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Review

The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene

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ABSTRACT

The cumulative impact of human activities has driven many species into severe declines across the globe. However, the recent focus on conservation optimism has begun to highlight case studies that go against this trend. Reforestation, agricultural abandonment, reintroduction and legislative change have led to a situation where large mammals have recovered and are now widespread across the European continent. This study summarizes the knowledge about wild ungulate distribution in Europe and review the diversity of ways in which they interact with humans. Drawn from a wide range of sources, we built distribution maps of European wild ungulates. Results show that 90% of Europe is home to at least 1 species of wild native ungulate, with roe deer and wild boar occupying 74% and 64% of Europe respectively. In contrast, wild native mountain ungulates only occupy 5% of Europe, and are often associated with protected areas. The wide distribution of most European ungulates combined with the extensive human activity within Europe result in a wide range of interactions between ungulates and humans. These interactions can be classified as services or disservices depending on the value orientation and economic position of the various stakeholders perceiving this relationship. Overall, our survey highlights the success of wildlife management policies in Europe and the potential for continental scale conservation of large mammals in human-dominated landscapes. However, maintaining the success of wild ungulate conservation requires actions from national and European institutions to improve coordinated management across jurisdictional borders and sectorial coordination for the whole landscape.

1. Introduction

There are currently many debates ongoing within conservation science concerning the best models for human – nature interactions. These include the debates about land sparing vs land sharing (Fischer et al., 2014), the role of protected areas vs multi-use landscapes (Sayer, 2009), and sustainable use vs protectionist ideals (Cretois et al., 2019). The science of spared landscapes (i.e. protected areas) is well developed, at least in part due to its robust conceptual foundations in island biogeography and the small population paradigm which were central to the early days of conservation biology (Caughley, 1994). However, critics of this approach note that the conceptual confinement of wildlife into “human-free” areas impedes our capacity to envision conservation strategies that do not include remoteness (López-Bao et al., 2017). In contrast, the science of coexistence, which promotes the presence of wildlife in multi-use landscapes, remains ad hoc and fragmented, and both the strategic utility and practicality of the whole approach are being contested. Despite recent attempts to conceptualise the approach (Carter and Linnell, 2016), there remains a dearth of good studies and analyses within the conservation science literature to illuminate the ongoing discussions.

The practice of wildlife conservation began many decades, even centuries, before the development of conservation science (Leopold, 1933). The results of these efforts can contribute valuable insights to inform ongoing debates. This is especially evident for species such as large mammals with which humans have a long and complex relationship, and which have been both directly exploited and directly managed. The relationship between Europeans and large ungulates goes

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back 30,000–40,000 years with the species serving as important contributions to early diet (Morin, 2008) and to early cultures (as objects of art; Fosse and Philippe, 2005). The distributions of species and the structures of communities have fluctuated dramatically during the post-Pleistocene and Holocene, driven by climate, human exploitation and human land-use (Boivin et al., 2016). As for most large mammals, the cumulative impact of human activities had driven most species into severe declines and regional extinctions by the end of the Holocene (i.e. late 19th and early 20th centuries). A trend that has continued for many of the planet's wild ungulates (Ripple et al., 2015). However, somewhat paradoxically with respect to global trends in species endangerment, the status of most European wild ungulates has dramatically improved during the 20th century's transition to the Anthropocene (Linnell and Zachos, 2010). For example the Alpine ibex (*Capra ibex*) was reduced to a few individuals localised in one hunting preserve (now Gran Paradiso National Park) and is now widespread all over the Alps with a population numbering more than 34,000 individuals in the late 1980's (Stüwe and Nievergelt, 1991). A combination of reforestation, agricultural-abandonment, rural-urban migration, legislative change, the development of wildlife management institutions and active re-introduction (mainly driven by hunters) has led to a situation where wild ungulates are now widespread across the European continent, making this an ideal case study to explore the challenges and opportunities associated to human wildlife coexistence.

Our objectives here are to take the case of wild ungulates in Europe, to summarise knowledge on their distribution across the continent, and examine the complex ways with which they interact with humans through the lens of the emerging coexistence discourse which is ongoing within conservation biology. This will include reviewing both the tangible and intangible aspects of their interactions with humans, which will also be viewed through the lens of ecosystem services and disservices.

2. Data gathering

2.1. Distribution maps and analysis

To our best knowledge, the only detailed wild ungulate range maps available are the ones published by the Global Mammal Assessment Group in 2008 and hosted by the IUCN Red List of Threatened Species (https://www.iucnredlist.org/). Although these maps are now a milestone for studies on ungulate ecology and conservation, updating them is demanding. However, ignoring new information can be detrimental to species conservation (Hughes, 2017). Moreover, it has already been noted that the IUCN species range maps lack precision at local scales (Ficetola et al., 2014).

To visualise the extent to which humans and ungulates presently share space, we have produced up-to-date continent-wide distribution maps of all of the native species of wild ungulates (see Fig. A1 in the online Appendix for a workflow illustration). This includes the following species: Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), moose (*Alces alces*), wild reindeer (*Rangifer tarandus*), European bison (*Bison bonasus*), Alpine and Iberian ibex (*Capra ibex* and *C. pyrenaica*), Northern chamois (*Rupicapra rupicapra*), Pyrenean chamois (*R. pyrenaica*) and wild boar (*Sus scrofa*) (Fig. 1). We also include other species like fallow deer (*Dama dama*) and mouflon (*Ovis ammon*), whose native status is unclear and contested (Chapman and Chapman, 1980; Lever, 1985), and species that are without doubt introduced, like white-tailed deer (*Odocoileus virginianus*), sika deer (*Cervus nippon*), Chinese water deer (*Hydropotes inermis*), Reeves's muntjac (*Muntiacus reevesi*), muskox (*Ovibos moschatus*) and barbary sheep (*Ammotragus lervia*) (Fig. A2 in the online Appendix). We do not include feral or extensively grazed free-ranging livestock like horses and semi-domestic reindeer. Data on distribution were drawn from many sources. The three volumes on ungulate management in Europe (Apollonio et al., 2010; Putman et al., 2011a; Putman and Apollonio, 2014) were central starting points. In addition, we added data from national mammal atlases, hunting statistics, citizen science databases, vehicle collisions, scientific papers that provided the location of their study sites or which reviewed the status and distribution of various species and populations, and expert assessments. Full details are provided in the online Appendix. Data were digitalised and represented on a 10 × 10 km grid, although it must be borne in mind that the real resolution of some underlying data may have been coarser. For example, some data were only available as polygon data representing counties, hunting grounds or other administrative units. From the 10 × 10 km grid we derived a spatial dataset containing 48,499 observations that we used to carry out GIS analysis and visualize the results. All analyses have been conducted using R (R Core team, 2018), and maps created using the R package tmap (Tennekes, 2018).

2.2. Hunting bags, ungulate–car collisions, and agriculture and forestry damage data

Because no overall European hunting bag and ungulate-car collision data exist, we gathered data from websites and reports publishing national statistics. If no data were found, we contacted wildlife managers and other administrative staff who had access to these data. Tables 1 and 2 summarize the data collected from national sources (see Table A1 in the online Appendix for a complete overview). Data on wildlife damages to agriculture and forestry are highly fragmented and hard to access. This illustrates that such costs are challenging both to map and quantify. For the purpose of this study, we mainly rely on the compilation found in Apollonio et al. (2010) and selected scientific case studies to illustrate the general types and magnitudes of issues.

3. Current distribution of wild ungulates in Europe

From the pool of 18 species that we included, we recognised 10 species as being native and 8 as being introduced (Linnell and Kaltenborn, 2019). About 90% of Europe's land area hosts from one to five species of wild native ungulate (Fig. 2A and C), with mountainous areas being generally the most species diverse. It should be noted that even though northern Scandinavia appears ungulate free or has a low ungulate diversity, semi-domestic reindeer thrive in most of this range (see Pape and Löffler, 2012 and Fig. A3 in the online Appendix). The introduced species tended to have more limited distributions, although a few areas have up to 4 sympatric species (Fig. 2B and D). Species had highly variable distribution areas. Roe deer and wild boar occupying respectively 74% and 64% (more than 3 million km^2) of the continent and the mountain ungulates (i.e. Northern and Pyrenean chamois, and Alpine and Iberian Ibex) occupying 5% or less of the European land area (less than 250,000 km^2). These differences in distribution area are also reflected in differences in the extent to which distributions were linked to protected areas. With the exceptions of the European bison and the muskox which are most associated with protected areas, the mountain ungulates tended to have the largest proportions of their distribution ranges within protected areas. However, the Pyrenean chamois was the only species to have more than 50% of their range within protected areas. For the other species, on average more than 70% of their distribution was outside protected areas.

4. Interactions with humans and human interests

The fact that most of the distribution area of wild ungulates is outside protected areas, combined with the fact that there is extensive human activity, including hunting, within all European protected areas (Linnell et al., 2015; van Beeck Calkoen et al., 2020), results in a wide range of interactions between wild ungulates and humans. In the following sections we review these interactions and their consequences on humans and their shared ecosystems and discuss how to improve coexistence with wild ungulates.

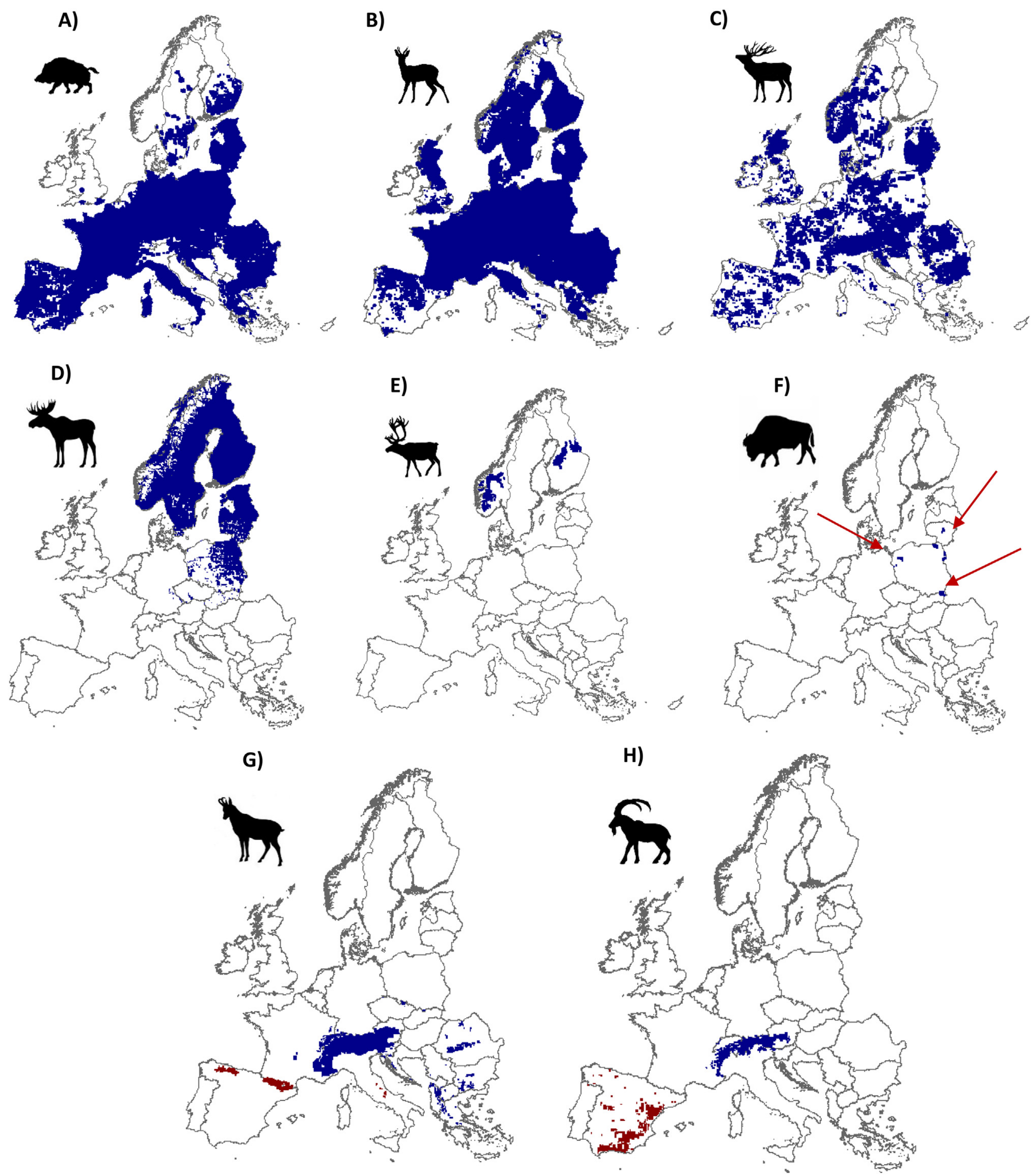

Fig. 1. Distribution maps for wild native ungulates in Europe. A) wild boar, B) roe deer, C) red deer, D) moose, E) wild reindeer, F) European bison, G) northern chamois (in blue) and Pyrenean chamois (in red), H) alpine ibex (in blue) and Iberian ibex (in red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Prey for predators and carrion for scavengers

The recovery of Europe's wild ungulates during the 20th century (Linnell and Zachos, 2010) preceded, and facilitated, the recovery of Europe's large carnivores in the latter half of the century (Chapron et al., 2014). There are currently an estimated 17,000 grey wolves (*Canis lupus*) and 9000 Eurasian lynx (*Lynx lynx*) in Europe (Linnell and Cretois, 2018). Presently, wild ungulates constitute the main part of the diet of both species across most of Europe, with the exception of some areas in the extreme north of Fennoscandia and the Mediterranean south where domestic animals constitute the main prey of lynx and wolves respectively (Breitenmoser et al., 2008; Zlatanova et al., 2014). Wolves prey extensively on moose, red deer, roe deer and wild boar, with lynx preying on roe deer, Northern chamois and red deer. Brown bears (*Ursus arctos*) in Scandinavia also prey on moose calves during spring (Rauset et al., 2012) and occasionally on adult moose. Wild

Table 1
Number of wild ungulates harvested in Europe for the most recent year available.

Countries	Years	Total shot per year	Wild boar	Roe deer	Red deer	Moose	Other deer[a]	Mountain ungulates
Germany	2017	2,111,695	836,865	1,190,724	76,794		2429	4883
France	2017	1,421,958	756,149	585,925	62,418		1516	15,950
Poland	2017	660,100	341,400	214,800	94,400		9500	
Austria	2017	413,355	40,297	285,718	61,545		1749	24,046
Czech Republic	2017	383,584	229,182	103,455	27,878		23,069	
Spain	2010	371,377	207,159	29,935	112,252		10,846	11,185
Sweden	2017	354,305	114,831	103,396	10,494	84,754	40,830	
Hungary	2017	249,608	102,600		101,464		34,725	10,819
Slovakia	2016	132,106	53,788	25,627			45,861	6830
Bulgaria	2013	123,654	49,513	64,889	6295		2205	752
Denmark	2017	116,086	190	96,193	9927		9703	73
Scotland	2017	115,037		42,543	61,640		10,854	
Norway	2017	111,816	226	33,280	42,541	31,613	4156	
Finland	2017	107,849	571	9392		56,581	41,285	20
Switzerland	2017	83,200	11,346	44,394	14,611			12,849
Italy (Lombardie)	2017	187,059	114,831	46,507	7978		4424	13,319
Latvia	2017	70,066	25,549	22,135	15,330	7052		
Lithuania	2016	63,792	32,624	23,828	5266	1796	278	
Slovenia	2017	56,150	12,238	34,156	7425			2331
Croatia	2017	49,645	30,000	15,400			4245	
Estonia	2015	46,969	32,580	6264	1252	6873		
Belgium (Wallonie)	2016	45,930	21,721	19,272	4635		139	163
Romania	2012	29,496	19,965	7457	1617		457	
Luxembourg	2017	14,052	6520	6868	468		144	52
Belgium (Flanders)	2017	7379	1550	5762	5		62	
Total		7,326,268	3,041,695	3,017,920	726,235	188,669	248,477	103,272

[a] Includes wild reindeer, sika deer, fallow deer and white-tailed deer. No available harvest data for Reeves' muntjac and Chinese water deer.

ungulates help reduce conflicts between predators and livestock producers as high livestock depredation rates are often linked to low wild prey densities (e.g. Gervasi et al., 2014; Odden et al., 2013).

Although Europe's large carnivores now prey on wild ungulates across much of the continent, the dynamics of these predator-prey relationships are highly modified by the direct and indirect impacts of humans on all trophic levels, i.e. harvest and modification of vegetation through forestry and agriculture, and hunting and traffic collisions that kill both wild ungulates and carnivores (Boitani and Linnell, 2015; Kuijper et al., 2016). This implies that Europe has established large predator – ungulate dynamics within a wide range of different novel ecosystem contexts rather than re-establishing natural dynamics.

4.2. *Ecosystem engineers*

In addition to providing a prey base for increasingly viable large carnivore populations in Europe, the carcasses of ungulates killed by carnivores, or dying from other causes, as well as the gut-piles left by hunters, provide a crucial source of carrion for a diverse guild of vertebrate and invertebrate scavengers (Melis et al., 2004, 2007; Wikenros et al., 2013). Many scavengers such as vultures are of conservation concern and often require the artificial provisioning of carrion, for example in so called "vulture restaurants" (Piper, 2005).

Wild ungulates are also directly associated with a wide range of ecological interactions with vegetation and soil that change the structure and distribution of plant species and soil nutrients. These processes include grazing and browsing, physical disturbance of the soil surface, seed dispersal, and redistribution of nutrients via urination and defecation. In turn, these ungulate-plant-soil interactions have cascading effects on a wide range of invertebrate and vertebrate species (e.g. Danell et al., 2006 and chapters therein).

Although the presence of wild ungulates is essential for restoring ecosystem processes, they have recovered to densities that probably surpass those from historical times in many parts of Europe. This is because of high access to anthropogenic food sources (from agriculture, forestry, and supplementary feeding) and from reductions in predator densities. These high-density ungulate populations have been widely shown to influence vegetation, including species composition, ground vegetation and tree regeneration (Bernes et al., 2018; Kuijper, 2011), as well as associated vertebrate and invertebrate communities (Foster et al., 2014). In some cases, these high grazing or browsing rates may have negative impacts on species of conservation concern and on ecosystem productivity (Ramirez et al., 2018; Velamazán et al., 2017). Grazing could also hinder ecological succession, hence preventing overgrowth in open ecosystems, which can be viewed as both a positive or negative effect depending on conservation and economic objectives.

4.3. *Quarry for hunters*

Most of the early restoration of wild ungulates was initiated and motivated by hunters with the intention of increasing hunting opportunities. Wild ungulates (with the exception of bison and muskox) are currently hunted in virtually all parts of their distributional range, including most protected areas (van Beeck Calkoen et al., 2020). Wild ungulate hunting in Europe is managed in different ways, with major differences existing between and within countries. Hunting management is usually delegated to local (sub-national) administrative levels where different socio-economic and political traditions and cultures lead to different approaches (Linnell and Kaltenborn, 2019). Even though some initiatives (e.g. project Artemis; artemis-face.eu) promote collaboration on hunting management between countries, there are no overall European hunting bag statistics. Nevertheless, Table 1 gives a fairly good estimate of the number of wild ungulates being harvested each year (see Table A2 in Appendix for detailed number of large ungulates harvested in Europe). The approximatively 7.3 million ungulates being harvested represent a considerable meat resource, as well as a source of income for landowners (that may offset some of the damages caused by ungulates) and rural communities, and many recreational opportunities for the estimated 7 million hunters in Europe (https://www.face.eu/).

4.4. *Wildlife viewing for rural residents and tourists*

Wildlife tourism, and in particular wildlife watching, is currently a

Table 2
Number of ungulate-vehicle collisions (!), number of ungulates killed in vehicle collision (†) or both (!†) each year in a selection of European countries.

Country	Years	Yearly number	Roe deer	Wild boar	Moose	Red deer	Fallow deer	Mountain ungulates	Source
Germany	2017–2018	233,070!	191,590!	34,550!		2920!	4010!		Deutscher Jagdverband (www.jagdverband.de/content/wilde-zeiten-auf-der-straße)
United Kingdom	2016	74,000!							The deer initiative (www.deeraware.com/uploads/publications/press-release-motorists-warne-28.pdf)
Sweden	2017	60,857†!	45,863†!	6082†!	5941†!	425†!	2546†!		Nationella Viltolycksrådet (www.viltolycka.se)
France	2009	53,418!	27,991!	20,665!		4762!			Christine St Andrieux, Personal communication
Austria	2017–2018	42,279†	40,897†	602†		663†	27†	85†	Project Roadkill (http://globalroadkill.net)
Norway	2017–2018	22,396†!	14,872†!		4226†!	3298†!			Norwegian deer registry (www.hjorteviltregisteret.no)
Estonia	2014–2018	18,401!	1300	2000	2000				Estonian Road Administration, pers. comm
Poland	2014–2018	18,000!							Jasinska K, pers. comm
Czech Republic	2017	12,043!	75%	15%					Bíl et al., 2017; Bil M, Personal communication
Spain	2006–2012	9042!	3441!	5005!		581!	15!		Sáenz-de-Santa-María and Tellería, 2015
Hungary	2011–2014	7650†	4500–5000†	2500–2000†		500–800†			András. W, Personal communication
Denmark	2017	6608!	85%			4%	7%		Miljø-og Fødevareministeriet (schweiss.dk/sites/default/files/trafikeftersoegninger_2017.pdf)
Latvia	2017	3190!							Lama A, Personal communication
Croatia	2016	2863 †	2457†	334†		72†			Bil. M, Personal communication
Finland	2017	1824!			1824!				Liikennevirasto (julkaisut.vayla.fi/pdf8/lti_2018-06_hirvionnettomuudet_2017_web.pdf)
Lithuania	Per year on average	1000–2000†							Balciauskas. L - Personal communication
Italy(South Tyrol)	2014	776†	686†			90†			Favilli et al., 2018
Belgium (Flanders)	2017	179†	127†	44†			8†		Waarnemingen.be (Citizen science project: waarnemingen.be/Observation.be)
Italy(Piedmont)	2011	148!							Tizzani P, Personal communication
Total		568,244†!	360,203†!	73,178†!	13,831†!	13,825†!	7068†!	85†	

growing sector in Europe with wild ungulates serving as a tourist attraction in many remote areas. For instance, the rising interest in 'moose safaris' in Norway and Sweden show the potential wild ungulates hold for local economies (Margaryan and Wall-Reinius, 2017; Thulin et al., 2015). Muskoxen in central Norway provide novel opportunities for wildlife watching and the basis for new nature tourism companies. This is both as direct targets for viewing, and more indirectly as part of the allure or branding of natural areas with multiple values (Schirpke et al., 2018). Furthermore, it is evident that many rural residents take pleasure in seeing wild ungulates close to their houses and during recreational activity in more remote areas. However, these intangible and non-consumptive interactions between humans and ungulates remain grossly understudied and unquantified.

4.5. Vehicle collisions

Europe is a highly and increasingly fragmented continent (Piorr et al., 2011), with an estimated 7.3 million km of public roads of various sizes criss-crossing the landscape (Central Intelligence Agency, 2018). This provides a consequent interface between traffic and ungulates (Bruinderink and Hazebroek, 1996; Putman et al., 2011b). Although up-to-date statistics are hard to find for the whole continent, Table 2 shows that for the selected countries or a subset of regions within some countries, more than half a million collisions with ungulates are recorded every year. These collisions result in damage to vehicles, human injuries and loss of human life, and represent a major source of ungulate mortality (Putman et al., 2011a). They also constitute an animal-welfare issue as an unknown proportion of ungulates are injured but not found after the accidents. In Norway, for instance, the number of moose-vehicle collisions is at least two times as high as the number of moose recorded killed in these accidents (http://www.hjorteviltregisteret.no). Many mitigation measures have been tested, but few have been consistently documented to effectively reduce collision frequency apart from fencing longer road sections in combination with wildlife crossing structures (Huijser et al., 2016; Rytwinski et al., 2016). With high, and in some countries and regions increasing, abundance of ungulates and increasing traffic there is a growing need to reduce the number of collisions (e.g. Rolandsen et al., 2011; Massei et al., 2015).

4.6. Damage to crops and forests

Although browsing and grazing are essential ecosystem processes provided by wild ungulates, they can be major sources of conflict with humans when they exploit species of importance to agriculture or forestry. In the absence of protection measures, browsing and grazing can have substantial economic consequences for some farmers. Regions of high moose, red deer and roe deer in regions of high densities are also frequently causing damage to tree species of interest to foresters, preventing the recruitment of some species and, through browsing or bark stripping, seriously reducing the growth rate of others. Estimating the costs of such damages is notoriously difficult, but in some countries, where damages are compensated, payments can reach 13 million euros (e.g. for Poland, see Table 3). Wild boar is one of the species that is most often causing damage to crops (Barrios-Garcia and Ballari, 2012) and is estimated to generate an economic loss of more than 30 million euros in the agricultural and forestry sector in Italy and France alone (Apollonio et al., 2010).

4.7. Diseases

There is a risk of increased pathogen transmission when people, livestock and wild ungulates share a landscape. An extensive investigation of emerging infectious disease found that 60% of disease events were caused by zoonoses. More than 70% of these originate in wildlife (Jones et al., 2008), and changing climate may increase the

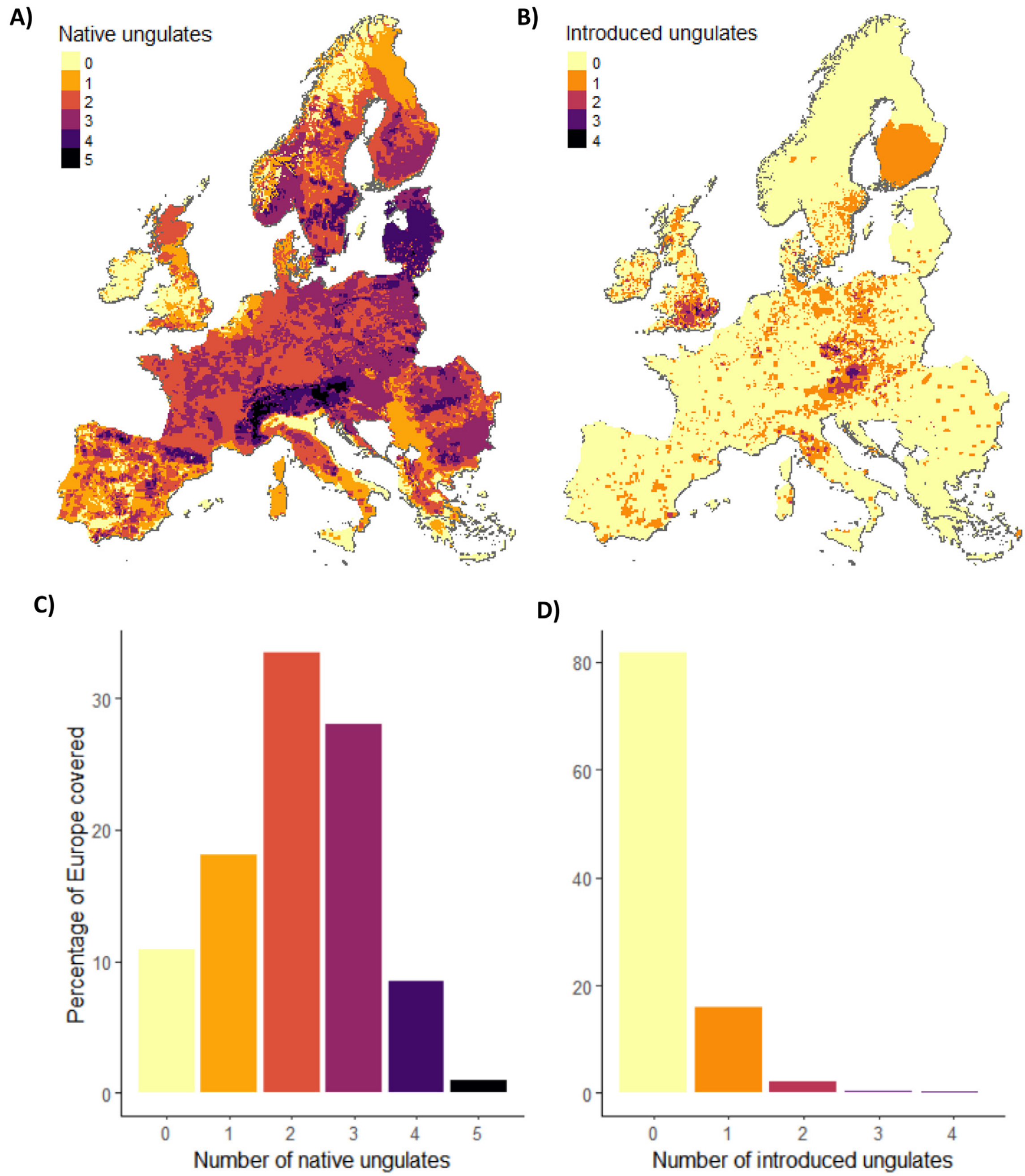

Fig. 2. Distribution maps and histograms of the number of native (A) (C) and introduced (B) (D) diversity in Europe.

occurrence of diseases (Altizer et al., 2011; Altizer et al., 2013). Lyme disease and tick-borne encephalitis, where deer are important tick reproduction hosts, are examples of common zoonoses with an increasing geographic distribution. Accordingly, ungulate density is one of several factors which influences their prevalence (Mysterud et al., 2016). Other zoonoses, involving ungulates as reservoirs, include tuberculosis, and brucellosis (Martin et al., 2011), while trichinellosis is an example of a disease that can be directly transmitted to humans by wild boar meat consumption (Rostami et al., 2018).

Livestock production may be affected by a large number of diseases including anaplasmosis, tuberculosis, paratuberculosis, African swine fever (ASF), classical swine fever, brucellosis, blue-tongue virus and Aujeszky's disease virus (Martin et al., 2011; Gortázar et al., 2007), all of which are on the World Organisation for Animal Health's (OIE) notifiable disease list (OIE 2019 - https://www.oie.int/animal-health-in-the-world/oie-listed-diseases-2019/). Diseases can also be transmitted from livestock to wild ungulate populations. For example, domestic sheep populations can act as a reservoir for *Mycoplasma conjunctiva*, an infectious eye disease that is normally not self-maintained in wild northern chamois (Belloy et al., 2003).

The recent geographic expansion of chronic wasting disease (CWD), into Norwegian wild reindeer (Benestad et al., 2016), moose (Pirisinu et al., 2018), and red deer (Vikøren et al., 2019), was listed among the top 15 most important global issues for biodiversity and conservation research (Sutherland et al., 2018). ASF and CWD are a cause of major concerns for wildlife and livestock health in Europe (Gavier-Widén et al., 2015; EFSA Panel on Biological Hazards, 2016), and may have effects that go far beyond the direct impact on wildlife and livestock as authorities often respond to outbreaks with powerful measures. This may include actions such as eradication of entire subpopulations (Mysterud and Rolandsen, 2018), building of fences to mitigate transmission (Mysterud and Rolandsen, 2019), and significant population

Table 3
Some examples of damage caused by wild ungulates to agricultural crops and forestry at various scales in Europe (most data from Apollonio et al., 2010).

Country	Damage to agriculture	Damage to forestry	Source
Europe	Estimated annual costs from wild boar of €80,000,000.		Apollonio et al. (2010)
Luxembourg	Compensation for wild boar damages was €900,000 in 2004.		Schley et al. (2008)
Slovenia	Compensation for wild boar damages was €575,000 in 2013.		Slovenia Forest Service (2014)
Italy	No consistent estimates available, but total annual costs are expected to exceed €10,000,000. In north eastern Sardinia, a total of €483,982 have been attributed for compensating wild boar damages to crops over a 7 years period.		Apollonio et al. (2010) Lombardini et al. (2016)
Lithuania	With more than 130 ha of crops damaged in 2017, the growth of the endangered European bison populations has led to increase costs in compensation.		Marozas et al. (2019)
Hungary	Compensation payment for crop damage reached €6,000,000 in 2008.	Compensation paid for forest damages in 2005 reached up €585,000.	Bleier et al. (2012) Csányi and Lehoczki (2010)
Poland	Compensation payment for crop damages was €13.7 million in 2010,in which €90,000 was attributed to bison damage.	Costs exceeded €15,000,000 in 2003.	Hofman-Kamińska and Kowalczyk (2012) Wawrzyniak et al. (2010)
France	Compensation for crop damages was more than €21,000,000 in 2005 (mainly wild boar).		Maillard et al. (2010)
Croatia	Compensation payment for damage to crops, forests and vehicles estimated to €685,000 yearly (mainly wild boar and red deer).		Kusak and Krešimir (2010)
Czech Republic		Annual costs estimated to reach up to €1,500,000 per year.	Bartoš et al. (2010)
Finland	Compensation payment in 2006 was €260,000 (mainly moose and white-tailed deer).	Amount of compensation payment in 2006 was €3,200,000 (mainly moose and red deer).	Ruusila and Kojola (2010)
England	Estimated annual costs at €6,560,000.		Putman (2010)
Slovakia	Compensation to crops was €320,000in 2005 (mainly wild boar).	Annual costs exceed €1,490,000 (mainly red deer, roe deer, mouflon and fallow deer).	Findo and Skuban (2007)
Sweden		Estimated annual loss €150,000.	Liberg et al. (2010)

reductions (EFSA, 2018). These actions can in extreme cases also influence entire countries' abilities to trade livestock and livestock products (EFSA, 2018; Schulz et al., 2019), and can be controversial both among the public, scientists and conservationists (Vicente et al., 2019; Mysterud and Rolandsen, 2018).

The interface between wild and domestic ungulates is influenced by livestock husbandry and wildlife management practices. For example, the widespread practice of supplementary feeding of wild ungulates (e.g. Mysterud et al., 2019; Putman and Staines, 2004) may create situations with high local densities and high interaction rates (Gortázar et al., 2006). Providing artificial waterpoints or saltlicks, may have similar effects. Another issue is the long-distance transfer of wild animals between hunting areas (Apollonio et al., 2017). The herding practice of livestock (i.e. enclosed, herded or free-ranging) may also affect the potential for disease transmission with wildlife and hence the level of biosecurity. Sheep, goats and cattle that are extensively grazing in alpine, heathland or forest pastures, have the greatest interface, while those kept on fields close to farms or indoors have the least (Gortázar et al., 2007).

4.8. Opportunity costs

Although many wild ungulates show an ability to tolerate anthropogenic land-use and habitat modifications, the level of tolerance needs to be considered in land-use planning of new developments. Including wild ungulates in the equation may incur opportunity costs for landowners and other property rights holders. One classic example concerns the vulnerability of wild mountain reindeer to virtually all infrastructures (e.g. roads, energy production plants, tourist resorts) and forms of human disturbances (e.g. hiking, skiing; Panzacchi et al., 2016; Beyer et al., 2016). Taking the needs of reindeer into account may require that such human activities are reduced and/or directed away from critical habitats (e.g. Gundersen et al., 2019). Mountain ungulates like ibex and chamois are also vulnerable to such disturbances (Pęksa and Ciach, 2015), and the potential mountains hold for the energy sector (wind and hydropower) have to account for the survival and wellbeing of these species. High ungulate densities may also impose opportunity costs on foresters and farmers as intense browsing pressure may exclude the possibility of planting certain tree species or growing certain crops.

5. A challenge or an opportunity? It's all in the eye of the beholder

The previous sections outlined the diversity of interactions that occur between humans and wild ungulates in shared landscapes. However, it is almost impossible to classify any as being unambiguously positive or negative (challenges vs. opportunities or services vs. disservices) because it depends on the basic value orientation and economic position of the various stakeholders. Conservationists may view predation on ungulates as a positive ecological process, whereas hunters may view this as competition for a valuable quarry (Bisi et al., 2010). Likewise, some conservationists may view herbivory as a positive ecological disturbance process, whereas foresters will view it as an economic loss. However, high herbivory pressure can also compromise conservation values and may as such be considered negative by some conservationists. While hunters obviously view the opportunity to hunt as a positive value, a certain proportion of the public will view it as morally unacceptable (Gamborg and Jensen, 2017). People may even view wildlife diseases in different ways depending on their basic view on whether these are important components of ecological processes and biodiversity (both of which include parasites and diseases as intrinsic components).

The result is that while there are many situations where ungulates cause costs to human economic assets and interests, there are also many conflicts between stakeholders over the way that ungulates should be managed (Bredin et al., 2015; Redpath et al., 2013). Interestingly, in the European context this is not only between conservationists and other stakeholders, but also within the conservation community, as there are many competing approaches to conservation in Europe (Linnell et al., 2015). Even individual stakeholders can have to face complex trade-offs in cases where they engage in the pluriactivity which characterises many European rural residents; for example, it is not uncommon for many farmers to also be hunters and/or foresters and/or engage in rural tourism. In such cases wild ungulates may have very different impacts on each of these different income streams. These complex trade-offs challenge all governance structures. Although economic valuation through ecosystem services is a popular approach to address such issues, it is likely to fail with regard to wild ungulate management. This is because so many of the costs and benefits are of an intangible nature, and not conducive to economic valuation. In addition, the distributions of costs and benefits fall on widely different spatial scales (Linnell, 2015) and within different value domains (Arias-Arévalo et al., 2018). As an example we point to the challenges of scale concerning the impact of ungulate-vehicle collisions. The benefits of high ungulate densities fall on local hunters and landowners, whereas the costs of accidents and mitigation measures are carried at wider societal scales. Finally, the density of ungulates varies across Europe and the impact that ungulates have is often density dependent implying that the relative strengths of different interactions will vary across the continent.

6. Looking into the future

The results of our mapping exercise illustrate that more than 70% of the European continent is now occupied by two or more species of native wild ungulates, with almost 1% hosting 5 species. This is a clear demonstration of the ability of these species to occupy heavily human-dominated landscapes, which is a prerequisite for coexistence. Although we have not formally examined the potential for further increases in distribution, it is highly likely that some species, especially wild boar, roe deer and red deer, have the potential to increase their distributions further in large parts of southern Europe, and in parts of Fennoscandia (Rosvold and Andersen, 2008; Vingada et al., 2010). However, the results of our examination of management issues illustrate the complexity of the human-wildlife and human-human interactions that stem from co-occupation of space. These interactions may be positive and/or negative, or both, and depend on the economic interests and basic values of different stakeholders. The extent to which we can regard the co-occupation with wild ungulates as coexistence depends very much on how these interactions are managed (Fig. 3).

Endangered species and those of clear conservation concern (like large carnivores) are subject to continental level management coordination due to their inclusion under the legal frameworks of the Habitats Directive and the Bern Convention (Linnell and Kaltenborn, 2019). In contrast, the wild ungulates that we consider in this article are normally managed at national or sub-national levels that do not always correspond to ecological scales (Linnell et al., 2015; Linnell and Kaltenborn, 2019). In some cases, this scale can be as low as the municipality or even the individual landowner. Furthermore, there is enormous variation in the extent to which management authorities provide research and administrative support to, and supervision of, these local decision-making structures. This decentralised and delegated approach may have functioned to acceptable levels in the past and has facilitated the recovery of ungulates whose results we are seeing today. However, there are many indications that changes in management structure are going to be needed to meet the challenges of the future.

The drivers of change are diverse, but include the following:

(1) Changing human pressure on the landscape through infrastructure development (transport, recreation, renewable energy production, Venter et al., 2016).
(2) Global change, including climate change, the re-emergence of diseases once thought to be under control, and the appearance of new diseases (Lindgren et al., 2012).
(3) Increased diversity of stakeholder perspectives with divergent, and often conflicting, perspectives on wild ungulate management. The increase in focus on new ideologies like animal rights and rewilding, for example, represent considerable challenges for conventional management structures that are centred around hunting as both an objective and a tool to reach other ecosystem goals (Kennedy and Koch, 2004).
(4) The return of large carnivores as predators on ungulates and competitors with hunters (Chapron et al., 2014).
(5) Constant changes in agricultural and forestry practices in response to shifting policy priorities (Persson et al., 2016).
(6) The controversial impacts of the increasing densities of ungulates, and their expansion into many areas, especially urbanised areas and those with intensive agricultural production create a number of challenges associated with the success of their conservation (Stillfried et al., 2017).
(7) New knowledge about movement patterns, demography, ecological interactions and disease processes that challenge existing management paradigms.
(8) The impact of shifting political directions that are currently dismantling, or restructuring, many of the wildlife management institutions that have developed during the 20th century.

6.1. The need for a bigger picture

Many of the drivers mentioned above affect human-wildlife interactions on large spatial scales, and their consequences can be seen in the need for increased coordination in several areas:

6.1.1. Coordinated management across jurisdictional borders

It is clearly challenging to achieve divergent management goals at spatial scales that are smaller than the biological scales at which the species in question operate (Linnell, 2015). A wide range of telemetry studies conducted during the last 40 years have demonstrated how mobile these species can be (Tucker et al., 2018). Therefore, there is a need to coordinate management actions across administrative and jurisdictional borders. This may include cooperation between multiple landowners, between state and private properties, between protected areas and neighbouring unprotected areas, or between different municipalities, counties, cantons, federal states or even countries.

It has been noted that the degree of transboundary management is currently unsatisfactory (Apollonio et al., 2010) so that there is considerable scope for improvement. Unfortunately, moving management up in scale removes it from the local acceptance that may be instrumental in bringing it to its present favourable situation (Linnell, 2015; Linnell and Kaltenborn, 2019).

Creating central databases of parameters like hunting bags, vehicle collisions and damage payments would be a crucial tool in this endeavour.

6.1.2. Sectorial coordination for whole landscape planning

Traditionally, ungulate management has been an issue mainly limited to the agricultural and forestry sectors. The new challenges require cooperation with a far broader set of sectorial interests. Their importance as prey for large carnivores and their interaction with wider biodiversity make wild ungulates a group of major concern for nature conservation authorities (Ripple et al., 2015). The transport sector represents another example because of the conflicts associated with vehicle collisions and the need to integrate crossing structures like green bridges or viaducts and safety structures like fences into road construction plans to constrain and facilitate ungulate movements (Gunson et al., 2011). The move towards renewable energy sources like solar, wind and hydropower leads to a rapid development of infrastructure, with associated human access, disturbance and barrier effects, in often previously undeveloped areas. These developments can have negative impacts on ungulates, requiring coordination with the energy sector (Northrup and Wittemyer, 2013). Likewise, the growth in recreation, and its associated infrastructure, can create disturbances in previously undisturbed areas, and requires that the wildlife management coordinate with the tourism and recreation sectors. The recent trend to build and refurbish border security fencing (Linnell et al., 2016) which can inhibit ungulate movement, also underlines the need to coordinate with the border security or defence sectors. A similar coordination is needed with the agricultural, veterinary and animal health authorities, given the potential role of wild ungulates in disease transmission.

Fig. 3. A) The area of distribution of wild ungulates in Europe (in % of total area) and B) the percentage of this distribution that is within protected areas.

The need for multi-sectorial coordination is not only necessary for the sake of wild ungulate conservation, but also for the possibility for other sectors to succeed in their own priorities. For example, the transport sector can build good roads, but failing to consider wild ungulates can lead to high accident rates. Similarly, a failure by veterinary authorities to consider the possible role of wildlife in disease transmission will frustrate attempts to eradicate or control diseases in livestock.

6.1.3. The need for planning human activity

The result of the issues highlighted in the last two sections is the need for both effective spatial planning of human activities and management of wild ungulate populations (Sandström, 2012). Spatial planning is the only existing policy arena where the interests and concerns of multiple sectors can be easily integrated. If the different sectors are aware of the need to consider wild ungulate issues, then spatial planning documents can help them identify areas of overlap and conflict. However, this presupposes an awareness of the need to consider these issues, which is often lacking. Rectifying this lack will require a great deal of awareness raising, and the provisioning of policy guidelines that outline the relevance of wild ungulates for the different sectors. A related aspect of this process also concerns the explicit integration of wild ungulate issues into environmental impact assessment procedures. Our maps of wild ungulate distribution on a continental scale are a first step in identifying and communicating the almost universal relevance of these issues across Europe. However, operationalising these concerns in planning processes will require much finer scaled and locally adapted mapping of areas of distribution and movement.

The other clear finding lies in the need for management of wild ungulates and of regulation of the ways humans interact with them. Hunting is the only readily available tool for influencing wild ungulate numbers on large scales, but the impacts of hunting extend beyond the numbers killed and also embrace the practices that hunters use to influence density, demography and distribution of animals (Milner et al., 2007). The need for hunting regulations to prevent over-harvest is obvious from a conservation point of view. However, it is also important to consider the conflicts (with other sectors) that can occur if too few animals are harvested, or if measures like supplementary feeding lead to too high densities, or aggregations in undesirable areas.

7. Conclusions – insights into coexistence and living with success

There are three main conclusions from this synthesis. Firstly, the survey identifies the high potential for conserving diverse wild ungulate communities across the entire landscape of the European continent, irrespective of whether it is private or public land, protected or unprotected areas. In other words, it reveals that there is a huge scope for a land-sharing form of conservation. Secondly, the diversity of interactions that occur with the humans who share this space underlines the need for a range of active management policies to deal with conflicting objectives and trade-offs. This implies that it is practically meaningless to expect a hands-off (i.e. "let nature take its course") management strategy to work or to use any form of "naturalness" (i.e. an absence of human influence) as a benchmark for setting management objectives (outside of some exceptional areas) as many rewilding or animal rights advocates would desire (Manfredo et al., 2019). Finally, because of the increasing diversity of interests and increasing conflict over objectives, there is a need to build on existing management structures to ensure greater transparency, scientific robustness and social legitimacy. The integration of all these elements is needed to ensure that this very successful cohabitation can continue to be termed coexistence (Carter and Linnell, 2016).

Data availability statement

The R script and the full dataset use to carry out the analysis are both made available to ensure full reproducibility and can be found at https://doi.org/10.17605/OSF.IO/N5P2U.

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.

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Appendix A. Supplementary data

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