

## REVIEW

## Hybridisation in European ungulates: an overview of the current status, causes, and consequences

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### ABSTRACT

1. Hybridisation and gene introgression are important sources of diversification, the relevance of which in the evolutionary processes is well recognised. Their fitness consequences in animal populations, however, are not sufficiently well understood, despite hybridisation rates becoming increasingly important worldwide following human-related activities such as domestication, game management and habitat alteration.
2. In Europe, the density and distribution of native ungulates have largely been influenced by humans since pre-historic times. This, alongside the introduction of non-native and domesticated species, may bear major consequences at the genetic and population levels. We provide an updated overview of recent hybridisation events in wild European ungulates; we describe their ecological drivers, extent, current distribution, potential consequences and proposed management strategies.
3. We reviewed the scientific literature published between 2000 and 2018 and found that confirmed hybridisation was described in 75 of the 89 references we included, involving nearly all the species that we investigated. Most researchers relied on genetic information for hybrid identification, which often involved a domestic counterpart. However, introductions and translocations also led to crossbreeding between wild ungulate (sub)species. Only 43 papers provided management recommendations, mostly focused on preventing hybridisation and removing hybrids.
4. Hybridisation proved to be relatively common in several ungulate taxa in Europe. Despite reported changes in phenotype and fitness-related traits in some species, the consequences of hybridisation for adaptation, life history, and evolutionary potential remain largely unknown. The current conservation paradigm aims to prevent the spread of domestic or non-native genes in native populations; accordingly, conservation plans should: 1) determine the genetic origin of possible source populations; 2) protect native populations from the risk of crossbreeding with non-native ones, and 3) establish permanent monitoring.

## INTRODUCTION

Hybridisation or crossbreeding – between individuals of different (sub)species – and gene introgression – the transfer of genes between (sub)species – play important roles in evolutionary processes (Rieseberg & Carney 1998). Hybridisation, for example, occurs naturally in 10% of animal species and acts as a source of genetic variation (Mallet 2005). It depends on the distribution and size of distinct populations, increasing when differences in densities are high, owing to restricted mate choice in the rarest population (Hubbs 1955). Consequently, anthropogenic activities such as habitat degradation, domestication and translocation of animal species have recently increased the rate of hybridisation events worldwide. Humans have favoured contacts between previously allopatric populations, either wild or domesticated, and the renewed sympatry has often resulted in new hybrid zones that may bear major consequences for native species, subspecies, and locally adapted populations (Allendorf et al. 2001). For example, native populations might lose local adaptation by introgression of non-native alleles (Barton 2001, Burke & Arnold 2001). Understanding the causes, extent and potential consequences of hybridisation events are thus pivotal for the conservation of native species.

### The ecology of hybridisation in European ungulates

Europe is a largely human-dominated landscape, and the importance of ungulates typically stands on ecological, cultural, and economic grounds. The impacts of ungulates on human society may span from negative to profitable – through either consumptive or non-consumptive use (Csányi et al. 2014) – therefore it is not surprising that the size and distribution of ungulate populations in Europe have been, and continue to be, influenced by humans, with profound consequences on the opportunity for hybridisation. The fate of European ungulates throughout history is inextricably related to human activities and attitudes. From the early hunter-gathering lifestyle, humans have progressively changed towards more agricultural and game hunting-oriented lifestyles, until the very recent awareness of the importance of biodiversity conservation (Linnell & Zachos 2011). Accordingly, the size and distribution of wild native ungulate populations have been profoundly influenced by changes in land-use patterns, overhunting and translocations for recreation and/or attempts to restore and increase biodiversity (Linnell & Zachos 2011). As a result, wild native ungulates are presently widely distributed in Europe, though their conservation status varies greatly, depending on the species, subspecies and region of interest.

The roe deer *Capreolus* spp., for example, is the most abundant and widely distributed ungulate in Europe (though it is absent on some islands), although the subspecies *Capreolus capreolus italicus* is rare (Lovari et al. 2016a). Similarly, the wild boar *Sus scrofa* is abundant and can be found throughout much of Europe (Herrero et al. 2007). The red deer *Cervus elaphus* is also abundant and widespread, albeit patchy (Lovari et al. 2016b). However, some taxa are of conservation concern (e.g. *Cervus elaphus corsicanus*, *Cervus elaphus italicus*, *Cervus elaphus barbarus*). Wild populations of reindeer *Rangifer tarandus* are geographically restricted to Fennoscandia and the species has been assessed as Least Concern at the European level on the International Union for Conservation of Nature's (IUCN) Red List (Henttonen & Tikhonov 2007), though the 2010 Red List of Finnish Species included the wild forest reindeer *Rangifer tarandus fennicus* as a near-threatened species (Rassi et al. 2010). The European bison *Bison bonasus*, with about 6600 individuals, is listed as vulnerable on the IUCN Red List (Raczyński 2017). Wild native *Caprinae* (ibex *Capra* spp., chamois *Rupicapra* spp.) are patchily distributed in the mountain ranges of southern-central Europe from Spain to Greece; no species is threatened, yet there is concern about the conservation of certain chamois subspecies (Corlatti et al. 2011), and the future decline of Alpine ibex *Capra ibex* populations should be prevented. The wax and wane of population size due to overexploitation, shifts in distribution related to land-use changes and translocations for consumptive or conservation reasons, may eventually favour the onset of hybrid zones among native (sub)species. The conservation of wild native ungulates in Europe, however, is further complicated by the introduction of non-native species and interactions with livestock.

Wild ungulates have been moved around by humans since early historic times, for sport hunting, food provision, recreation, and gifts; the current distribution of non-native ungulates is thus a result of intentional releases and escapes from public and private properties, and these species have occasionally founded naturalised populations (Spear & Chown 2009). European examples include Barbary sheep *Ammotragus lervia*, American bison *Bison bison*, European mouflon *Ovis aries musimon*, fallow deer *Dama dama*, axis deer *Axis axis*, wapiti *Cervus canadensis*, sika deer *Cervus nippon*, Chinese muntjac *Muntiacus reevesi*, Chinese water deer *Hydropotes inermis*, and white-tailed deer *Odocoileus virginianus* (Ferretti & Lovari 2014). Populations of wild non-native ungulates are spread across almost all European countries, with the greatest number of taxa found in Germany, Czech Republic, and the UK (Ferretti & Lovari 2014). Consequences of their introduction span from habitat alteration and disease spreading to interspecific competition and hybridisation events (Spear

& Chown 2009, Ferretti & Lovari 2014). Additionally, European livestock farming has a long history that originated in the Neolithic and post-Neolithic eras around the Mediterranean basin (Zeder 2008). Today, it is widespread throughout the continent, although its importance varies between regions and livestock types (Neumann et al. 2009): the highest density of cattle, for example, occurs in northern-central Europe (UK, France, the Netherlands, Germany, and northern Italy), while pig farms mainly occur in central Europe (northern France and Germany, the Netherlands, southern Denmark, northern Italy, Spain). Sheep and goats are mainly found in the Mediterranean countries (Greece, Spain, France, and Italy), though sheep farming is also of key importance in the UK (Ataide Dias et al. 2008).

This complex pattern of land use, exploitation, and translocations of wild (either native or non-native) and domestic ungulates sets the ground for hybridisation issues in Europe, following widespread and uncontrolled diffusion of domestic species, and changes in abundance and distribution of wild populations.

### How can we detect hybrids?

Hybridisation can be detected in a variety of ways, either morphologically or through use of molecular data. Morphological alterations in some cases led to the identification of hybrids – later confirmed by molecular data – in both Alpine ibex and wild boar populations (Giacometti et al. 2004, Šprem et al. 2011, 2014). However, phenotypic traits can be misleading in the case of rare mutations or undescribed epigenetic effects (Clark et al. 2017), can be problematic to detect in the wild (Pérez-Espona et al. 2011) or can fail to detect crossbreeding altogether (Lorenzini et al. 2011). Molecular genetics can integrate hybrid detection and gene introgression between taxa (Avise & Hamrick 1996). Based on their transmissions and evolutionary dynamics, molecular markers can be categorised into two groups: nuclear and uniparental. The most commonly used uniparental marker is mitochondrial DNA (mtDNA), as it is more prone to introgression than the nuclear genome. Complete mtDNA replacement can be observed even in the absence or presence of low nuclear introgression (Abbott et al. 2013). Sometimes, however, mtDNA lineages are shared by closely related species, thus reducing the power of haplotype analysis to detect introgression (Mallet 2005). This can be explained by the maternal inheritance of the mtDNA genome: in species evolution, intraspecific gene flow at organelle loci occurs at a much lower rate than at nuclear loci (Birky et al. 1989). Y-chromosome markers might uncover the male impact of translocations. Unfortunately, these markers are less variable than mtDNA and are thus of limited applicability (Petit et al. 2002). High variability associated

with biparental nuclear microsatellites provides an appropriate marker system for detecting hybridisation between individuals from different populations or taxa (Zane et al. 2002). Nonetheless, microsatellites quickly accumulate homoplasy, and thus have low statistical power for inferring population structure when samples are obtained from a hybrid population, especially when admixture proportions are high (Haas & Payseur 2010). For these reasons, microsatellites cannot always accurately estimate gene flow between free-ranging individuals and their domestic counterparts. Recently, genomic studies have taken advantage of thousands of single nucleotide polymorphisms (SNPs) to understand the dynamic nature of hybridisation and introgression. Such studies aim to have a good coverage of markers distributed across the (nuclear) genome, with high marker density, to detect introgressed genes accurately (Alves et al. 2003a, Herrero-Medrano et al. 2013).

### Where do we stand?

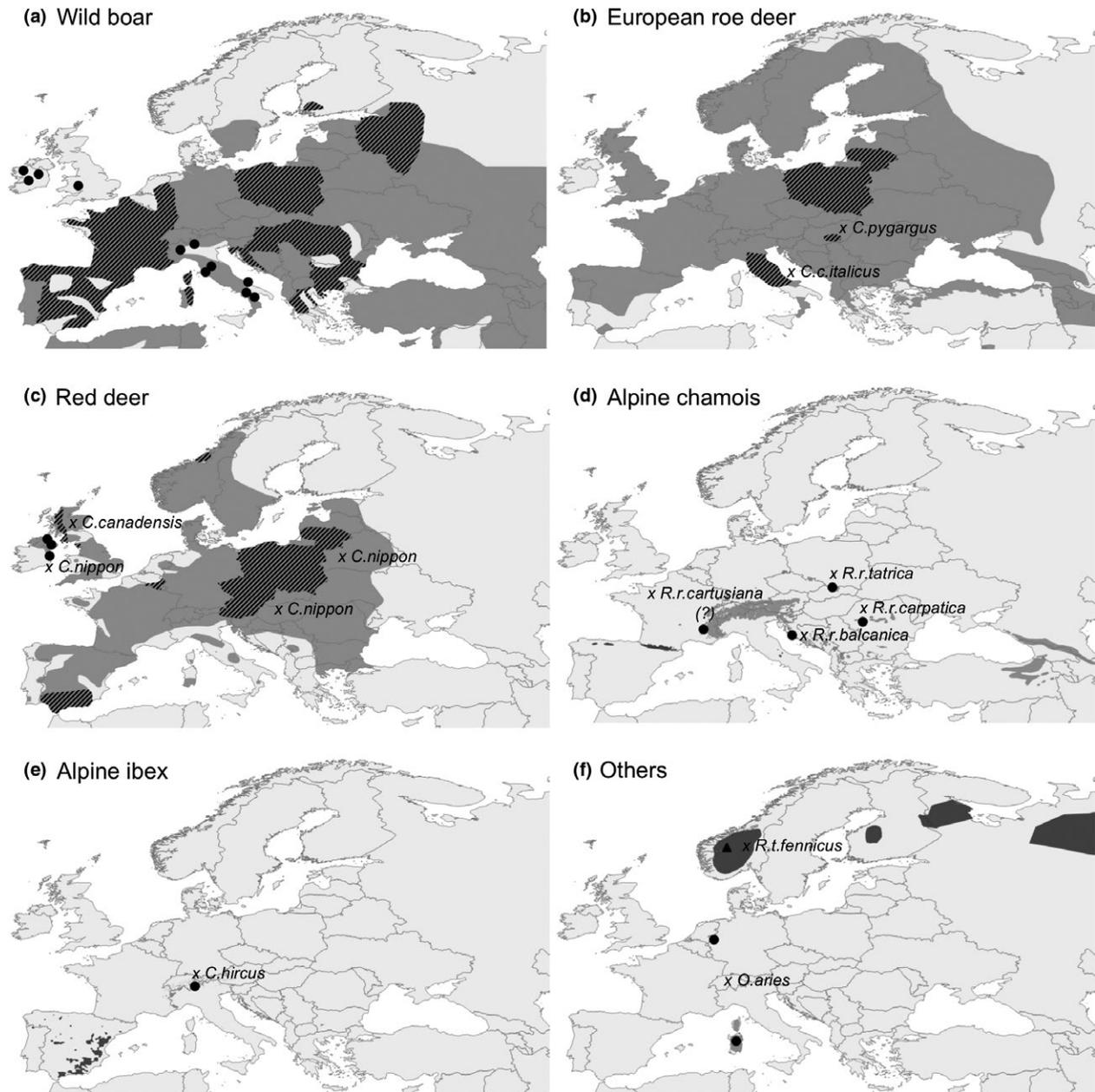
Although hybridisation is generally perceived negatively when considering conservation and management of natural resources (e.g. Allendorf et al. 2001, Wolf et al. 2001), it may be of key importance for the survival of some taxa under rapidly changing environmental conditions. However, in the current management paradigm that aims to minimise interventions to populations, human-mediated hybridisation is often seen as ‘genetic pollution’ (Zachos & Hartl 2011) and hybrid populations are not given equal protection in many countries, compared to ‘pure’ populations (Allendorf et al. 2004). Thus, genetic monitoring and the dissemination of relevant empirical data are expected to support conservation actions, including the implementation of officially accepted molecular protocols aimed at identifying the genetic status of populations, and to estimate contemporary vs. historical patterns of hybridisation. The possibility of identifying the impact of past (re)introduction activities on genetic variability and its geographical distribution are of primary interest when implementing conservation and management strategies (King & Burke 1999, Apollonio et al. 2014).

In this review, we discuss the many facets of hybridisation in the context of European ungulates. In particular, we aim to: 1) provide an overview of hybridisation patterns (location, levels, species, and subspecies involved) in wild European ungulates; 2) outline the methods used to identify admixed individuals; 3) report the ecological causes of hybridisation; 4) summarise the effects of hybridisation and their consequences for the conservation of European ungulates; and 5) review current management strategies to limit the consequences of hybridisation.

## METHODS

Wild European ungulates included in this review were selected according to Temple and Terry (2007). To find all

the relevant literature, a systematic search was conducted in the Scopus database. We searched for titles, abstracts, and keywords using the following combinations: 'species\_name hybridisation', 'species\_name hybrids', 'species\_name



**Fig. 1.** Geographic ranges of ungulates and their hybrids in Europe; shaded areas correspond to the species' geographical ranges, redrawn from IUCN Red List maps; hybridisation is represented by crosshatching where it is extensive and by dots (approximate locations) where it is geographically confined. (a) Wild boar, showing the hybrids: *Sus scrofa scrofa* × *Sus scrofa domestica*; (b) European roe deer, showing the hybrids: *Capreolus capreolus* × *Capreolus pygargus*/*Capreolus capreolus italicus*; (c) red deer, showing the hybrids: *Cervus elaphus* × *Cervus* spp. (see text for details); (d) Alpine chamois, showing the hybrids: *Rupicapra rupicapra rupicapra* × *Rupicapra rupicapra* spp.; (e) Alpine ibex, showing the hybrids: *Capra ibex ibex* × *Capra hircus*; (f) other species, showing reindeer and the hybrids: *Rangifer tarandus tarandus* × *Rangifer tarandus fennicus* in Fennoscandia and Russia, and European mouflon and the hybrids: *Ovis aries musimon* × *Ovis aries* in Corsica and Sardinia. When hybridisation involved multiple (sub) species, the corresponding taxon names are reported. Panels (d) and (e) also show, in the Iberian Peninsula, the geographic ranges of *Rupicapra pyrenaica* and *Capra pyrenaica*, respectively, though no hybridisation has been reported so far for these species.

crossbreeding', and 'species\_name introgression'. Searches were performed using both the English and the scientific names of species. We used all papers in English that were published in the period between 2000 and June 2018. Relevant literature on ungulate hybridisation not present in the search results using the aforementioned keywords, or published outside of the timeframe 2000-2018, was included in the review when appropriate according to the authors' expertise. We found and included a total of 89 papers providing information on eight taxa (Appendix S1).

## RESULTS

### *Sus scrofa*

Cases of hybridisation between the wild boar and its domestic counterpart *Sus scrofa domesticus* have been reported in several European countries using a variety of molecular and morphological markers (see Appendix S1 and Fig. 1a). However, hybridisation between different wild boar subspecies (namely between European wild boar *Sus scrofa scrofa* and Italian wild boar *Sus scrofa majori* or Sardinian wild boar *Sus scrofa meridionalis*) has also been detected (Vernes et al. 2003, Scandura et al. 2011). The screened literature (42 papers on *Sus scrofa*, see Appendix S1) shows variable levels of hybridisation, ranging from absent (Iberia, using mtDNA and SNPs; Alves et al. 2003b, Herrero-Medrano et al. 2013) to high (Ireland, using microsatellites and mtDNA; McDevitt et al. 2013). The geographic distribution of the phenomenon differs greatly. For example, Scandura et al. (2011) found that in Sardinia, introgression from the domestic pig was mostly limited to a smaller island off the northeast coast, while in the Netherlands it was geographically widespread (Goedbloed et al. 2013). However, introgression is usually related to human practices, be it release of admixed individuals or free-range farming practices (Appendix S1). Having the same legal status as the wild boar throughout Europe, hybrids are regularly hunted. When crossbreeding leads to a lack of camouflage, this might increase the chances of hybrids being spotted by human hunters or predators (Canu et al. 2016). On the contrary, Fulgione et al. (2016) report that introgression from the domestic pig into the wild boar population might lead to improved fitness. Improvement in meat quality has been observed after introgression of wild genes into the domestic pig population (Matiuti et al. 2010). However, the most commonly reported effects are alterations to the local gene pool (in 14/42 screened papers), including loss of adaptation (2/42), increased population size (5/42), increased invasiveness (3/42), and morphological changes (4/42; see Appendix S1). To limit the spread of hybrids, several management practices have been proposed, primarily focusing on genetic monitoring

of local populations and individuals used for restocking, including farmed ones, and on an integrated management strategy and stricter regulations for animal release and movement (see Appendix S1). Only one of the papers highlights the importance of increasing public awareness on this topic. Although mtDNA has been the most commonly used marker (21/42), it cannot resolve hybridisation between European taxa. Some authors thus strongly recommend the use of a combination of markers, including at least one autosomal, as they might lead to different results (e.g. Frantz et al. 2013, Canu et al. 2016).

### *Bison bonasus*

The European bison went extinct in the wild in the 1920s, but populations were soon restored from 12 zoo captive animals. One of them was the last representative bull of a distinct subspecies, the Caucasian bison *Bison bonasus caucasicus* (Tokarska et al. 2011).

In 1950, individuals with Caucasian bison genes were separated from the pure lowland bison, creating two isolated genetic lines of European bison: the hybrid Lowland-Caucasian (LC) line and the Lowland line, the latter representing the pure *Bison bonasus bonasus* subspecies (Pucek et al. 2004). The LC line is considered the only remaining source of Caucasian bison genes. The Status Survey and Conservation Action Plan for the European bison (Pucek et al. 2004) states: 'Pure Lowland and LC lines should be separated in the wild, as well as in enclosed breeding centers, up to the time of their likely natural contact. This isolation is of particular importance for preserving the genetic variability within LC line'. Although no hybridisation event has been reported in the 16 screened papers (Appendix S1), potential hybridisation between the two populations is described as a threat to the conservation of the remaining European bison.

The European bison range expansion brought the two lines into contact in the Białowieża Forest, at the border between Poland and Belarus. According to estimates from 2011, around 52% of all free-ranging Lowland line bison live in the Białowieża Forest. The population has been divided by a border fence since 1981 (Tokarska et al. 2011), leading to differentiation into two subpopulations. Tokarska et al. (2015), using 19 microsatellite and 1512 bovine SNP markers, revealed highly significant differences between the Polish and Belarus subpopulations from the Białowieża Forest. Their data showed that at least some of the genetic variants found in the Belarus subpopulation, but not in the Polish one, were of Caucasian origin. The authors suggest that the separation of the two Białowieża Forest lines is now vital for the protection of the world's largest free-roaming population of Lowland line bison (Tokarska et al. 2015). Since the border fence between

Poland and Belarus – which prevents contact between the two bison subpopulations – is a human construct of current politics, potential hybridisation between these two lines, and consequentially their genetic status, are unpredictable.

## Capra

The screened literature (six papers) reported hybridisation events mostly between wild *Capra* spp. and domestic goats *Capra hircus* (Appendix S1, Fig. 1e); however, information is limited.

The strongest evidence for hybridisation has been reported between Alpine ibex and domestic goats in the Swiss Alps. While earlier studies based on multilocus enzyme electrophoresis did not find compelling evidence (Randi et al. 1990), microsatellite markers (Giacometti et al. 2004), major histocompatibility complex analysis, and SNPs (Grossen et al. 2014) recently confirmed the occurrence of ibex × goat hybrids. Introgression is likely to have resulted from natural and captive breeding with domestic herds, the former due to more or less recent spatial overlap during winter, the latter due to early re-introduction attempts (Stüwe & Nievergelt 1991, Giacometti et al. 2004, Grossen et al. 2014). The consequences of ibex hybridisation with domestic goats span from morphological changes such as increased body size, longer male horns with smaller nodes, prominent leg markings, and dark brown colour in young individuals (Giacometti et al. 2004), to maladaptive alteration of reproductive biology (Stüwe & Nievergelt 1991) and potentially improved immune responses (Grossen et al. 2014). Turček and Hickey (1951) report anecdotal evidence for hybridisation of Alpine ibex with Nubian ibex *Capra nubiana* and bezoar *Capra aegagrus* in the Tatra Mountains of Slovakia, where all these species were introduced for hunting purposes; consequences of introgression included early rutting season and anticipated parturition, which may have pushed the hybrid population to extinction. In western Europe, Iberian ibex *Capra pyrenaica* and domestic goats have long co-existed in the mountainous regions of Spain, yet firm evidence of hybridisation in the wild is lacking (Sarasa et al. 2012, Herrero et al. 2013). While introgression has been confirmed in the Rute-Priego Mountains (using major histocompatibility complex genes) in semi-captive breeding conditions (Alasaad et al. 2012), physiological and behavioural reproductive incompatibility between domestic goats and Iberian ibex might prevent interbreeding in the wild (Fernández-Arias et al. 1999, Herrero et al. 2013). Anecdotal evidence of hybridisation with domestic herds has also been reported for wild goats, or bezoar, in the mountains of Turkey; consequences of interbreeding include longer body hair, big floppy ears, and horns that flare out at

the ends (Damm & Franco 2014). The other European ‘wild’ goats (including Mallorcan and Cretan goats) are considered feral descendants of primitive domestic stock (Giannatos et al. 2007, Masseti 2009); not surprisingly, on the mountains of Mallorca and Crete, hybrids with domestic herds have been anecdotally reported (Giannatos et al. 2007, Papaioannou 2010). To limit the spread of hybrids, management recommendations generally include the removal of domestic herds from core areas of wild species, surveys of morphological traits where hybridisation is suspected and, possibly, removal of hybrids.

## Rupicapra

Evidence for hybridisation has been reported (seven papers) only between different *Rupicapra* subspecies (Appendix S1, Fig. 1d). Using mtDNA, Šprem and Buzan (2016) confirmed the occurrence of hybrids between Balkan chamois *Rupicapra rupicapra balcanica* and Alpine chamois *Rupicapra rupicapra rupicapra* in the Velebit Mountains (Croatia), resulting from the introduction of both species for hunting purposes. Similar patterns may occur in the Rhodope Mountains in Bulgaria, although the signals of introgression (using microsatellites) for the Balkan population are not unequivocal (Markov et al. 2016b) and further screenings are desirable (Valchev et al. 2006). Interbreeding has been suggested to occur also between Balkan and Carpathian chamois *Rupicapra rupicapra carpatica* at the contact zone of the natural ranges of the two subspecies, in Djerdap National Park (Serbia; Damm & Franco 2014). In the Low Tatras (Slovakia), the occurrence of hybrids between the endemic Tatra chamois *Rupicapra rupicapra tatrica* and Alpine individuals introduced for hunting purposes has been confirmed using cytochrome b (Crestanello et al. 2009). Subsequent analyses using microsatellites, sex-determining region Y gene, major histocompatibility complex and mtDNA confirmed up to 19% of male-biased introgressive hybridisation between the two subspecies (Zemanová et al. 2015). Finally, potential issues of hybridisation have been suggested to occur in the Chartreuse Massif in the French Alps, where the genetic identity of the endemic subspecies *Rupicapra rupicapra cartusiana* is put at risk by translocations of individuals of the Alpine subspecies for hunting purposes (Roucher 1999), although evidence of hybridisation is currently lacking. Damm and Franco (2014) anecdotally reported possible hybridisation between Alpine and Chartreuse chamois in the Vosges Mountains (France) during the 1950s, where both subspecies were introduced. Overall, the consequences of hybridisation between chamois subspecies remain largely unknown. Zemanová et al. (2015) suggested that the effects might include the disruption of local genetic adaptations, outbreeding depression, local extinctions, the increase of

genetic variation, and enhanced adaptability to environmental change in populations with reduced genetic diversity. Future research on the effects of hybridisation on fitness-related traits is thus of paramount importance for planning appropriate conservation measures. To date, management recommendations to avoid the spread of hybrids generally include the removal of non-endemic populations, the definition of conservation units for different chamois taxa – that should cautiously consider translocations of individuals carrying the appropriate genetic background (Corlatti et al. 2011) – and careful monitoring of potential ongoing hybridisation events.

### *Ovis aries musimon*

The European mouflon was introduced to the Mediterranean islands of Corsica and Sardinia by humans during the first wave of domestication, ca. 6000–7000 years ago (Barbato et al. 2017). On those islands, after feral populations became established (Chessa et al. 2009), the species is considered ‘historically autochthonous’ and is protected. Since the 18th century, mouflon from Corsica and Sardinia have been introduced to many countries in mainland Europe as game animals.

Evidence of European mouflon × domestic sheep hybridisation has been reported (4/17 papers; Appendix S1, Fig. 1f). In Corsica and Sardinia, mouflon populations have coexisted with domestic sheep populations since the second domestication wave (Barbato et al. 2017), and admixture between them has occurred. The genetic link between Sardinian domestic sheep breeds (Sardinian white and Sardinian ancestral black sheep) and Sardinian mouflon was identified using the 50k SNP chip by Ciani et al. (2014). Genetic differences between mouflon and domestic sheep are difficult to detect, due to the similarities of their genomes. For example, both mouflon and European domestic sheep breeds belong to the sheep mitochondrial haplogroup B (Hiendleder et al. 1998, Tapio et al. 2006), therefore mtDNA markers cannot be used to infer gene flow between them. However, autosomal markers allow for the identification of the two parental populations and their hybrids. Arnaud et al. (2007) and Chessa et al. (2009) used the provirus endogenous jaagsiekte sheep retrovirus insertion in chromosome 11 to distinguish old European domestic breeds, including mouflon, from modern domestic breeds. Forensic investigations using microsatellites have detected signs of crossbreeding in samples phenotypically attributed to mouflon (Lorenzini et al. 2011). Similarly, Schröder et al. (2016) combined endogenous jaagsiekte sheep retrovirus-18 and microsatellites to detect hybrids in western Germany. More recently, Barbato et al. (2017) compared European mouflon populations with 16 sheep breeds using 50k SNPs. Their results

showed that signals of domestic sheep introgression into mouflon were stronger in a fenced mouflon population in Sardinia, probably as a result of extensive recent crossbreeding, while hybridisation signatures were weaker in mainland Europe (Barbato et al. 2017).

The causes of this difference might be related to the regulatory effect of hunting and management and the rarity of free-range sheep farming in continental Europe; in Sardinia the mouflon is protected and free-range sheep farming practices are common. Consequences of crossbreeding with the domestic form are usually reported to affect the phenotype (Schröder et al. 2016). However, Barbato et al. (2017) showed that genes with functions related to innate immunity and bitter taste have been introgressed from mouflon into numerous sheep breeds, giving an example of positive selection. None of the screened papers provided management recommendations.

### *Capreolus*

To date, two independent cases of hybridisation within the genus *Capreolus* have been reported in Europe. The first case (6/12 screened papers) occurred between European roe deer *Capreolus capreolus* and Siberian roe deer *Capreolus pygargus*, two distinct but very closely related species (Appendix S1, Fig. 1b). The second case (6/12) was between European roe deer and the endemic subspecies, Italian roe deer (Appendix S1, Fig. 1b).

Hybridisation between Siberian and European roe deer might have been caused by natural processes, e.g. range expansion during the Middle Ages, or by more recent human-mediated introductions of Siberian roe deer within the range of European roe deer for hunting purposes, with the aim to increase body mass and trophy size (Hewison & Danilkin 2001, Matosiuk et al. 2014a, Olano-Marin et al. 2014). The main hybridisation event between the two roe deer species took place 2000 km from the current geographic range of the Siberian roe deer, and hybridisation levels range from low (3% in the Pannonian region; Markov et al. 2016a) to high (nearly 50% in Poland and Lithuania; Lorenzini et al. 2014; Appendix S1).

In central and southern Italy, hybridisation between the European and Italian roe deer represents the main threat to the genetic integrity of the endemic Italian subspecies (Gentile et al. 2008, Biosa et al. 2015), and is a consequence of reintroduction and restocking operations by humans (Battisti et al. 2015). The first restocking attempts were conducted in Abruzzo National Park in the 1930s (Battisti et al. 2015); subsequently, the European roe deer expanded its range northwards (e.g. into Tuscany and Emilia Romagna; Randi 2005, Mucci et al. 2012).

Hybridisation between the Siberian and European roe deer can be detected by mtDNA, while autosomal microsatellite loci and Y chromosome markers did not show signs of introgression (Appendix S1). In the case of European and Italian roe deer, both mitochondrial and nuclear markers proved useful in the identification of hybrids (Mucci et al. 2012, Biosa et al. 2015). The lack of divergence in nuclear DNA between Siberian and European roe deer, but not between European and Italian roe deer, may be evidence that introgression in the former case happened more than 200 years ago (Lorenzini et al. 2014). This estimate is concordant with documented introductions (Lorenzini et al. 2014), and is likely to be too long ago to be detected by microsatellites, due to their inheritance and high recombination rate (Bhargava & Fuentes 2010).

Whereas only Markov et al. (2016a) discussed the importance of preserving the genetic diversity of European roe deer through the prevention of crossbreeding with Siberian roe deer, specific conservation and management measures for the Italian subspecies are listed in the Italian roe deer Action Plan (Focardi et al. 2009). The main recommendations include: genetic identification and mapping of pure Italian roe deer individuals and populations; permanent monitoring of hybridisation and introgression from alien European roe deer; and establishment of new pure Italian roe deer populations geographically separated from the introduced European roe deer populations (Focardi et al. 2009).

Consequences of hybridisation may include morphological and behavioural changes, and hybridisation could cause disruptions of locally adapted traits, threatening the viability of populations (Battisti et al. 2015, Biosa et al. 2015). However, hybrids possessing Siberian roe deer mtDNA may show better adaptation to severe winters, an important agent of roe deer mortality in Eastern Europe (Matosiuk et al. 2014b, Olano-Marin et al. 2014). Both hybrids within the genus *Capreolus* still have undefined legal status in Europe.

## **Cervus**

Introgression of red deer genes – of non-native or captive origin – into native populations is relatively frequent throughout Europe, as a consequence of translocations. Hybridisation (from rare to moderate) has been confirmed in different regions, where native red deer and introduced sika deer occur sympatrically (Appendix S1, Fig 1c). Conversely, introgression of wapiti genes into Irish and Scottish red deer populations is very low (Appendix S1, Fig 1c).

Translocations of red deer occurred already in the Neolithic period, representing one of the most significant

forms of human intervention and management practice for this species throughout Europe (Appendix S1). Particularly in Central Europe, it is uncertain if truly native red deer populations exist; as the species has substantial dispersal abilities, introduced animals and/or their offspring may have dispersed into other populations (Linnell & Zachos 2011). The available literature on red deer hybridisation (14 papers) shows variable levels of introgression after restocking, introduction or illegal translocation of different subspecies or phylogenetic lineages (Appendix S1). MtDNA and microsatellite loci have been widely used to study red deer genetic ‘pollution’, even at small geographic scales. However, Frantz et al. (2017) suggest that only large-scale microsatellite genotypic datasets can detect the presence of non-autochthonous red deer introgression into indigenous stocks.

Nonetheless, the management of subspecies and hybrids (all with undefined legal status) remains particularly challenging, owing to the ongoing discussion on red deer taxonomy. The genetic distinctiveness and low variability of Sardo-Corsican red deer *Cervus elaphus corsicanus*, Barbary red deer *Cervus elaphus barbarus* and Mesola red deer *Cervus elaphus italicus*, however, are well documented (Fernández-García et al. 2014, Zachos et al. 2014), highlighting the need to prevent hybridisation with non-autochthonous stock(s). Hybridisation between different deer species has substantial phenotypic consequences, which are likely to alter life-history traits and complicate management. One of the best examples is hybridisation between sika deer and red deer. Originally from Japan, the sika deer is strongly genetically differentiated from the red deer; they nevertheless hybridise, especially in some parts of the British Isles (McDevitt et al. 2009, Senn & Pemberton 2009, Senn et al. 2010, Smith et al. 2014), and extensive introgression has occurred, both in enclosures (Bartoš 2009) and in the wild (Senn & Pemberton 2009). Moreover, hybridisation between native red deer hinds and introduced sika deer stags in continental Europe was reported, using both mtDNA and microsatellite, in five regions of Poland, in the Kaliningrad District (Russia), in Lithuania (Biedrzycka et al. 2012), in the Czech Republic (Bartoš 2009), and in Austria (reviewed in Zachos & Hartl 2011). Hybridisation increases the body mass of both sika-like males and females, and increases incisor arcade breadth and jaw length of sika-like females (Senn et al. 2010). There is concern that introgression may not only compromise the genetic integrity of native red deer stocks, but also reduce the trophy value of red deer (sika deer antlers are much smaller than those of red deer). Where red and sika deer populations overlap, several management practises have been proposed (see Smith et al. 2018 for a critical overview). However, identification of hybrids in the field can be problematic even for experienced

personnel and improved training on this aspect is highly desirable (Smith et al. 2018).

Introductions of wapiti into English deer parks and the Scottish Highlands were common practice in the past, aiming to improve body mass and antler size of native red deer. However, hybridisation between the two species is rare (Pérez-Espona et al. 2011, 2013), and there is limited evidence of reduced reproductive success (Asher et al. 2005).

### **Rangifer**

In reindeer, hybridisation may occur between two wild subspecies, the mountain reindeer *Rangifer tarandus tarandus* and the forest reindeer, as well as between wild and domestic animals (Appendix S1, Fig 1f).

The only large remaining native population of reindeer in Norway received considerable gene introgression from domestic herds (Røed et al. 2011). Indeed, except for the forest reindeer in Finland, both wild and domestic reindeer in Fennoscandia belong to the same subspecies: *Rangifer tarandus tarandus*. The genetic data in Røed et al. (2008) illustrated a clear genetic distinction in both microsatellites and mtDNA between the domestic reindeer in eastern Finland and the endangered forest reindeer. In south-eastern Russia, introgression was detected with mtDNA markers between domestic and forest reindeer (Røed et al. 2008). Native wild reindeer in Scandinavia show two typical mtDNA lineages, while domestic reindeer carry two different lineages, indicative of a non-indigenous origin (Flagstad & Røed 2003, Røed et al. 2008, 2011). However, there is no information about the influence of hybridisation on reindeer populations and their life-history traits, and presently reindeer hybrids have undefined legal status.

## **DISCUSSION**

The literature showed the pervasiveness of hybridisation in the most common European ungulates, with 75 confirmed cases described in 89 papers. Potential biases should be considered: it is likely that mostly positive results, in consequence of targeted investigations, were published, whereas spatial information may be limited by different scientific interests and/or funding availability. Yet, this figure represents the state of the art knowledge of the scientific community. Overall, gene introgression can be observed between wild (sub)species (32/75 papers) or between the wild population and its domestic counterpart (44/75). In both cases, it is often related to human practices (56/75), as is often the case for other taxa where a domesticated or human-managed counterpart co-occurs (*cf.* Russo et al. 2018). Introgression from the domestic

counterparts is usually due to range overlap of wild and domestic populations, either intentional or accidental, whereas crossbreeding between wild (sub)species is generally related to introductions or translocations, often carried out for hunting purposes (Appendix S1).

### **Uncertainties in the taxonomic resolution**

It is worth noting that for some species, taxonomic classification is still a matter of debate. For example, it is unclear whether or not the living populations of *Capra pyrenaica* should be split into two subspecies: *Capra pyrenaica hispanica*, that occurs mainly in southeastern Spain, and *Capra pyrenaica victoriae*, in northwestern Spain (Pérez et al. 2002). Whereas a study based on mtDNA did not support this subdivision (Manceau et al. 1999), it has been suggested that 'single-locus analyses only show single gene trees that need not be in accordance with organism-level phylogeny' (Linnell & Zachos 2011), and that hemiplasy or recent hybridisation between these subspecies may have reduced potential differences between them. Pérez et al. (2002) also called for careful evaluation of the sources of translocated individuals of Spanish ibex. Thus, it seems important to acquire new data to help the decision-making process on the conservation of Spanish ibex populations (Linnell & Zachos 2011). However, a similar issue also stands for red deer subspecies, with few exceptions (*i.e.* Sardo-Corsican, Barbary, and Mesola red deer), and should be considered in conservation and management of the species. Additionally, it has been recently suggested that the identification of meaningful taxonomic units for conservation should not be based exclusively on the species definition (Zachos 2018).

### **Hybrid detection and consequences of introgression**

The methods used to investigate hybridisation vary greatly, and so does their success in identifying introgressed individuals. Researchers largely rely on genetic markers (73/89 papers), with mtDNA being the most widely used (45/73), followed by autosomal microsatellites (35/73) and, more recently, SNP (11/73; Appendix S1). The power of these methods to detect hybrids varies depending on the target species and on the number of generations since the admixture event. For example, mtDNA cannot resolve hybridisation between mouflon and European sheep breeds (Hiendleder et al. 1998, Tapio et al. 2006), but is the only marker that can detect Siberian roe deer introgression in the European population (Lorenzini et al. 2014, Matosiuk et al. 2014a, Markov et al. 2016a). Although morphological alterations have often been reported as consequences of

hybridisation, individual variation, health status, and age might complicate the interpretation of results. We thus recommend combining these data with genetic information for hybrid detection. Considering the different mutation rates and transmission patterns, we suggest using a combination of markers for hybrid detection, comparing autosomal fast-evolving markers with slow-evolving or with uniparentally inherited ones, as they might lead to different results (e.g. Frantz et al. 2013, Canu et al. 2016). This rule of thumb is not without exceptions though, for mtDNA is fundamental in the detection of red  $\times$  sika deer hybrids (Senn & Pemberton 2009), whereas large numbers of microsatellites are necessary to identify non-native red deer (Frantz et al. 2017). Additionally, aspects such as budget and research question need to be considered in marker selection.

Although hybridisation is not negative *per se*, it can have detrimental consequences if introgressed traits are maladaptive or can decrease survival rates in the wild, and so hybridisation may raise management concerns, especially when domestic animals or farmed wild animals are involved. With the exceptions of *Rangifer* and *Rupicapra*, where data are lacking on this aspect, there are reports of morphological and/or behavioural changes due to hybridisation (Appendix S1). Whereas improved disease resistance, an improved immune system (Grossen et al. 2014, Zemanová et al. 2015, Barbato et al. 2017), increased litter size, and increased growth rate (Frantz et al. 2013, Goedbloed et al. 2013, Fulgione et al. 2016) may be beneficial, maladaptation (Battisti et al. 2015, Canu et al. 2016), reduction in fitness-related traits (Stüwe & Nievergelt 1991), increased invasiveness (e.g. Goedbloed et al. 2013, Manunza et al. 2016), and enhanced chances of disease spread (e.g. Manunza et al. 2016) may have important negative consequences for management and population ecology. This issue might be particularly relevant for some species, such as the wild boar, that has recently been recognised as a potential agent for the introduction of African Swine Fever in disease-free countries of the European Union (Bosch et al. 2017). However, information on the genes involved and the potential impacts on the species' evolutionary potential is still patchy.

## Hybrid distribution and management

Throughout Europe, the evidence of hybridisation between ungulates varies greatly (Fig. 1). In some countries, it has never been reported (e.g. Portugal), whereas in others, multiple species show signs of introgression (e.g. UK and Poland). This review highlights the need for further investigation in specific areas, such as Corsica and parts of the Balkans, and for certain species, such

as chamois, to shed light on current anecdotal information. Management recommendations, provided in only 41/89 papers, are generally aimed at reducing hybridisation through the prevention of future events (27/41) and by the removal of hybrids (9/41). In some cases, negative effects may have outweighed the positive ones in introductions or reintroductions as a management tool for the recovery of ungulate populations.

Hybrids may become a socially relevant issue, especially if they are likely to carry anthropogenically or unintentionally selected traits (Russo et al. 2018). While the latter case may apply to wolf  $\times$  dog hybrids, for ungulates the biggest concerns may involve the uncontrolled diffusion of hybrids with high invasive potential and intentional crossbreeding for trophy hunting, which might trigger market distortions and represent a threat to biodiversity.

Given the uncertainty about the consequences of hybridisation, under the current management paradigm, three priorities should remain in conservation planning: 1) determine the genetic origin of possible source populations (*cf.* Russo et al. 2018); 2) protect native populations from the risks of crossbreeding with non-native ones, especially for species of social concern (*cf.* Russo et al. 2018); and 3) establish permanent monitoring (*cf.* Apollonio et al. 2014). We recommend the development of international databanks, as already created for certain species (e.g. carnivores and wild boar), with common criteria and protocols to support the implementation of goals (1) and (2) and to allow direct comparison of results across geographic areas. This last aspect was one of the challenges in the present work due to the different methodologies implemented and the lack of geographic details in many publications.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1.** References and information on hybridisation studies used in this review.