Title: 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 7 wild ungulates of high management interest across 25 European countries. We identified different temporal trends in hunting bags and for roe deer, red deer, wild boar, fallow deer, and mouflon, we also evaluated the social and environmental drivers of their abundances.

Number of harvested red deer, fallow deer, and wild boar increased steadily across Europe, with minor differences among countries, despite variations in land use and climate. On the contrary, roe deer harvest has decreased in six European countries since the late 1990s, probably due to reduced ecotone areas and locally also due to predation, intraspecific competition, and/or climate severity. 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 and climate change and the growing presence of large carnivores, will affect populations of species already showing signs of decline, like European roe deer and 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 the shared the marked decrease from the beginning of the XX century till the end of the War (Schwenk 1985). Since then, wild ungulates have increased their geographical range and numbers, being nowadays generally abundant and widespread (Apollonio et al. 2010).

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 (Milner et al. 2006; Apollonio et al. 2010). 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 (Gortazar 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 (Chiriboga et al. 2019; 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 dynamics 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 dynamics 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 red deer, roe deer and wild boar, *ii*) conserved species with limited distribution but abundant local populations such as 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 dynamics 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 build 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.

2. Methods

2.1 Data collection

To quantify long-term trends in wild ungulate populations, we collected data about annual harvests of wild ungulates across 25 European countries. Among these countries we selected the 19 countries that had hunting bag dataset starting from 1975 till 2018 for ungulate species. Although some studies highlighted the potential limitations of hunting bags in reflecting the population densities and temporal dynamics of wild ungulates (Pettorelli et al. 2007; Imperio et al. 2010), we used this data as they were the only figures available for such a long-time span. In this paper, we do not consider hunting bags as a direct indicator of population biological parameters but rather as an index representing the interaction between environmental factors and the harvest rate of different ungulate species, which can reflect long-term changes in populations (Massei et al. 2015; Aebischer 2019).

Data collection focuses on seven species that are regularly harvested or controlled to reduce their impacts on human activities and ecosystems: 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 forest structure (see the Discussion section).

Because individual countries have different living conditions and, therefore, very different ungulate populations, we standardized counts in each country, 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. 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.

2.2 Statistical analysis

For each species, we used longitudinal cluster analysis (Den Teuling et al. 2021), based on Dynamic Time Warping (DTW; Sardá-Espinosa 2019), to identify groups of countries with similar long-term trends. The optimal number of clusters was identified by inspecting the silhouette index. As DTW clustering does not allow us to compare a solution with two clusters against a solution with a single cluster, we used a cutoff of 0.5 for the silhouette index: in case there were groups with truly diverging long-term trends in each species, the silhouette index would have been higher than this cutoff (for an explanation of these metrics, see Den Teuling et al. 2021).

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. Wild ungulates are generally deemed to be favored by forest cover, which can provide regular (Spitzer et al, 2020) and pulsed (Bisi et al. 2018; Barrere et al. 2020; Touzot et al. 2020) food resources, a refuge against human disturbance (Bonnot et al. 2013; Carbillet et al. 2020; Jasińska et al. 2021; Salvatori et al. 2023; Dupke et al. 2017), and shelter from temperatures above critical thresholds (van Beest et al. 2012; Ewald et al. 2014; Reiner et al. 2021, 2022; Kramer et al. 2022). 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 1950s 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 (Martin et al. 2011; Chirichella et al. 2014). 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 et al. 2010) or numerical increase of large carnivores (Chapron et al. 2014).

In random forest modeling, we did not model either the hunting bags of moose nor those of the 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 dynamics of wild ungulates (Apollonio and Chirichella 2023; 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 either 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).

3. Results

Between 1975 and 2018, Europe-wide hunting bags increased for all 7 studied species of ungulates (Table 1, Fig. 1). This increase was considerable and yet quite heterogeneous among countries. Even when excluding particularly extreme increases (Table 1), the median increase of harvest per species during the 43-year study period was as follows: European roe deer (1.97 folds), red deer (10.95), wild boar (10.20), fallow deer (5.58), mouflon (14.58), northern chamois (2.27), and moose (1.33), respectively. In case of wild boar, it is worth mentioning that the species was absent from

Sweden until its accidental introduction in the wild during the late 1970s, but in 2018 a total of 112,352 wild boar were harvested (Fig. 2). Moreover, in Finland, approx. 1,000 roe deer were culled in 2013; in 2023/2024, this number has risen to 16,555 individuals (Ilpo Kojola, personal communication).

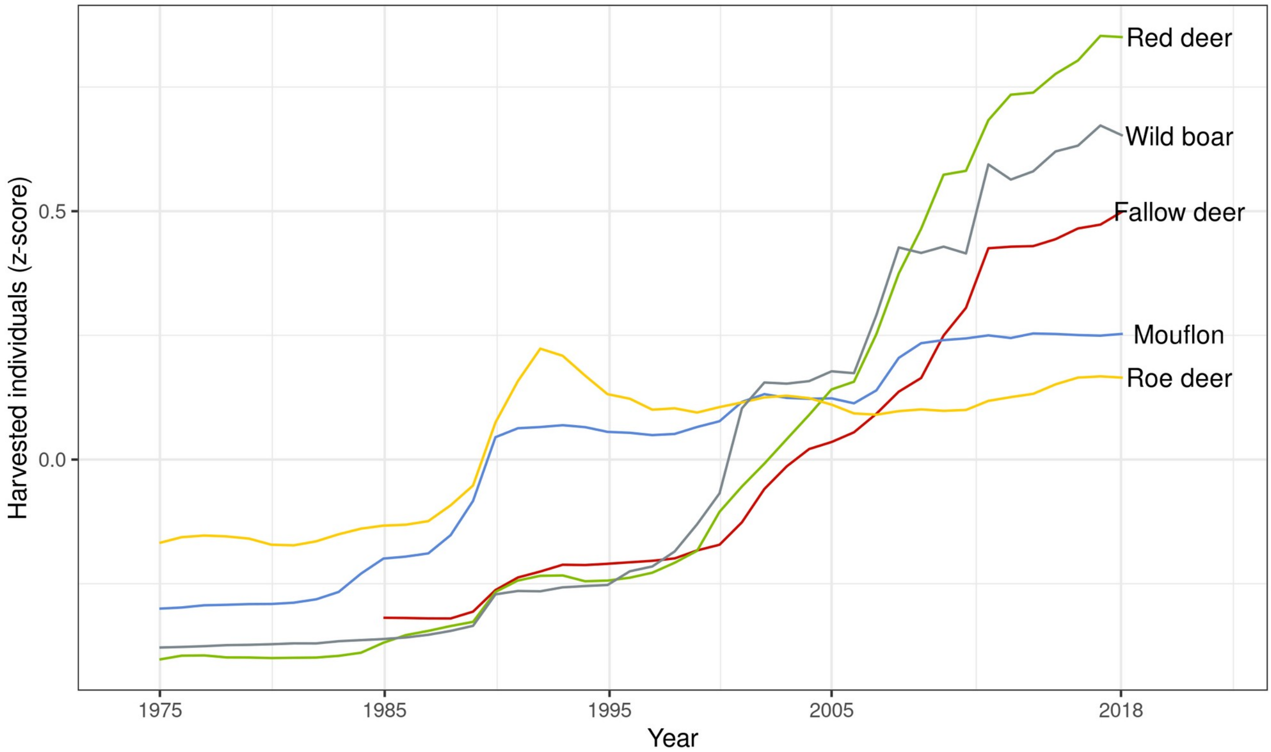

Fig. 1. Conditional effects plots, representing the evolution in the average number of harvested individuals, across the different species, according to random forests. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

The only ungulates with an overall decrease in their harvests were northern chamois in Austria and Switzerland, and 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 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) for a two-cluster solution was always below the cutoff of 0.5 (Fig. 3). This indicates that clusters had poorly distinguished long-term trends, with hunting bags in 2018 being consistently higher than those in 1975. However, the graphical inspection of cluster centroids sometimes revealed different groups of countries concerning short-term fluctuations or emerging differences.

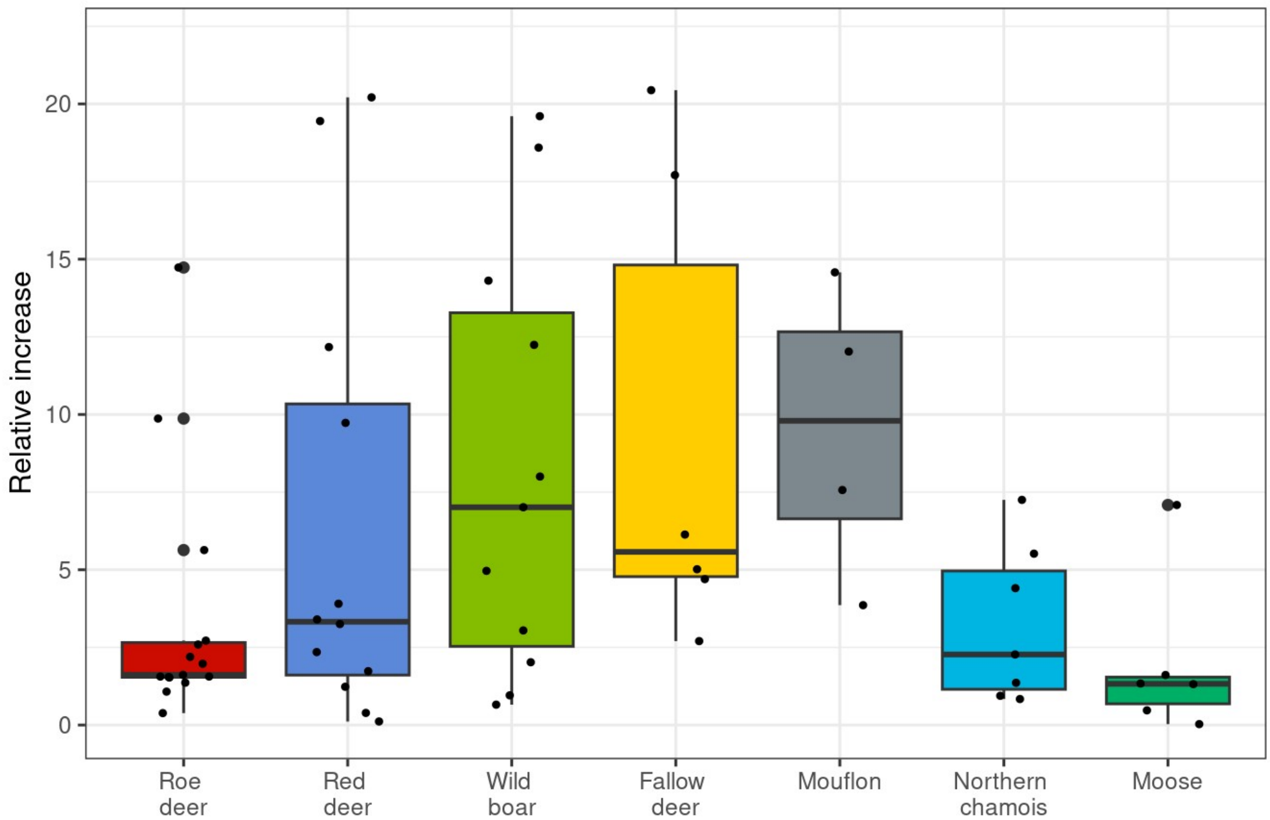

Fig. 2. Relative increase in the number of wild ungulates, across European countries (see Table 1 for detailed data in particular countries). The relative increase indicates how larger the number of harvested individuals was in 2018, compared to 1975. To make comparisons clearer, we omitted those countries where harvests had increased more than 25 times (see the Results section).

When considering roe deer (SI = 0.37; Fig. 3), hunting bags have decreased since the late 1990s 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 1990s, roe deer harvests have boomed.

Harvests increased steadily across most of Europe in case of red deer (SI = 0.37; Fig. 3). However, in Estonia, Latvia, Lithuania, Poland, Slovakia, and Slovenia, harvests of this species peaked in the early 1990s, 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 its harvests (SI = 0.23; Fig. 3), 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 1990s 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. 3). Harvests increased between 1975 and the early 1990s 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. 3), two groups of countries emerged. In Sweden, Estonia, Latvia and Lithuania, harvests increased until the late 1980s, declined until the mid-1990s, and increased again. Norway and Finland instead constituted a second group of countries with somewhat different temporal dynamics. In Norway, moose harvests increased until the late 1990s, 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 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 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: hunting bags for these two species were much higher in those countries with a marked increase in forest cover. 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 in countries with little rural depopulation. Other predictors seemed to have a comparatively smaller effect (Table 2).

When comparing the trends of roe deer and red deer harvests with data from 1948 in Austria, Denmark, Sweden, and Switzerland, we noticed that the two species exhibited two types of connected trends. In the first case, there were years when 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 roe deer harvests largely anticipated that of red deer. This was the case for Sweden, where roe deer harvests started booming in the mid-1980s and those of red deer increased in the 2010s, and in Denmark, where roe deer harvests increased around 1980 and red deer in the early 2000s (Fig. 5).

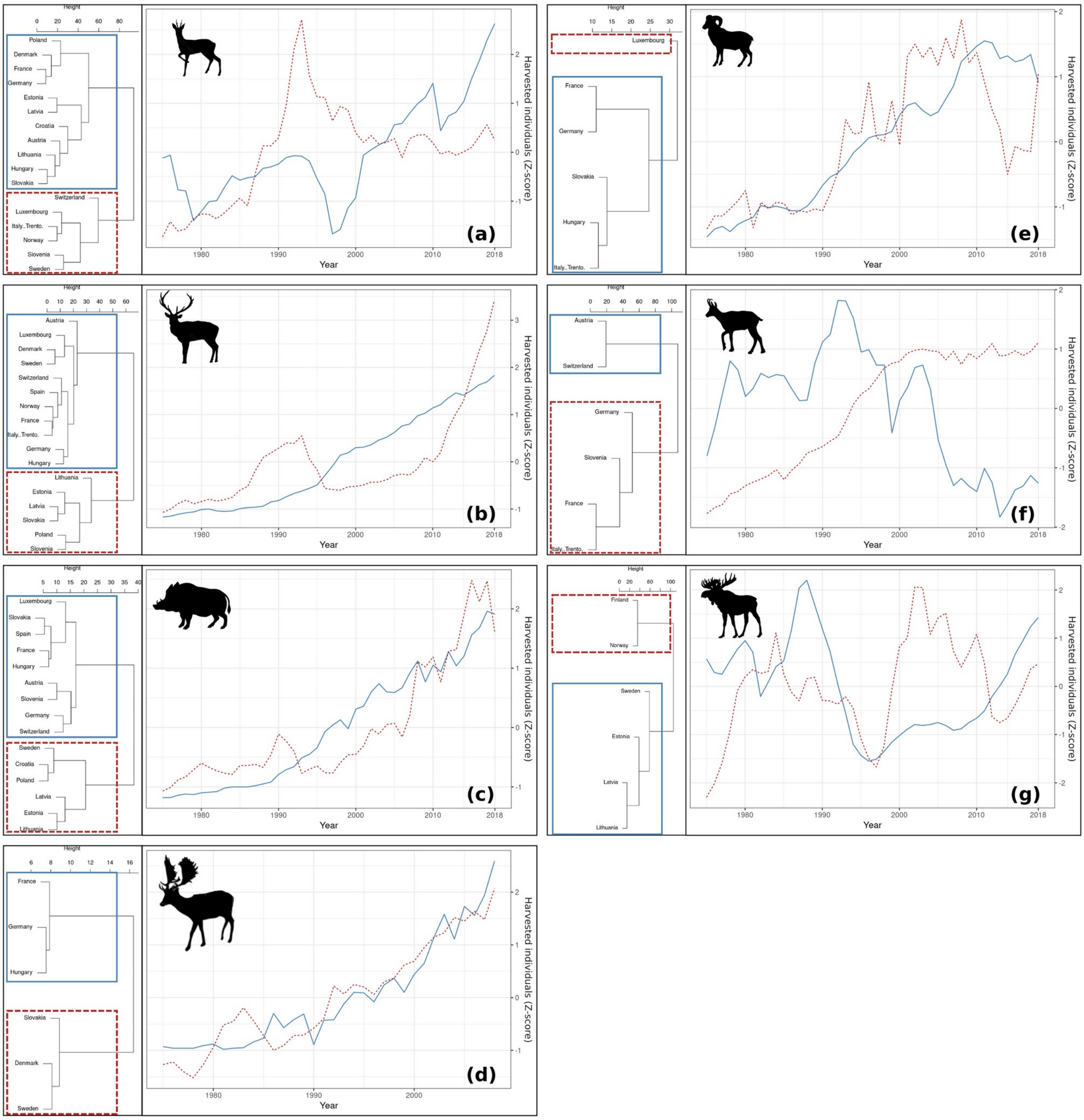

Fig. 3. Cluster centroids and dendrograms for the various species: roe deer (a), red deer (b), wild boar (c), fallow deer (d), mouflon (e), northern chamois (f), moose (g). For temporal changes in moose harvests in Finland and Norway, see Fig. S2. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

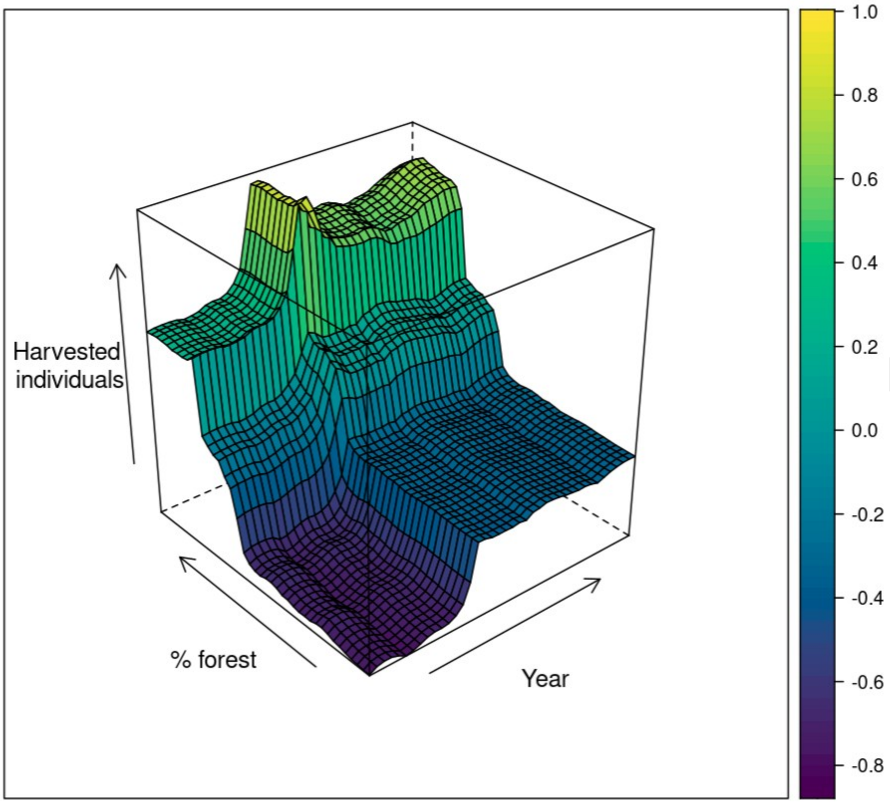

Fig. 4. Conditional effect plot, representing the change in the number of harvested roe deer according to time and relative change in forest cover.

4. Discussion

If we compare changes in large mammal distribution and abundance in Europe, we can appreciate a difference between ungulates and large carnivores. Chapron et al. (2014) reported that 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. Instead, the general picture about wild ungulates in Europe suggests that these species could regain 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. Our study shows that in the last decades, the trends of European ungulates' harvest (which is also a proxy of their abundance) 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 abundance in Europe, with a correspondent change in management issues like those related to the development of locally overabundant populations (Carpio et al. 2021; Valente et al. 2020).

Many previous studies have already confirmed that human development shapes wildlife populations (Tucker 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 dynamics 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). Indeed, the future of northern chamois conservation will further depend on several different environmental factors, with impacts on demography and life history traits that still need to be fully clarified (Chirichella et al. 2021; Corlatti et al. 2022). Available data and studies revealed the importance of environmental heterogeneity in shaping the population dynamics of wild ungulates, especially in response to ongoing climatic and land use changes (Mason et al. 2014; Chirichella et al. 2021; Hoste et al. 2024; Reiner et al. 2021), concerning the expansion and increase of potential competitors (e.g., red deer: Corlatti et al. 2019; Donini et al. 2021), and predators (Chapron et al. 2014; Vogt et al. 2024). Another species with limited distribution but abundant local populations, i.e. moose, revealed country-specific patterns in dynamics (e.g., Bobek et al. 2005; Kojola et al. 2021). These results confirmed the importance of site-specific management/conservation issues to maintain sustainable populations of a species susceptible to human-caused disturbance, vehicle collisions, illegal killings, and rising temperatures (Janík et al. 2021). The best example of this is the moose population in Poland, where it –in spite of the lowest harvest rate in Europe– has faced almost complete extermination and where recovering populations are still limited by low environmental connectivity (Bluhm et al. 2023).

On the other hand, although our findings highlighted a long-term increase in the harvests of roe deer and wild boar, we also found emerging short-term differences. 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 evaluating the effect of the impact wild boar abundance fluctuations due to ASF on habitats and communities, included other wild ungulates species (and their hunting and predation by large carnivores).

Another differentiation of harvest rates among countries occurred in the case of roe deer, whose hunting bags in 5 countries have declined since a peak in the early 1990s. This decline in roe deer harvests is likely to have been driven by changes in forest structures at the landscape scale (Fig. 4), and locally by the recovery of large carnivores as in the case of Eurasian lynx *Lynx lynx*; in Sweden (Andrén and Liberg 2015). This point might be clarified when simultaneously considering the harvests of roe and red deer over a long period. However, roe deer is still expanding its distribution range in certain regions, like central and southern Iberia (Virgós and Telleria 1998). 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 roe deer reached a plateau or even started declining (Fig. 5). Moreover, roe deer did not show an increase comparable to that of red deer despite the steady increase of forest cover in Europe. The former is, in fact, typical of pioneer species, linked to the early stages of forest development that provide important resources like access to cover (Mysterud and Ostbye 1999) and high quality and diversity forage, particularly at ecotones in proximity to open areas (Andersen et al. 1998; Saïd and Servanty 2005). 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 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 dynamics could be widespread across Europe and might produce a decline in roe deer populations over the next few years. Moreover, locally, other factors like, for example, the influence of golden jackal (*Canis aureus*) in the Balkans and Hungary (Bijl et al. 2024) or, in the case of the Danube and its tributaries and in Central Europe, the increase of American liver fluke (*Fascioloides magna*), a non-native liver parasite, could be important factor in the decline of roe deer (Csivincsik et al. 2023). This shows that multifactorial processes are influencing single ungulate species distribution and abundance in Europe.

The increase in forest area partially contributed to explaining red deer harvest dynamics, 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 populations dynamics (for a review, see Melis et al. 2006 and Scandura et al. 2022).

In our analysis, the temporal component was not the most predictive factor for roe deer, mouflon, and fallow deer. The change in the percentage of forest area was the most relevant driver for 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 dynamics of this species (and their drivers) have received poor attention, especially in northern/central Europe and for free-ranging populations.

Climate shaped the distribution of European mammals (Santos et al. 2020), and its effects are foreseen to become increasingly important (Levinsky et al. 2007). However, in this study we did not investigate the effect of climatic factors over the population dynamics of European ungulates. This choice was motivated by the mismatch between local climatic conditions in each country and our country-level Nevertheless, considered that climate affects the distribution and dynamics of cold-adapted ungulates (i.e. species with a low thermal neutral zone) (Lovari et al. 2020), as well as those of species with a wide distribution (e.g., wild boar: Markov et al. 2022; deer species: Apollonio and Chirichella 2023), we believe that it is important to address this gap to guide the management of wild ungulates in European landscapes facing climate change.

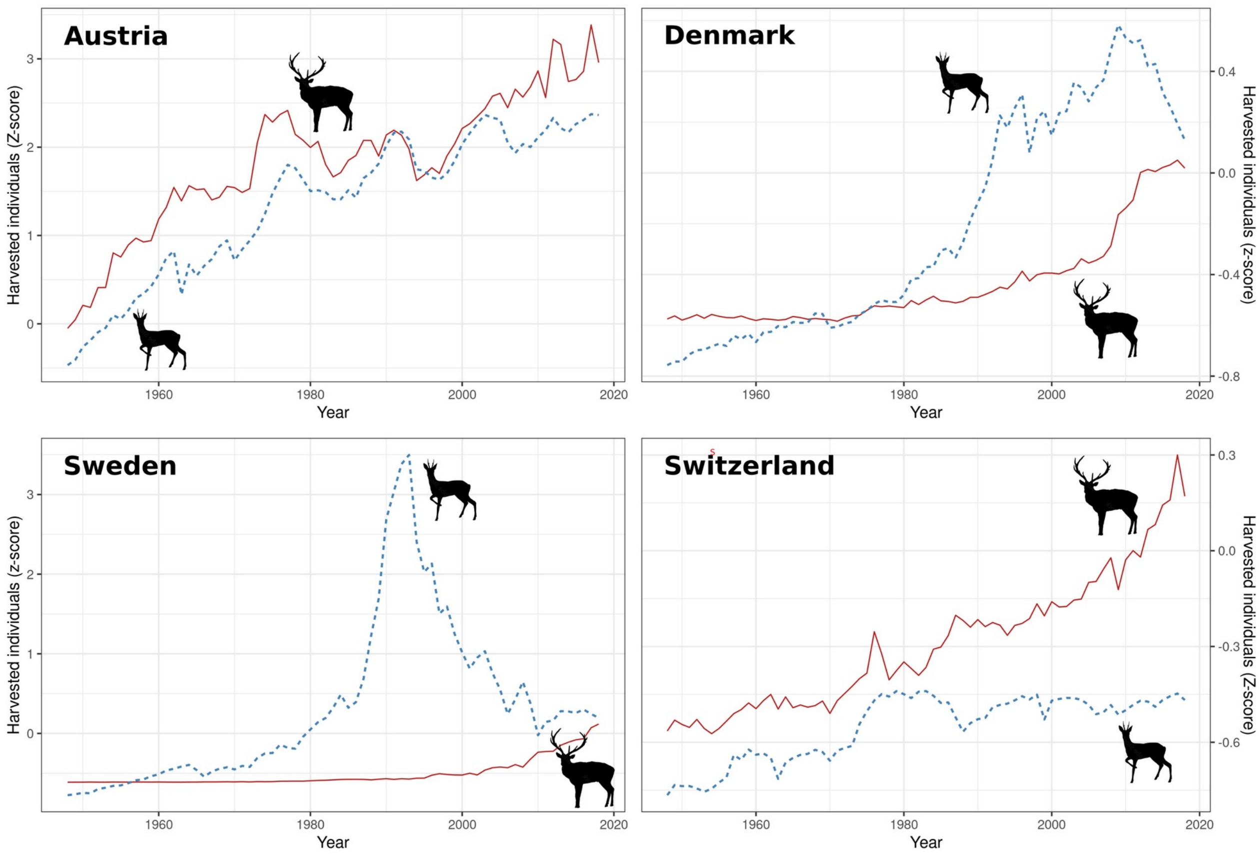

Fig. 5. Temporal trends of roe deer (dashed line) and red deer (solid line) harvests, between 1948 and 2018, in four countries: Austria (top-left), Denmark (top-right), Sweden (bottom-left), and Switzerland (top-right). The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

5. 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 monitoring schemes, aiming to better understand the demography of wild ungulates (Carpio et al. 2021; ENETWILD consortium, 2023), which is essential to implement and/or improve policies for their science-based management and conservation.

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Marco Apollonio - **Funding acquisition**

Data availability

Data and software code are available from the Open Science Framework, at the following link:

https://osf.io/uvfcs/

Funding

RC and MA were funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender no. 3138 of 16 December 2021, rectified by Decree no. 3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree no. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP J83C22000870007, Project title “National Biodiversity Future Center – NBFC”

Acknowledgments

We are grateful to Prof. Rory Putman and Prof. Reidar Andersen, for having pioneered large-scale research about the ecology and management of wild ungulates in Europe. We would also like to express our gratitude to prof. Sipke E. van Wieren Alterra and with dr. Reinhard Schnidrig, who shared data about the Netherlands and Switzerland.

Conflict of interest

The authors declare that they have no competing interests.

Ethical approval

Not applicable

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Supplementary figures

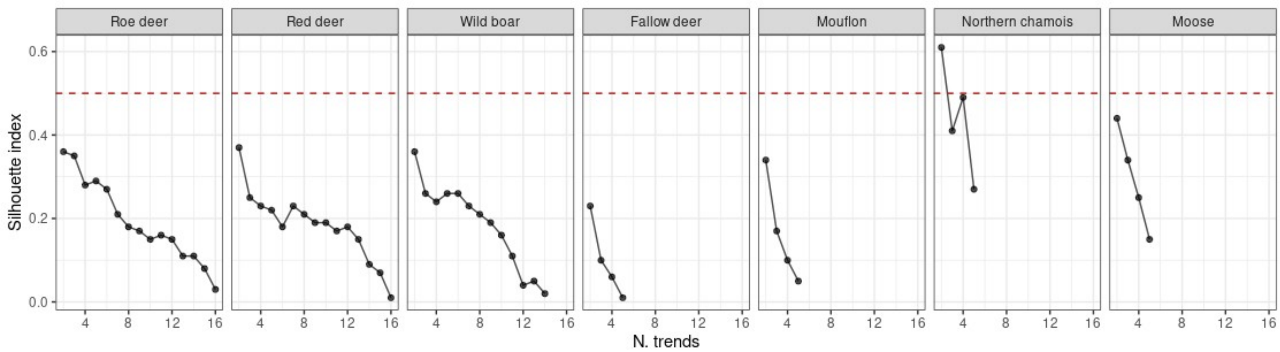

Fig. S1. Evolution of the Silhouette index for a growing number of temporal trends, in each species. Higher value of the index reflects more pronounced differences between long-term trends of cluster centroids. The horizontal line represents the cutoff value of 0.5, which is the threshold to identify clusters with different long-term trends according to Den Teuling et al. (2021).

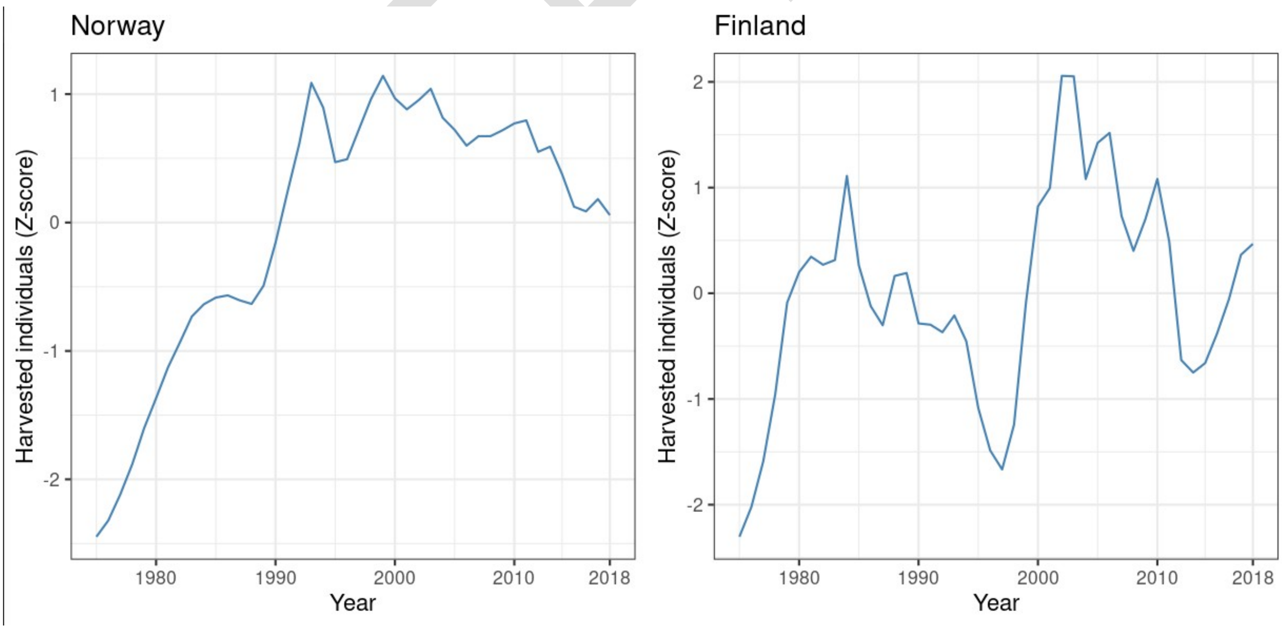

Fig. S2. Temporal trends in harvested moose in Norway and Finland. The number of harvested individuals was transformed to a Z-score and is represented in terms of standard deviations, from the mean value of each country.

Tables

Table 1. Number of harvested individuals, for each species per country, in 1975 and 2018 (- = no data or not considered; / = 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 1970s and was not hunted for years.

Species/year	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	54977	4,355	30,542	-	-	-	-	21,953	20,685	/	/
Croatia	4,204	16,160	1,674	3,933	2,418	29,599	-	971	-	497	12	87	/	/
Denmark	36,044	93,477	1,130	9,745	-	-	1,901	9,537	-	-	/	/	/	/
Estonia	16,390	24,146	5	2,757	4,977	4,761	-	-	-	-	/	/	5,441	7,163
Finland	-	-	-	-	/	/	-	-	-	-	/	/	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	/	/
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	/	/
Hungary	54,337	119,287	16,642	65,040	14,050	159,855	3,394	15,949	583	4,412	/	/	/	/
Italy (Trento)	2,119	4,185	9	2,287	-	-	/	/	2	270	541	2,985	/	/
Latvia	10,086	27,422	882	17,825	7,535	15,238	-	-	-	-	/	/	5,583	7,474
Lithuania	10,400	28,931	405	7,876	9,690	18,016	/	/	/	/	/	/	3,270	2,317
Luxembourg	4,493	7,016	131	426	972	7,777	-	-	2	119	/	/	/	/
Norway	5,240	29,520	3,807	43,800	/	/	/	/	/	/	/	/	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	/	/
Spain	-	-	11,843	144,134	19,038	373,225	-	-	-	-	/	/	/	/
Sweden	61,349	99,165	138	11,267	-	112,352	2,849	50,449	-	-	/	/	51,544	83,059
Switzerland	39,377	42,389	3,552	12,081	489	6,997	/	/	-	-	13,358	11,192	/	/

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
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