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RESEARCH

Trends of ungulate species in Europe: not all stories are equal

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Abstract
Wild ungulates have deep impacts on socio-ecological systems, and analyzing large-scale population trends in a multispecies set can identify their environmental and socio-economic drivers. We collected annual hunting bags (n = 11,046, period 1975–2018) of European roe deer, red deer, wild boar, fallow deer, mouflon, northern chamois and moose, across Europe. We identified different temporal trends in their hunting bags and evaluated the social and environmental drivers of their relative abundances. The number of harvested red deer and fallow deer, increased steadily across Europe, with minor differences among countries, despite variations in land use and climate. On the contrary, European roe deer harvests have decreased in six European countries since the late 1990s, probably due to landscape changes and locally also due to predation, interspecific competition, and/or increasing temperatures. Northern chamois harvests in Austria and Switzerland have decreased markedly, probably due to increasing temperatures, which decrease the survival of kids at high altitudes. Wild boar harvests have decreased in Poland, Estonia, Latvia, and Lithuania since the African Swine Fever outbreak in 2013–2014. Minor differences emerged between countries adopting different management regimes for wild ungulates. While many studies pointed out landscape changes as the cornerstone for the increase in wild ungulates across Europe, our research emphasizes important species-specific differences. There is a need to predict how landscape dynamics, climate change and recovering large carnivores will affect populations of species already showing signs of decline, like the European roe deer or the northern chamois.

Keywords Wild ungulates · Hunting bags · Time-series analysis · Wildlife management · Reforestation · Rural abandonment

Introduction

The cumulative impact of human activities had driven most large mammals into severe declines and regional extinctions by the end of the Holocene (i.e., in late 19th and early 20th centuries; Ripple et al. 2015). As for wild ungulates living in the Global North, particularly in Europe, a prolonged decrease started in the 18th century and lasted until the end of the II World War (Linnell and Zachos 2010; Putman et al. 2011; Beguin et al. 2016; Carpio et al. 2021). Some Central European countries like Austria experienced a different trend in the XIX century but then shared the marked decrease from the beginning of the XX century till the end of the War (Schwenk 1985). Since then, wild ungulates have

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increased their geographical range and numbers, being nowadays generally abundant and widespread (Apollonio et al. 2010; Linnell et al. 2020).

The members of the Cervidae family, such as red deer (*Cervus elaphus*) and European roe deer (*Capreolus capreolus*), as well as wild boar (*Sus scrofa*) are increasingly ubiquitous and abundant in most European countries, accounting for over 90% of total wild ungulate biomass (Apollonio et al. 2010; Milner et al. 2006; Linnell et al. 2020). These species can have strong ecological impacts (Fuller and Gill 2001; Carpio et al. 2021), as they can damage soil properties (Harada et al. 2020) and remove plant biomass (Marchiori et al. 2012) or curtail forest regeneration (Côté et al. 2004; Pépin et al. 2006), thus affecting also animal communities (Barasona et al. 2021; Dawson et al. 2024; Mori et al. 2020; Oja 2017; Palmer et al. 2015; Rae et al. 2014) and ecological successions (Perea et al. 2014; Suzuki 2024). Moreover, wild ungulates transmit diseases to other wildlife, domestic ungulates and humans (Gortázar et al. 2007), sometimes with major economic impacts, like in the case of the African swine fever (hereinafter ASF; Bergmann et al. 2021). However, (native) wild ungulates are also very important compositional part and key species of terrestrial ecosystems, where they have several important ecological roles/functions which are essential for existence and functionality of those ecosystems (Pokorny and Jelenko 2014; Pokorny et al. 2017; Smit and Putman 2011), but they also have several important values for humans (Csanyi et al. 2014; Pascual-Rico et al. 2021).

In the respect of global changes that may influence population trends of wild ungulates, the current situation in Europe stemmed from the synergy between three large-scale processes of human land-use that started in the late 1940s: the exodus from rural to urban areas (Baudin and Stelter 2022), which reduced human disturbance, increased the amount of land available to wild ungulates and fostered a shift in wildlife value orientations that allowed the subsequent emergence of conservation policies (Manfredo et al. 2020); the decrease in the amount of land used for agricultural production and livestock breeding (Jepsen et al. 2015), which eased human pressures on the environment and progressively increased biomass available to wild ungulates; the development of institutions and laws that govern the reforestation of rural areas, the creation of protected areas, the implementation of intensive wildlife management systems, and the reintroduction or translocation of wild ungulates (Fuchs et al. 2015).

Understanding how these processes have influenced the population trends of different wild ungulates, across European countries, is needed to manage them adequately. However, differences between European countries, in terms of their environment and society, make it hard to completely generalize the numerical and geographical expansion of wild ungulates.

In this study, we summarized large-scale population trends of wild ungulates, by using annual hunting bags as a proxy of different species abundances across Europe and identified their most relevant environmental and socio-economic drivers in a framework of human-wildlife coexistence (Carpio et al. 2021). In particular, over the last few decades, wildlife agencies in Europe have: *i*) managed common and widespread species with relevant hunting and commercial interest, such as the red deer, European roe deer and wild boar, *ii*) conserved species with limited distribution but abundant local populations such as the moose (*Alces alces*) and northern chamois (*Rupicapra rupicapra*), *iii*) taken decisions about controlling emerging diseases, like in the case of ASF in wild boar, or chronic wasting disease in deer species, and *iv*) controlled introduced species with widespread (i.e., fallow deer, *Dama dama*) or local (i.e., mouflon, *Ovis gmelini musimon*) distribution. In consequence, these diverse practices could have had contrasting effects on the population demography of different species.

This paper analyzes the population trends of seven ungulate species to identify species-specific or species-country-specific differences in their trends and highlight their environmental and socio-economic drivers. The results of this study can contribute to building a background to predict how emerging factors like climate change as well as the recovery of large carnivores and (imported) diseases could add to their influence in affecting populations of more widespread species.

Materials and methods

Data collection

To quantify long-term trends in wild ungulate populations, we collected data about annual harvests of wild ungulates across 25 European countries (Fig. 1). Data were provided by co-authors, asking the total number of harvested individuals, for each species, to relevant environmental and wildlife agencies. For Denmark data were downloaded from the FAUNA portal of Aarhus University (https://fauna.au.dk/en/hunting-and-game-management/bag-statistics) and for Switzerland from the public website of the Office Federal de environment (https://www.jagdstatistik.ch). For Italy, data were obtained only for the autonomous province of Trento. Annual harvests were therefore referred to entire countries (or the autonomous Province of Trento), without considering the distribution range of each species. This choice was motivated by the long-time interval covered by the study,

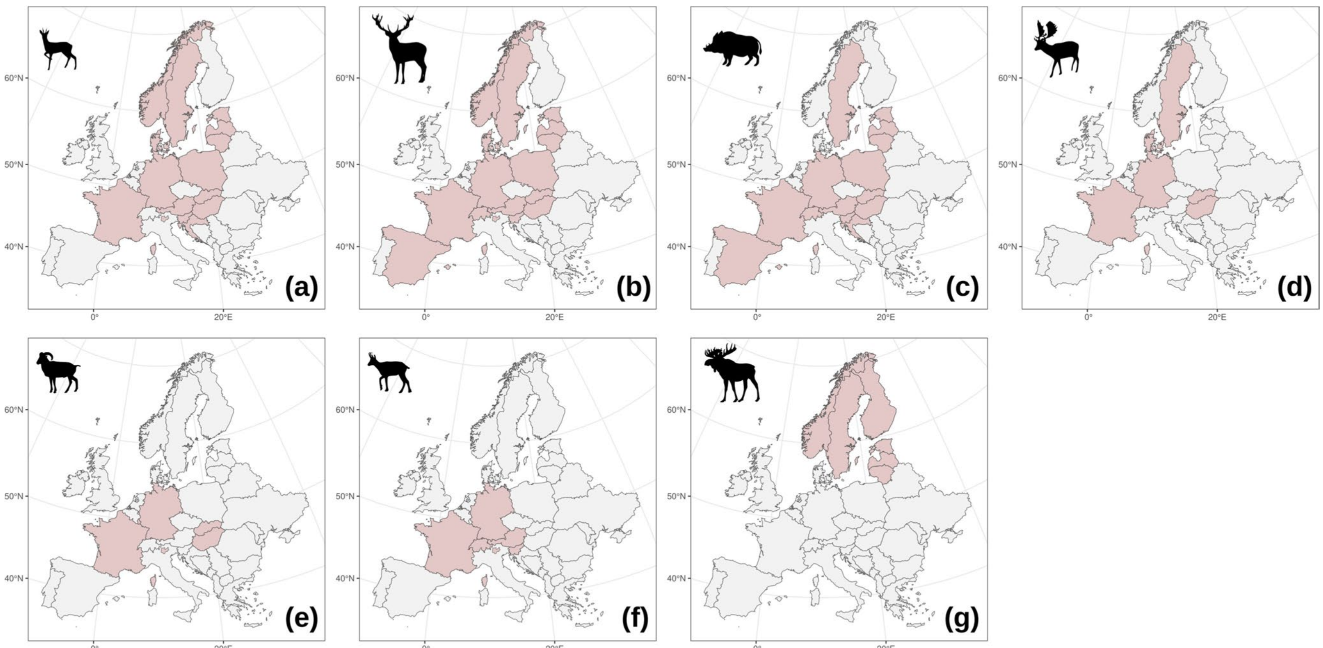

Fig. 1 Map representing the distribution of harvests for the seven species of wild ungulates, between different European countries: European roe deer (**a**), red deer (**b**), wild boar (**c**), fallow deer (**d**), mouflon (**e**), northern chamois (**f**), moose (**g**). Harvests are at the national level, without considering the distribution range of the various species within each country. For Italy only the autonomous province of Trento was considered

and the lack of information about pan-European changes in the distribution of wild ungulates through time.

Among these countries we selected the 19 countries that had hunting bag datasets of wild ungulates starting from 1975 till 2018 (Fig. 1). While hunting bags are not a perfect measure of the number of wild ungulates in the environment (Pettorelli et al. 2007; Imperio et al. 2010), they can be used as a proxy for their relative abundance, to reconstruct changes in space (ENETWILD-consortium 2022; Murphy et al. 2023) or time (Aebischer 2019; Massei et al. 2015). Unfortunately, we did not adjust for hunting effort, a crucial factor affecting the interpretation of hunting bags as a proxy of wild ungulate populations, as official estimates were not available for most our study area.

Data collection focuses on seven species that are regularly harvested or controlled to reduce their impacts on human activities and ecosystems (Fig. 1): the European roe deer (17 countries), red deer (17), wild boar (15), fallow deer (6), mouflon (6), northern chamois (6), and moose (6). For all these 7 species, we collected hunting bags from 1975 to 2018. Moreover, we also compared the 1948–2018 trends in roe and red deer hunting bags in Austria, Denmark, Sweden, and Switzerland to better understand their simultaneous temporal evolution concerning landscape change (see the Discussion section).

Because individual countries have different living conditions and, therefore, very different ungulate populations, we converted counts in each country to Z-scores, by subtracting the mean and dividing by the standard deviation. This allowed us to compare time series from different countries, represented as standardized values of each time series, that would have been on different scales otherwise (Fig. S1-S3). We did not divide hunting bags according to the area of each country (calculated bag densities), as this value was larger than the distribution range of the various species, which for decades ago was often unknown.

Statistical analysis

For each species, we used longitudinal cluster analysis (Den Teuling et al. 2021), based on Dynamic Time Warping (DTW; Sardá-Espinosa 2017), to identify groups of countries with similar long-term trends. The optimal number of clusters was identified by inspecting the silhouette index, which quantifies how similar values from a certain time series are to those of a certain cluster, compared to those of time series from other clusters. The Silhouette index ranges from -1 to $+1$, with higher values indicating more compact clusters (Den Teuling et al. 2021). Indeed, only values greater than 0.5 indicate the existence of groups of time series with truly diverging long-term trends. However, the exploration of cluster silhouettes, corresponding to the "median" trend of each cluster, for the number of clusters with the highest value of the Silhouette index, can be used to identify short-term differences which are not captured by DTW clustering. In out case, these differences could indicate emerging trends in ungulate harvests which had not resulted into a long-term change yet.

Then, we also used the random forests algorithm (Breiman 2001) to quantify the effect of different landscape and socio-economic dynamics on the temporal evolution of hunting bags. Random forests were fit with the "randomforest" package in R, by using 500 regression trees, a minimal node size of 5 and number of random predictor variables at each split point equal to one third of the total number of predictors. Wild ungulates are generally deemed to be favored by forest cover, which can provide regular (Spitzer et al. 2020) and pulsed (Barrere et al. 2020; Bisi et al. 2018; Barukčić 2020; Touzot et al. 2020) food resources, a refuge against human disturbance (Bonnot et al. 2013; Carbillet et al. 2020; Dupke et al. 2017; Jasińska et al. 2021; Salvatori et al. 2023), and shelter from temperatures above critical thresholds (Ewald et al. 2014; Kramer et al. 2022; Reiner et al. 2021, 2022; van Beest et al. 2012). Therefore, we also included changes (1975–2018) in the proportion of forested areas of each country as a covariate in the model. The amount of forest cover in each country was obtained by combining official data from the Food and Agriculture Organization with data from forestry inventories of the various countries. Moreover, as some ungulate species are also affected by the availability of understory and secondary successions (Hewison et al. 2009; Reiner et al. 2023; Vannini et al. 2021; Zong et al. 2023), we also calculated the percentage of forests that in 1975 were less than 20 years of age. This value was obtained from Vilén et al. (2012) and aimed to identify countries subjected to intense afforestation policies in the 1950 s and the 1960s. Moreover, in Europe, forest expansion followed agricultural land abandonment, particularly in mountainous or marginal areas (MacDonald et al. 2000; Levers et al. 2018). Therefore, we also used changes in the percentage of the population living in rural areas (https://data.worldbank.org/indicator/SP.RUR.TOTL.ZS) and changes in the proportion of surface that was covered by croplands (https://data.worldbank.org/indicator/AG.LND.AGRI.ZS) in individual countries as predictors in our model.

In most cases, rural abandonment also corresponded to a decrease in the presence of livestock in the environment, which can compete with wild ungulates for resources and transmit infectious and parasitic diseases (Chirichella et al. 2014; Martin et al. 2011). Therefore, we also controlled for differences in livestock units of each country (https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Glossary:Livestock_unit_(LSU)) between 1975 and 2018.

Finally, as European countries differ in their game management systems, we also controlled different management policies' effects on wild ungulates. Namely, following Apollonio et al. (2010) and Putman et al. (2011), we compared countries *i*) with a centralized, top-down approach, where overall hunting quotas are established by national agencies and subsequently divided across regions, *ii*) with a decentralized top-down approach, where national wildlife agencies fix overall quotas, but their implementation is up to management districts, *iii*) where wildlife agencies define the boundaries of management units, but these units are then entirely responsible for the determination of hunting quotas, *iv*) countries with a "bottom-up" approach, where hunting quotas are determined by each district and where districts could aggregate between them, and *v*) countries with a "libertarian" approach, where hunting quotas are entirely up to landowners.

In random forests, we also controlled for the year of each hunting bag in each country to model overall temporal trends, which could have been caused by unmeasured factors, such as climate change (Mysterud and Sæther 2010) or numerical increase of large carnivores (Chapron et al. 2014).

In random forest modeling, we did not model neither the hunting bags of moose nor those of the northern chamois, as we had too few countries and, therefore, little variation in model covariates. Moreover, our analyses did not include variables representing climatic conditions. Although climate is a key factor affecting the population trends of wild ungulates (Apollonio and Chirichella 2023; Markov et al. 2022; Malpeli et al. 2024), which can be represented by indexes such as the North Atlantic Oscillation (Mysterud et al. 2003), climate conditions in Europe are not homogeneous neither between, or within countries. For example, they vary according to the latitude, elevation, or distance from the coast of different areas. However, aggregating these gradients at the national scale would have resulted in the so-called "ecological fallacy" and biased our findings (Salkeld and Antolin 2020).

All continuous predictors were converted to z-scores. As random forests average between multiple regression trees, the relative importance of each predictor was measured as the decrease in node impurities through the residual sum of squares. Statistical analyses were carried out using R (R Core Team 2024).

Results

Between 1975 and 2018, Europe-wide hunting bags increased for all 7 studied species of ungulates (Fig. 2). However, despite this general increase, significant variations characterized different countries (Fig. 3), even after discarding extreme observations that exceeded the third quartile of the distribution of species-specific relative increases, such as the red deer in Estonia, Sweden and the autonomous province of Trento (Italy) (Table 1). In the case of the wild boar, it is worth mentioning that the species was absent from Sweden until its

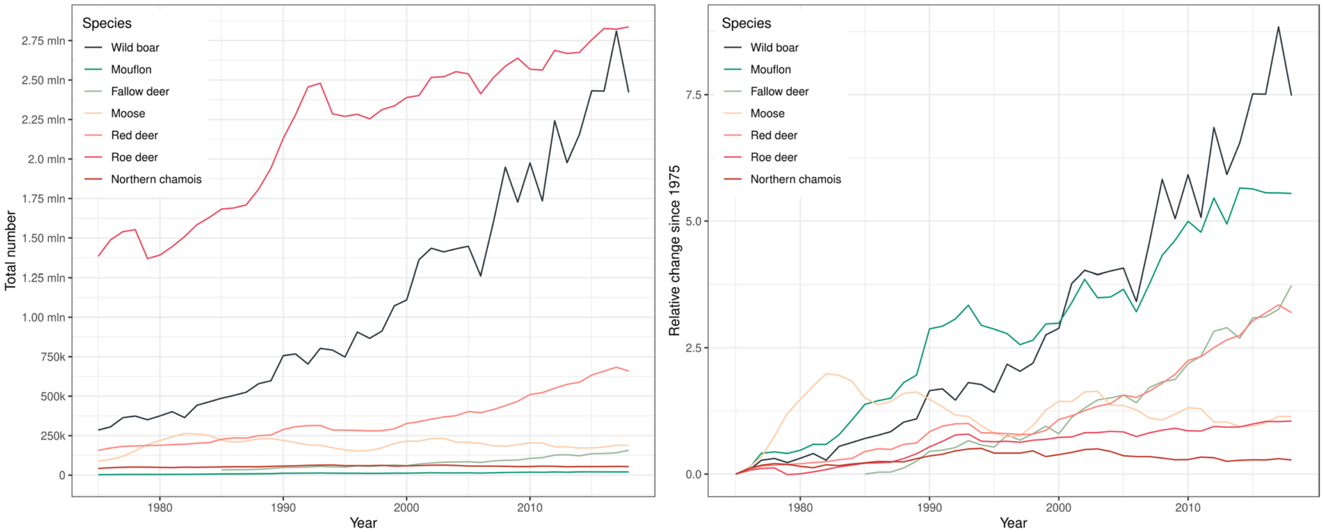

Fig. 2 Temporal evolution of the harvests of wild ungulates in our entire study area: total number of harvested individuals (left) and relative change since 1975 (right). The spatial coverage of data for the various species is shown in Fig. 1. For fallow deer, relative change was calculated since 1985

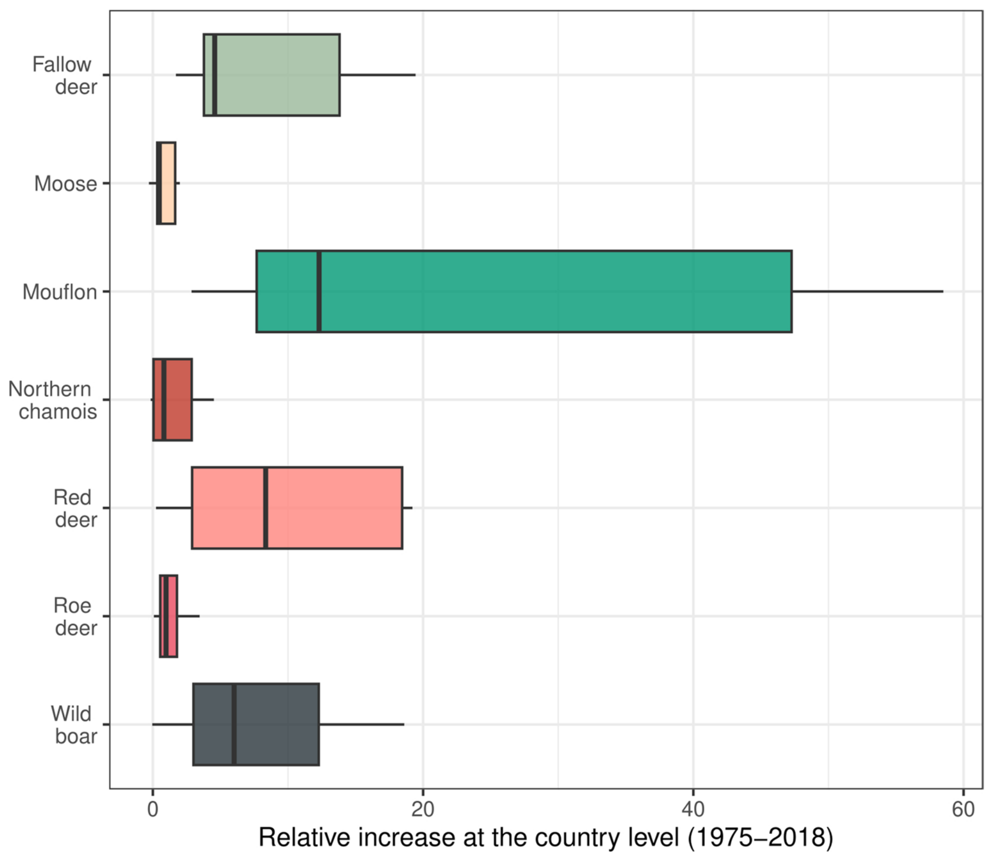

Fig. 3 Distribution of the relative increase in the harvests of wild ungulates calculated at the country level (see Table 1 for detailed data in particular countries). The relative increase indicates how larger the number of harvested individuals was in 2018, compared to 1975, in a certain country. To make comparisons clearer, we omitted those countries where harvests exceeded the 90th percentile of the distribution. For the fallow deer, 2018 data were compared to 1985 data

accidental introduction in the wild during the late 1970s, but in 2018 a total of 112,352 wild boar were harvested (Table 1). Moreover, in Finland, approx. 1,000 European roe deer were culled in 2013; in 2023/2024, this number has risen to 16,555 individuals (Ilpo Kojola, personal communication).

The only ungulates with an overall decrease in their harvests were the northern chamois in Austria and Switzerland, and the moose in Lithuania (Table 1). Furthermore, in Poland, 560 moose were hunted in 1975, with harvests peaking in 1989 (1,670 individuals), but hunting was

Table 1 Number of harvested individuals, for each species per country, in 1975 and 2018 (- = no data or not considered; 0 = no presence). For fallow deer, data started in 1985. For moose in Poland, data were not considered as hunting was suspended in 2001. We also did not consider wild Boar in Sweden, whose population originated from a reintroduction in the late 1970 s and was not hunted until the 1990s

Species/year	European roe deer		Red deer		Wild boar		Fallow deer		Mouflon		Northern chamois		Moose	
Country	1975	2018	1975	2018	1975	2018	1985	2018	1975	2018	1975	2018	1975	2018
Austria	208,886	284,916	44,598	54,977	4,355	30,542	-	-	-	-	21,953	20,685	0	0
Croatia	4,204	16,160	1,674	3,933	2,418	29,599	-	971	-	497	12	87	0	0
Denmark	36,044	93,477	1,130	9,745	-	-	1,901	9,537	-	-	0	0	0	0
Estonia	16,390	24,146	5	2,757	4,977	4,761	-	-	-	-	0	0	5,441	7,163
Finland	-	-	-	-	0	0	-	-	-	-	0	0	12,285	58,190
France	59,426	586,464	6,709	65,275	45,830	747,367	217	1,331	191	2,784	2,815	12,407	0	0
Germany	787,806	1,206,445	44,517	77,212	120,831	599,862	24,127	65,226	1,869	7,214	2,131	4,843	0	0
Hungary	54,337	119,287	16,642	65,040	14,050	159,855	3,394	15,949	583	4,412	0	0	0	0
Italy (Trento)	2,119	4,185	9	2,287	-	-	0	0	2	270	541	2,985	0	0
Latvia	10,086	27,422	882	17,825	7,535	15,238	-	-	-	-	0	0	5,583	7,474
Lithuania	10,400	28,931	405	7,876	9,690	18,016	0	0	0	0	0	0	3,270	2,317
Luxembourg	4,493	7,016	131	426	972	7,777	-	-	2	119	0	0	0	0
Norway	5,240	29,520	3,807	43,800	0	0	0	0	0	0	0	0	10,218	30,600
Poland	47,100	210,133	10,200	95,365	40,400	266,047	-	-	-	-	-	-	-	-
Slovakia	16,557	25,856	10,993	42,937	13,696	41,723	718	14,677	461	5,544	-	-	-	-
Slovenia	19,969	30,875	1,600	6,268	1,257	8,250	70	275	50	459	1,625	2,212	0	0
Spain	-	-	11,843	144,134	19,038	373,225	-	-	-	-	0	0	0	0
Sweden	61,349	99,165	138	11,267	-	112,352	2,849	50,449	-	-	0	0	51,544	83,059
Switzerland	39,377	42,389	3,552	12,081	489	6,997	0	0	-	-	13,358	11,192	0	0

suspended in 2001 due to the dramatic decline of the population (Bobek et al. 2005).

Longitudinal cluster analysis confirmed the pan-European, long-term increase in hunting bags. Except for northern chamois, for which two groups of countries with clearly diverging trends emerged, the Silhouette Index (hereinafter, SI) was always below the cutoff of 0.5 (Fig. 4). This indicates that clusters had poorly distinguished long-term trends, with hunting bags in 2018 having an overall increase compared to those from 1975. However, the graphical inspection of cluster centroids sometimes revealed different groups of countries distinguished by emerging differences. These emerging differences corresponded to temporal changes in the evolution of harvests that had not translated

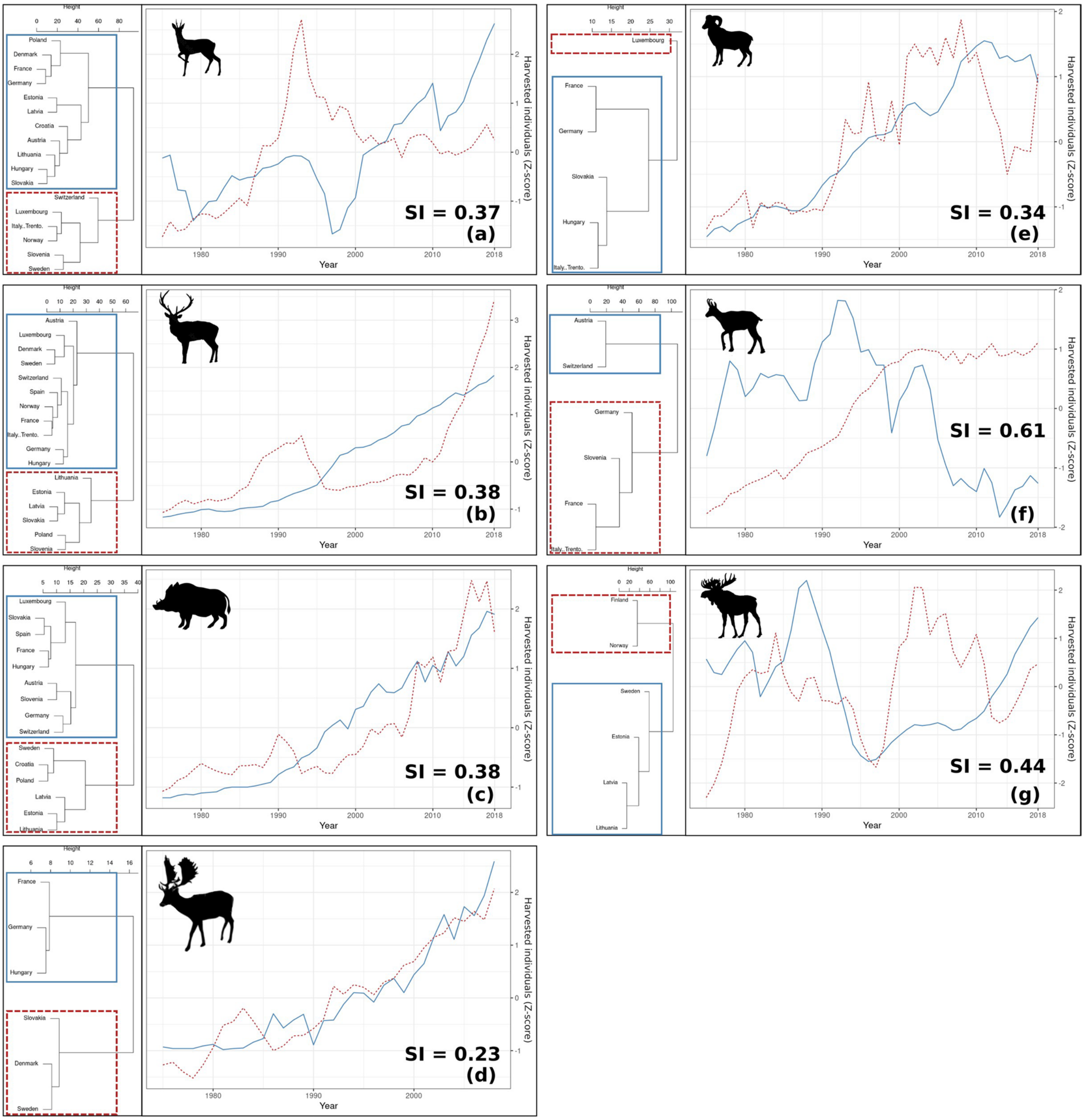

Fig. 4 Cluster centroids and dendrograms for the various species: European roe deer (**a**), red deer (**b**), wild boar (**c**), fallow deer (**d**), mouflon (**e**), northern chamois (**f**), moose (**g**). For temporal changes in moose harvests in Finland and Norway, see Fig. S2. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviation units, from the mean value of each country. The silhouette index (SI) is shown for each species

yet into any long-term trend, because they were relatively recent. For example, a group of time series with a strong increase in hunting bags for 33 years, followed by their partial decrease for 10 years might not be distinguished by the Silhouette Index and DTW clustering from a group of time series where hunting bags consistently increased throughout 43 years. Yet, the exploration of cluster centroids for these two groups can reveal well distinguished emerging differences.

When considering European roe deer (SI = 0.37; Fig. 4), hunting bags have decreased since the late 1990 s in Luxembourg, Norway, Switzerland, Slovenia, Sweden, and the autonomous province of Trento (Italy). On the other hand, in the rest of Europe, after a decrease in the late 1990 s, European roe deer harvests have boomed.

Harvests increased steadily across most of Europe in case of red deer (SI = 0.37; Fig. 4). However, in Estonia, Latvia, Lithuania, Poland, Slovakia, and Slovenia, harvests of this species peaked in the early 1990 s, then decreased and subsequently increased again with a change point around 2010. In some Eastern European countries, these patterns might occur at different levels due to the political changes after the collapse of socialism (1989/1990), as shown by Bragina et al. (2018).

Wild boar experienced a steady increase across most of Europe. However, the increase in wild boar harvests was temporally lagged in Croatia, Poland, Estonia, Latvia, Lithuania, and Sweden, where it started after 1995. Noteworthy, in Poland and Baltic countries, wild boar harvests also decreased after 2013–2014, when an outbreak of ASF occurred in this area (Cwynar et al. 2019).

Fallow deer had even less pronounced differences in long-term trends of their harvests (SI = 0.23; Fig. 4), which increased homogeneously across Europe. Homogeneity also characterized mouflon (SI = 0.34), whose harvests also increased markedly across the 6 European countries for which we had data. Luxembourg was the only country with a different trajectory, where harvests of mouflon boomed in the 1990 s and then dropped in 2015.

The only species characterized by well-distinguished opposite harvest trends in two groups of countries was northern chamois (SI = 0.61; Fig. 4). Harvests increased between 1975 and the early 1990 s in Austria and Switzerland, where they subsequently declined in recent years. On the other hand, the number of harvested individuals continuously increased in France, Germany, Slovenia, and the autonomous province of Trento (Italy).

As for moose harvests (SI = 0.44; Fig. 4), two groups of countries emerged. In Sweden, Estonia, Latvia and Lithuania, harvests increased until the late 1980 s, declined until the mid-1990s, and increased again. Norway and Finland instead constituted a second group of countries with somewhat different temporal trends. In Norway, moose harvests increased until the late 1990 s, then slightly declined. In Finland, on the other hand, harvests fluctuated highly, with two peaks, i.e. from 1980 to the mid-1990s and from 2000 to 2010, with two sharp declines in between (Fig. S2).

Random forests predicted well hunting bags of European roe deer (R^2 = 0.81; MSE = 0.18), red deer (R^2 = 0.92; MSE = 0.07), fallow deer (R^2 = 0.94; MSE = 0.06), wild boar (R^2 = 0.90; MSE = 0.09), and mouflon (R^2 = 0.92; MSE = 0.08). However, random forests also revealed species-specific differences in the most important correlates of hunting bags (Table 2). Overall, hunting bags were positively associated with the years within the time series, which aligns with the fact that each species increased in the number of harvested individuals over time. The year of each hunting bag was the most important predictor for red deer and wild boar.

However, the temporal component was not the most predictive factor for European roe deer, mouflon, and fallow deer. The change in % of forest cover of each country was the most important predictor for roe deer and mouflon: particularly for the European roe deer hunting bags were much higher in those countries with a marked increase in forest cover (Fig. 5). The change in the percentage of the human population that lived in rural areas was the most crucial factor predicting hunting bags in fallow deer, with peak

Table 2 Relative importance of the various predictors, expressed as the decrease in node impurities through the residual sum of squares. This value tells how well trees can split variables (the higher the better)

	Year	Changes in % of area covered by forests	Changes in livestock density	Changes in % of population in countryside	Changes in % of area covered by croplands	% of forests which had 20 years of age or less in 1975	Management regime
European roe deer	0.19	0.65	0.07	0.12	0.12	0.13	0.04
Red deer	0.58	0.16	0.03	0.05	0.06	0.01	0.01
Wild boar	0.45	0.06	0.02	0.01	0.15	0.01	0.01
Fallow deer	0.22	0.03	0.01	0.33	0.08	0.01	0.01
Mouflon	0.14	0.26	0.01	0.04	0.17	0.00	0.00

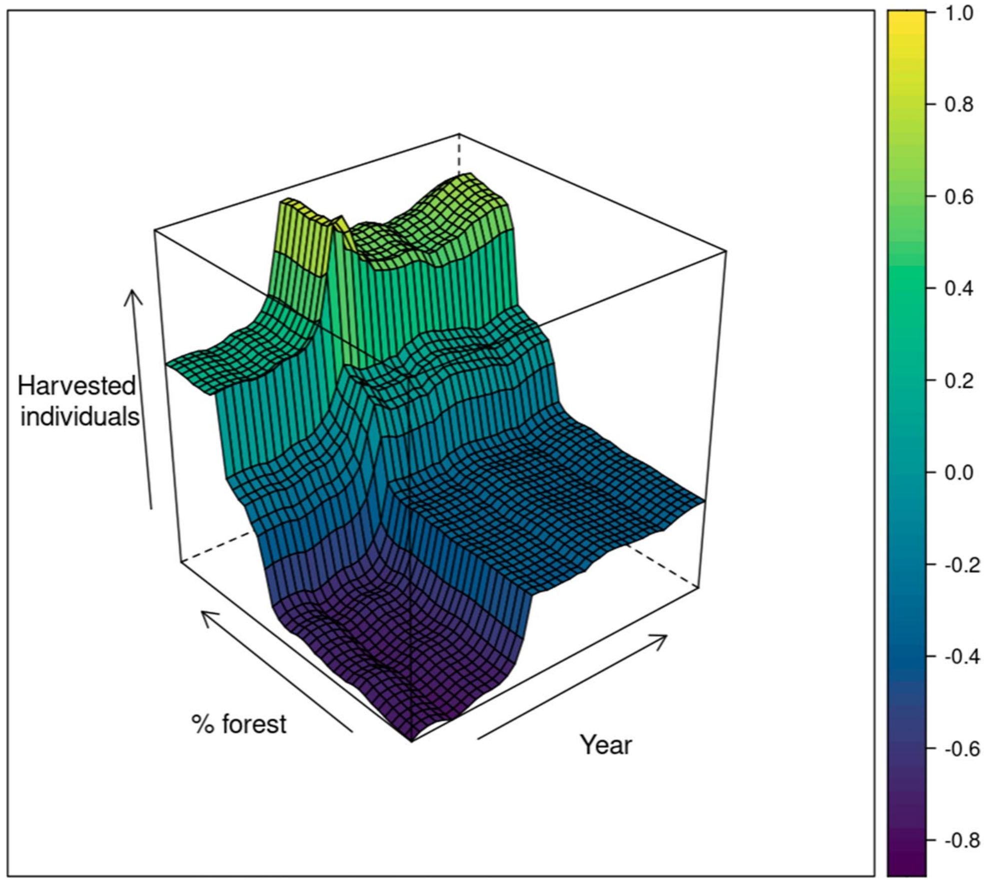

Fig. 5 Conditional effect plot, representing the change in the number of harvested European roe deer according to time and relative change in forest cover

in countries with little rural depopulation. Other predictors seemed to have a comparatively smaller effect (Table 2).

When comparing the trends of European roe deer and red deer harvests with data from 1948 in Austria, Denmark, Sweden, and Switzerland (Fig. 6), we noticed that the two species exhibited two types of connected trends. In the first case, there were years when European roe deer harvests started stagnating or declining, corresponding with a marked increase in red deer harvests. This happened in Switzerland in 1980, Austria in the mid-1990s, and Denmark in the early 2010s. On the other hand, sometimes the peak in European roe deer harvests largely anticipated that of red deer. This was the case for Sweden, where European roe deer harvests started booming in the mid-1980s and those of red deer increased in the 2010 s, and in Denmark, where European roe deer harvests increased around 1980 and red deer in the early 2000s.

Discussion

When comparing changes in large mammal distribution and abundance in Europe, we can appreciate a difference between wild ungulates and large carnivores. The success of large carnivores in Europe stemmed from coordinated legislation shared by many European countries (e.g., Council Directive 92/43/EEC; Bern Convention), context-specific management practices, and institutional arrangements (Chapron et al. 2014), which significantly reduced their large-scale mortality from humans. Instead, wild ungulates were capable of regaining a landscape that had significantly changed when human pressure shifted towards urbanized areas, while at the same time being intensively managed all over the continent, with millions of individuals being harvested each year (Apollonio et al. 2010; Linnell et al. 2020). Our study shows that in the last decades, the trends of European ungulates' harvest increased, following socio-economic changes associated with the shift from rural economies, characterized by low production applied to large areas, to industrial and post-industrial economies. Indeed, according to our results, ungulates have experienced a significant increase in their relative abundance across Europe, with a correspondent change in management issues like those related to the development of locally overabundant populations (Carpio et al. 2021; Linnell et al. 2020; Valente et al. 2020).

Many previous studies have already confirmed that human development shapes wildlife populations (Tucker

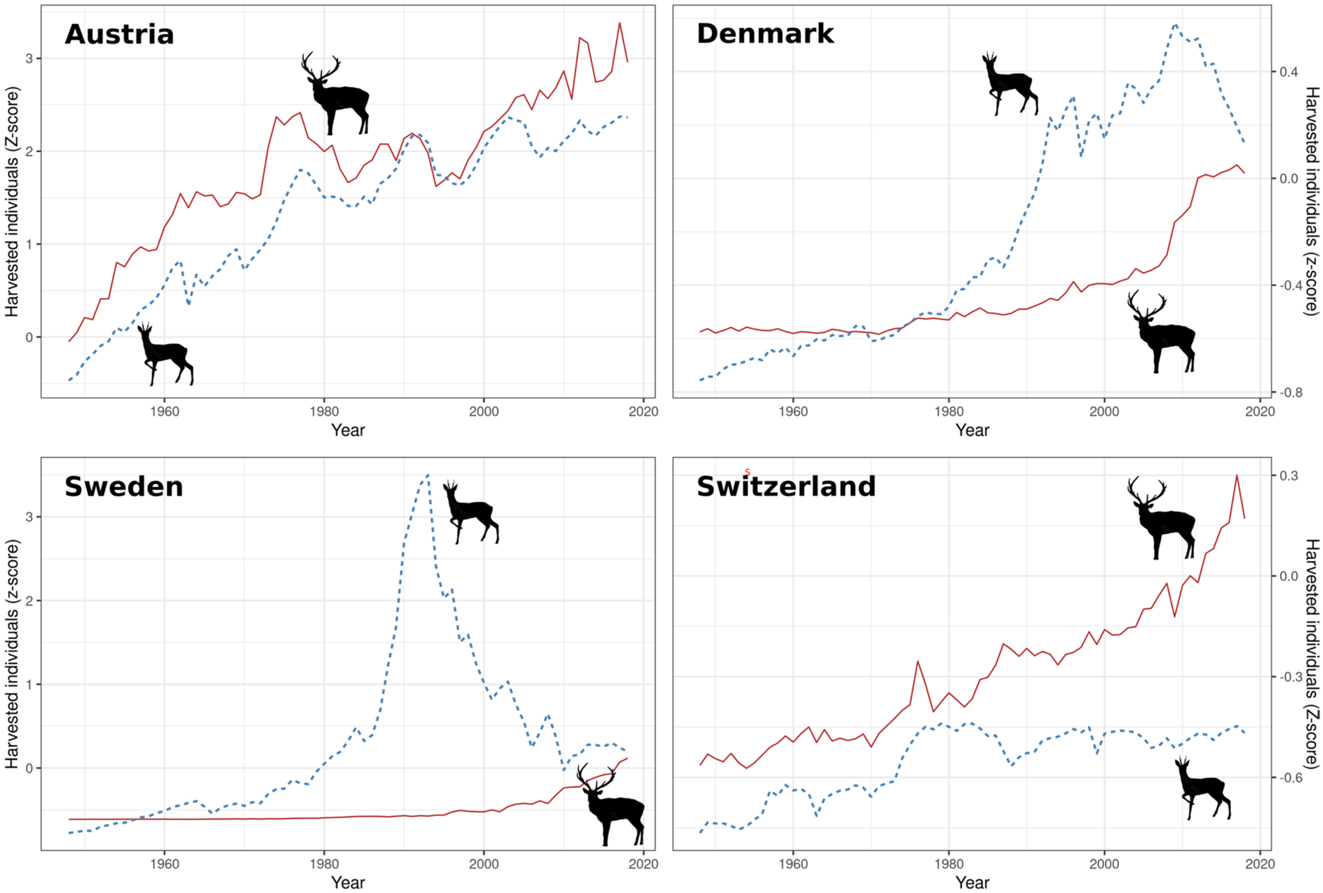

Fig. 6 Temporal trends of European roe deer (dashed line) and red deer (solid line) harvests, between 1948 and 2018, in four countries: Austria (top-left), Denmark (top-right), Sweden (bottom-left), and Switzerland (top-right). The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviation units, from the mean value of each country

et al. 2021; Johnson et al. 2023), and in this context our approach revealed: *i*) marked country-specific differences in the long-term trend of cold-adapted species, *ii*) country based emerging differences for European roe deer and wild boar, *iii*) the complementary and sometimes opposite temporal development for deer species with a different ecology, *iv*) similarities and differences in the overall weight of environmental factors across different species or among different population of the same species. These results can be helpful in predicting how landscape, climate change, and emerging diseases could affect the trends of future wild ungulate populations.

First, for Alpine/boreal species like northern chamois and moose, we found evident variations in the temporal trend of their harvests between countries. In the case of northern chamois (*Rupicapra rupicapra rupicapra*), while harvests increased between 1975 and the early 1990s in Austria and Switzerland, where they subsequently declined, a permanent increase was revealed in France, Germany, Slovenia, and autonomous province of Trento (Italy). Available literature indicates that changes in climate and land use (Chirichella et al. 2021; Hoste et al. 2024; Lovari et al. 2020; Mason et al. 2014; Reiner et al. 2021), as well as the increase in potential competitors (e.g., red deer: Corlatti et al. 2019; Donini et al. 2021) and predators (Chapron et al. 2014; Vogt et al. 2024) can affect the behavior and ecology of chamois. Although their impacts on demography and life history traits still need to be fully clarified (Chirichella et al. 2021; Corlatti et al. 2022), our findings call for the need of large-scale analyses, aimed at addressing their influence and better understanding large-scale diverging trends.

Moose harvests also showed emerging differences between countries, although these still need to translate into completely diverging trends. Moose population in Europe are affected by human disturbance, collisions with vehicles, illegal killing and low environmental connectivity (Bluhm et al. 2023), with some of them still recovering (e.g. Poland, Dziki-Michalska et al. 2019). Considering that moose are susceptible to high temperatures (Janík et al. 2021) and many populations depend upon wetlands (Borowik et al. 2024), the current pace of climate change calls for the continuous monitoring of the long-term evolution of their harvests, with the goal of informing their conservation and management.

On the other hand, although our findings highlighted a long-term increase in the harvests of European roe deer and wild boar, we also found short-term differences emerging. In the case of wild boar, some countries experienced an average reduction in hunting bags between 2013 and 2014. This differentiation could have been due to the impact of ASF in Poland, Estonia, Latvia, and Lithuania (Cwynar et al. 2019), Recent data collected by the ENETWILD Consortium indicates a recovery of wild boar populations in the Baltic countries affected by ASF since 2019/2020 (ENETWILD Consortium 2023; EFSA 2024). It will be interesting to evaluate the effect of fluctuations in wild boar abundances, due to ASF and its impact on predation by large carnivores, on habitats and communities, including other wild ungulates species.

Another emerging differentiation in harvests involved the European roe deer, whose hunting bags in 5 countries have declined, after a peak in the early 1990s. This decline could have been driven by changes in landscape cover and forest structure and the return of large carnivores (e.g. *Lynx lynx*, Andrén and Liberg 2015; e.g. *Canis lupus*, Randon et al. 2020), two factors which might act in synergy (Melis et al. 2009). As for the influence of landscape dynamics on European roe deer trends, this might be clarified when simultaneously considering them altogether with those of the red deer. In Austria, Denmark, Sweden, and Switzerland, where the harvest of these two species had been recorded from 1948, we noticed that the change points of the time series of the two species coincided and then exhibited a symmetrical pattern: harvests of red deer always increased when those of European roe deer reached a plateau or even started declining (Fig. 6). Moreover, European roe deer did not show an increase comparable to that of red deer despite the steady increase of forest cover in Europe. The European roe deer depends upon the early or post-disturbance stages of forest development (Oeser et al. 2021), that provide access to cover (Mysterud and Østbye 1999) and high quality food resources (Andersen et al. 1998; Saïd and Servanty 2005), in turn affecting body condition (Hewison et al. 2009; Reiner et al. 2023). On the contrary, red deer is more adapted to live among all different environments occupied, in mature forests, forest-agriculture mosaics, and even in artificial conifer plantations, being a mixed feeder with a better capacity to exploit poor quality forage (Hoffman 1989; Gordon and Prins 2019). A comparative analysis of the trends of the two species for the countries with available pre-1975 data has shown a greater growth rate in European roe deer in the pre-1975 period with a subsequent slowdown. On the contrary, faster growth in the post-1975 period is noted for red deer, a species able to benefit from the late successional stages of forests deriving from post-WW2 agriculture decline (Mattioli et al. 2022). These symmetrical trends were already noticed in the Italian Alps (Chirichella et al. 2017). Finding them in four countries indicates that similar trends could be widespread across Europe and might produce a decline in European roe deer populations over the next few years.

Emerging differences in European roe deer harvests might also stem from the phenotypic plasticity of different populations, and their capacity to cope with shifts in plant phenology caused by climate change (e.g. by anticipating parturition, see Hagen et al. 2021).

The increase in forest area partially contributed to explaining red deer harvest trends, as reported in other studies (e.g., Heurich et al. 2015; Chirichella et al. 2017). While in the case of wild boar, due to the ecological adaptability and invasive potential of this species, it is more difficult to find a primary driver of expansion and increase, the changes in the percentage of area covered by croplands were found in our study to be most important after the temporal component. Indeed, many studies reported the effect of different drivers (i.e., climate, both harshness, and warming; habitat, agriculture, both current diversity and possible change; large carnivore presence and abundance; hunting management practices; supplementary feeding) as limiting or promoting factors in shaping wild boar population trends (for a review, see Melis et al. 2006 and Scandura et al. 2022). While our findings agree with the overall increase reported by Massei et al. (2015), they also highlighted the influence of African Swine Fever over long-term trends (Barukčić 2025). In the near future it will be interesting to see if ASF will further differentiate long-term trends in harvests, or if wild boar populations in Europe will manage to fully recover.

In our analysis, the temporal component was not the most predictive factor for European roe deer, mouflon, and fallow deer. The change in the percentage of forest area was the most relevant driver for European roe deer and mouflon: hunting bags for mouflon were much higher in those countries with a marked increase in forest cover. Moreover, the percentage of area covered by croplands was also an important factor driving the abundance of mouflon (see Garel et al. 2022; for a review about mouflon).

Similarly, the change in the percentage of the human population that lived in rural areas was the most important factor in predicting hunting bags in fallow deer. As De Marinis et al. (2022) reported, fallow deer is one of the most widespread introduced mammals in Europe as it has been established in most European countries; if they are not present in the wild, then they are kept in farms, reserves, or parks (Bijl and Csányi 2022). Its distribution/density is, therefore, a direct consequence of human activity (Bijl and Csányi 2022; Masseti 1996, 2002; Sykes et al. 2011). However, to date, the population trends of this species (and their drivers) have received poor attention, especially in northern/central Europe and for free-ranging populations. Our findings nevertheless confirm that fallow deer populations are increasing, in line with Bijl and Csányi (2022). Considering its capacity to cope with large carnivores through behavioral changes (Lazzeri et al. 2024), it will be interesting to see if fallow deer harvests in Europe will keep increasing, in the near future. This would be extremely important, considering the ecological role of this species as a browse (Fattorini et al. 2025).

It is important to emphasize three key limitations of our study. The first one is the geographical imbalance of data, with most of them coming from Western and Central Europe and widespread gaps in Eastern Europe and the Balkans, as well as Czech Republic, Italy, Ireland and the United Kingdom. Future studies should try to collect long-term data on ungulate harvests there, to provide a truly pan-European picture, accounting for long-term changes between different biogeographical regions. Another key limitation is the lack of any measure of hunting effort, which would be crucial to improve our interpretation of total harvests. The total number of harvested wild ungulates is just a proxy of their total number in the environment, which partially varies according to the number of hunters and the effort they put at hunting ungulates. Although quantifying hunting effort for entire countries is probably unfeasible, future studies might focus on collecting data from single administrative units throughout Europe (e.g. regions or NUTS2). This would allow to better understand long-term changes in the number of hunters and their hunting activity, also by linking them to long-term socioeconomic changes (Manfredo et al. 2020). Finally, it would also be important to store meta-data about the data centralization workflow, between different wildlife agencies. Due to the long timespan covered by our study, it was not possible to assess if reporting criteria for hunted ungulates has changed through time, an aspect which could have influenced total harvests. For example, it is plausible that some estimates might not include animals that were shots during wildlife control operations (e.g. due to crop damaging).

Conclusion

A combination of reforestation, agricultural abandonment, and rural-urban migration has led to a situation where wild ungulates are widespread across Europe. Nevertheless, the main drivers of change differ among species, as well as between different socio-economic and environmental contexts. Wild ungulates are hunted in virtually all parts of their distributional range, including most protected areas (van Beeck Calkoen et al. 2020), with major differences between and within countries. Hunting seems to be the major source of mortality in wild ungulates and therefore the main anthropogenic driver of population density (Bassi et al. 2020; van Beeck Calkoen et al. 2023). In this context, it is extremely important not to generalize the increase in ungulates but to consider their local status and short-term fluctuations, to support proper management strategies for the different species. Our findings confirm the need for long-term national and international harmonized monitoring schemes, aiming to better understand the demography of wild ungulates (Carpio et al. 2021; ENETWILD Consortium 2023) and to collect information on hunters and hunting effort, which will be essential to implement and/or improve policies for their science-based management and conservation.

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Data availability Data and software code are available from the Open Science Framework, at the following link: https://osf.io/uvfcs/.

Declarations

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