natusch, D.J.D., Mayer, M., Lyons, J.A., Shine, R., 2017. Interspecific interactions between feral pigs and native birds reveal both positive and negative effects. Austral Ecol. 42, 479–485.

Nuñez, M.A., Bailey, J.K., Schweitzer, J.A., 2010. Population, community and ecosystem effects of exotic herbivores: a growing global concern. Biol. Invasions 12, 297–301.

Osofsky, S.A., 2019. The global burden of (how we manage) animal disease: learning lessons from southern Africa. J. Wildl. Dis. 55, 755–757.

Owen-Smith, N., 1989. Megafaunal extinctions: the conservation message from 11,000 years B.P. Conserv. Biol. 3, 405–412.

Pascual-Rico, R., Morugán-Coronado, A., Botella, F., García-Orenes, F., Sánchez-Zapata, J.A., 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Appl. Soil Ecol. 127, 136–143.

Pascual-Rico, R., Martín-López, B., Sánchez-Zapata, J.A., Morales-Reyes, Z., 2020. Scientific priorities and shepherds' perceptions of ungulate's contributions to people in rewilding landscapes. Sci. Total Environ. 705, 135876.

Pascual-Rico, R., Morugán-Coronado, A., Pereg, L., Aldouri, S.S., García-Orenes, F., Sánchez-Zapata, J.A., 2021. Effects of diversionary feeding on abundance of microbes involved in soil nitrogen cycling on a Mediterranean mountain. Pedobiologia 85–86, 150724.

Paterlow, S., Schlüter, A., von Wehrden, H., Jänig, M., Senff, P., 2017. A sustainability agenda for tropical marine science. Conserv. Lett. 11, e12351.

Perea, R., Gil, L., 2014. Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically-defended shrubs. For. Ecol. Manag. 312, 47–54.

Pullin, A.S., Knight, T.M., 2009. Environmental program and policy evaluation: Addressing methodological challenges. In: Birnbaum, M., Mickwitz, P. (Eds.), Data credibility: a perspective from systematic reviews in environmental management. New Directions for Evaluation 122, pp. 65–74.

Rasmussen, L.V., Christensen, A.E., Danielsen, F., Dawson, N., Martin, A., Mertz, O., Sikor, T., Thongmanivong, S., Xaydongvanh, P., 2017. From food to pest: conversion factors determine switches between ecosystem services and disservices. Ambio 46, 173.

Rduch, V., Jentke, T., 2021. Alarming decline of bovids in kasanka National Park, Zambia: a case study of the puku antelope (Kobus vardonii). Afr. J. Ecol. 59, 387–398.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C., Watt, A., Gutierrez, R.J., 2013. Understanding and managing conservation conflicts. Trends Ecol. Evol. 28, 100–109.

Roberts, D.W., 2016. Package 'labdsv'. Ordination Multivar. 775.

Sankaran, M., Hanan, N., Scholes, R., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Toux, X.L., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., et al., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., Van Mantgem, P.J., 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122, 297–305.

Sebastián-González, E., Morales-Reyes, Z., Botella, F., Naves-Alegre, L., Pérez-García, J.M., Mateo-Tomás, P., Olea, P.P., Moleón, M., Barbosa, J.M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., et al., 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. Ecography 43, 1143–1155.

Senserini, D., Santilli, F., 2016. Potential impact of wild boar (Sus scrofa) on pheasant (Phasianus colchicus) nesting success. Wildl. Biol. Pract. 12, 15–20.

Shackleton, C.M., Ruwanza, S., Sanni, G.K.S., Bennett, S., de Lacy, P., Modipa, R., Mtati, N., Sachikonye, M., Thondhlana, G., 2016. Unpacking pandora's box: understanding and categorising ecosystem disservices for environmental management and human wellbeing. Ecosystems 19, 587.

Sidorovich, V.E., Tikhomirova, L.L., Jedrzejewska, B., 2003. Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. Wildl. Biol. 9, 103–111.

Sitters, J., Kimuyu, D.M., Young, T.P., Claeys, P., Venterink, H.O., 2020. Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. Nat. Sustain. 3, 360–366.

Taylor, W.A., Lindsey, P.A., Nicholson, S.K., Relton, C., Davies-Mostert, H.T., 2020. Jobs, game meat and profits: the benefits of wildlife ranching on marginal lands in South Africa. Biol. Conserv. 245, 108561.

Teichman, K.J., Nielsen, S.E., Roland, J., 2013. Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. J. Anim. Ecol. 82, 1288–1299.

Tubiana, J., 2005. Relations between wild ungulates and pastoralists in the Sahara: the case of Teda-daza and beri people (Chad, Niger, Sudan). Parc de la Haute Touche, France, p. 71.

Valente, A.M., Acevedo, P., Figueiredo, A.M., Fonseca, C., Torres, R.T., 2020a. Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mammal Rev. 50, 353–366.

Valente, A.M., Acevedo, P., Figueiredo, A.M., Martins, R., Fonseca, C., Torres, R.T., Delibes-Mateos, M., 2020b. Dear deer? Maybe for now. People's perception on red deer (Cervus elaphus) populations in Portugal. Sci. Total Environ. 748, 141400.

Vanbergen, A.J., 2013. Insect pollinators initiative. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259.

Velamazán, M., Perea, R., Bugalho, M.N., 2020. Ungulates and ecosystem services in Mediterranean woody systems: a semi-quantitative review. J. Nat. Conserv. 55, 125837.

Walter, W.D., Lavelle, M.J., Fischer, J.W., Johnson, T.L., Hygnstrom, S.E., VerCauteren, K.C., 2011. Management of damage by elk (Cervus elaphus) in North America: a review. Wildl. Res. 37, 630–646.

Wilson, D.E., Mittermeier, R.A. (Eds.), 2011. Handbook of the Mammals of the World. Vol. 2. Hoofed Mammals. Lynx Edicions, Barcelona.