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Hunting as a source of alien species: a European review

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Abstract Hunting activities are responsible for the translocation and restocking of millions of animals throughout Europe, including the introduction of alien species. In a context of the growing use of game translocations and of increasing concern about the impact of biological invasions, our goal is to review the role of alien species introduced primarily for hunting purposes on the European scale. In particular, we explore: (1) the relative importance of game species in the context of alien species introductions; (2) the temporal evolution of the number of species introduced for hunting purposes; (3) the contribution of different taxa; (4) the pattern of introduced game species composition across countries (in terms of similarity), and (5) the underlying human demographic factors driving the diversity of introduced game species per country. According to our results, 24.3% of the mammals and 30.2% of the birds introduced into Europe during the last century were released primarily for hunting purposes, in total, 93 species (63 birds and 36 mammals), the most important taxa being Artiodactyls, Anseriformes and Galliformes. The species composition differed among countries, with a higher diversity of introduced game species in larger countries and in those with a higher human population density and proportion of hunters. This review stresses that hunting was a significant

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pathway for the introduction of invasive species into Europe in the last century. Since some of the game species introduced have had severe environmental impacts on many European regions, and introductions of non-native game species are still occurring, it is essential to improve regulations and increase public awareness regarding invasive game animals. This will help to preserve biodiversity and improve the sustainability of current hunting schemes in increasingly managed European ecosystems.

Keywords Alien species · Biological invasions · Game species · Hunting · Invasion pathways

Introduction

Invasive alien species (IAS) have been identified as one of the most important direct drivers of biodiversity loss, ecosystem degradation and ecosystem service changes (Pejchar and Mooney 2009; Pyšek and Richardson 2010). The threats posed by IAS have consequently been addressed through the development of many international policy instruments, guidelines and technical tools (Monaco et al. 2013). In this context, understanding the pathways of species introductions constitutes a key issue as regards managing and preventing further invasive events. The most common motivation for the introduction of plant and animal species into new areas has by far been the establishment of new food sources (Lambdon et al. 2008; Shimono and Konuma 2008). Other common introduction pathways related to human activities include the wild-bird trade (Carrete and Tella 2008), aquarium fish commerce and inland fisheries (Gertzen et al. 2008), maritime activity (López-Legentil et al. 2015), the commerce of species for aesthetic purposes (Mack and Lonsdale 2001) and horticulture, in addition to unintentional introductions (Hulme et al. 2008).

In Europe, hunting is a social and cultural activity in which millions of people are involved as both participants and beneficiaries, and it is undertaken on millions of hectares of land and wetland. In general, hunting is currently practiced for recreation and involves the harvest of game species and the management activities that are undertaken to enhance these harvests. In this context, wildlife is frequently introduced in order to create or improve hunting opportunities, especially when native game species have become scarce (Blackburn and Duncan 2001; Long 2003). Some of the most commonly used techniques in game management are the relocation of wildlife species for the purpose of introduction (attempts to establish a species outside its recorded distribution), re-introduction (attempts to establish a species in an area that was formerly part of its range, but from which it was extirpated or became extinct) or supplementation (when individuals are added to an existing population of conspecifics) (Griffith et al. 1989; Wolf et al. 1996; Fischer and Lindenmayer 2000). Animals are also commonly released from farms for intensive hunting without the aim of creating or reinforcing populations (e.g. pheasants, partridges or mallards; Champagnon et al. 2009; Caro et al. 2014). From this perspective, hunting is usually considered to be among the most common motivations for the introduction of alien species (Yiming et al. 2006; Genovesi et al. 2012). Although recreational fishing is also a frequent pathway of species introductions (Savini et al. 2010), we have focused on hunting because the ecological, economic and social settings associated with both activities are clearly different.

It is often difficult to distinguish species introduced merely for hunting purposes from those initially introduced for other purposes (e.g. for their fur or for aesthetic purposes) and that were later hunted. Nevertheless, this review focuses only on those species introduced primarily for hunting purposes, and species released for other reasons and that were later harvested as hunting resources have, therefore, been excluded. The transportation and introduction of species are only two of the stages in the invasion process, which also includes the stages of establishment and spread (Kolar and Lodge 2001, 2002; Blackburn et al. 2011). The aim of this review was not to carry out an in-depth assessment of the role of hunting in all of these stages. However, we did consider all the species released primarily for hunting purposes, regardless of the stage at which each species was in the invasion process.

There are numerous studies on biological invasions, including their ecological and economic impacts (Olson 2006; Pejchar and Mooney 2009; Keller et al. 2011; Barnes et al. 2014), along with the way in which

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non-native species have been introduced (Hulme 2009; Sanchirico et al. 2010; Hulme 2015). However, the role of hunting as a source of alien species has received relatively little attention in comparison with other aspects like those previously mentioned (Blackburn and Duncan 2001; Jeschke and Strayer 2006). It is, therefore, important to quantify the number of species that have been introduced primarily for hunting purposes, in addition to assessing their origin, distribution and consequences. This review is relevant because most wildlife and habitat management throughout Europe currently occurs in hunting areas. This sector must, therefore, actively participate in conservation policies whose intention is to protect biodiversity based on the premise of the sustainable use of resources, and particularly to reduce the impact of alien species. Our general objective was to identify cases of alien species that were introduced into Europe primarily for hunting purposes during the twentieth century. We restricted our review to the last century because historical sources of information do not always exist for a wide range of species (like those covered in this review), and if they do exist, are often not easily available (e.g. Delibes and Delibes-Mateos 2015). In addition, differences between Europe and other continents as regards biogeography, history, culture, traditions, ecology and hunting styles, among other things, prevented us from expanding our review to other continents. We defined five specific goals, which were: (1) to review the relative role of game species in the general context of alien species introductions; (2) to assess the temporal evolution of the number of species introduced for hunting purposes; (3) to assess the relative importance of different taxa; (4) to identify similarity patterns in the composition of introduced game species across countries, and (5) to assess the underlying human demographic factors that drive their diversity in Europe. The final goal was to provide conservation managers with further useful insights and to guide future research on the topic.

Methods

Data collection

We reviewed several lists of species that had been introduced into Europe, which we obtained from either scientific papers, books and technical reports (Jeschke and Strayer 2005; Wolfe et al. 2007; Genovesi et al. 2009, 2012; Nentwig et al. 2010; Kumschick et al. 2011; Baker et al. 2014), or official databases such as the Global Invasive Species Database ("GISD"), and Delivering Alien Invasive Species Inventories for Europe ("DAISIE"). Scientific papers that particularly addressed the introduction of species for hunting purposes were searched using three main web engines: Google Scholar™, ISI Web of Knowledge® and Scopus®. We used the following search terms: 'alien species' OR "exotic species" OR 'introduced species' AND 'hunting' OR 'game species' AND 'Europe'. The Canary Islands, Madeira and Cyprus were excluded from this study because they lie in different biogeographical zones to the rest of Europe (Beierkuhnlein 2006). The list of sources of information used for this review is shown in Table S1. As mentioned above, we identified those species that were, according to the bibliography consulted, primarily introduced for hunting purposes. We defined "introduced game species" as those introduced species that are deliberately sought and legally harvested from the wild, whether for sport, individual consumption, or commercial harvest (Jeschke and Strayer 2006). Game species that were introduced for other purposes (e.g. fur farms), but were later hunted, were not therefore considered in this review. We then combined all this information to obtain one unified database. The full list of species introduced primarily for hunting purposes is depicted in Table S2. This table also shows the stage of the invasion process at which each species is at the European level. According to "DAISIE" and "GISD", the stages of the invasion process are: "Extinct" (completely vanished), "Not Established" (have disappeared from natural environments, but are maintained on farms, parks…), "Established" (occur successfully in the natural environment) and "Invasive" (officially declared as invasive at a European level). We calculated the proportion of mammal and bird species found in each invasive stage.

The biogeographic region from which each species was derived was also identified (Palaearctic, Nearctic, Indo-Malaysia, Afrotropics, Neotropics, Australasia and Oceania), and those widespread species that occupy several regions were classified as either Holarctic, New World or multiregional (Abellán et al. 2015; see Fig. S1). Finally, we evaluated in which country or countries each species occurs (Fig. S2a).

Analyses

Similarities in the composition of alien game species throughout the countries studied were explored using cluster analyses. Hierarchical clustering analyses were performed using Ward's method, in which information is quantified as the sum of squared distances of each element with regard to the cluster centroid (Mirkin 2012). This was done by first calculating the mean vector for all variables and the multivariate centroid for each cluster and then calculating the squared Euclidean distances between each element and the centroid (mean vector) of all the clusters. Finally, the distances for all elements were combined. This clustering method was deemed the most appropriate, since it provides a flexible approach and does not assume any specific distributions of variables (Oteros et al. 2013). The clustering variable was the presence of different introduced game species in each country (Fig. S2a). After clustering the countries, we analysed each group in order to describe the distribution of species composition. The proportion of each species in each cluster as a function of the number of countries in which each species is present was then depicted as a matrix plot using R statistical software (R Core Team). This ranges between 1 (i.e. species present in all countries of one sub-cluster) and 0 (i.e. species absent in all countries of one sub-cluster; Fig. S2b).

In order to determine the underlying human demographic factors driving the diversity of introduced game species per country, two Generalised Linear Models (GzLM) were performed using the total number of introduced game species in each country (model 1) and the proportion of game species in relation to the total number of introduced species in each country (model 2) as response variables. Model 1 fitted a gamma distribution with a log link and model 2 fitted a binomial distribution with a log link, respectively. The variables country size, human population density, percentage of rural population, percentage of hunters and the gross domestic product (GPD) per capita were included as explanatory variables in both models (the data source is shown in Table S1). The selection of the most plausible models was carried out by comparing Akaike's information criterion (AIC) in the models (Burnham and Anderson 2002) following a backward procedure (Zuur et al. 2009). In particular, we compared the Akaike information criteria for small sample sizes (AICc value) in each candidate model and the best model (that with the lowest AICc). As a rule, a $\Delta i < 2$ suggests that the candidate model has a similar explanatory power to the a priori best model (Burnham and Anderson 2002). We therefore selected all the models in which $\Delta i < 2$ with regard to the best model. Statistical analyses were performed using IBM SPSS Statistics 20 software.

Results

Game species in the context of alien species introductions in Europe

According to our results, 24.3% of the mammals (34 out of 140 species) and 30.2% of the birds (59 out of 195 species) introduced into Europe during the last century were released primarily for hunting purposes. Of these 93 introduced species, 68 are currently exploited as small game species, and 25 as big game species. We specifically noticed that 34 mammal species (29%) and 59 bird species (34%) of the 117 mammals and 175 birds introduced into Europe according to the DAISE list were introduced primarily for hunting purposes. In the case of GISD, at least 17 (25%) out of the 68 alien mammal species and 8 (25.8%) out of the 31 alien birds species are hunted in their non-native range. In addition, we found that 33% of the mammals ($n = 3$) and 50% of the birds ($n = 14$) introduced into Europe according to Jeschke and Strayer (2005) were released for hunting purposes. Genovesi et al. (2009, 2012) showed that hunting was the origin of 24% ($n = 7$) of introductions of mammals into Europe. Another European review pointed out that food and game were the primary introduction pathways for birds (61 species, which represented 25.8% of total bird introductions) and mammals (31 species, which represented 20% of total mammal introductions) (Hulme et al. 2008). Overall, our results further show that 56.1% of the birds and 60.6% of the mammals introduced for hunting purposes are currently successfully established in the wild (Table S2).

Within Europe, the introduction of these species has not been spatially uniform, and countries such as France, Italy, Germany or UK stand out in this respect (20 or more introduced game species). On the contrary, other areas such as the Balkans or Baltic states have a much lower incidence of game species introductions (Fig. 1).

In addition, the origin of these species is also highly heterogeneous. The Palaearctic biogeographic region stands out as the source of the majority of introduced species (46%). It is followed by the Nearctic (16%), the Neotropics (9.6%), Indo-Malaysia (7.5%) and the Afrotropics (6.45%), with similar proportions in both taxa; the Neotropics were the exception as they were the origin of 11.8% for birds but no introduced game mammal came from this region (see Fig. S1).

Temporal evolution of the number of species released for hunting purposes in Europe

The introduction of new species as a game management tool has historically been a frequent practice in Europe (Long 1981). However, it has become much less common over the last few decades (Monaco et al. 2013). The aforementioned authors showed that the number of intentional introductions of new alien species for hunting purposes (specifically birds and mammals) has decreased by approximately 50% since the 1980s, reaching its lowest value after 2000. In addition, the rate of introduction events for hunting purposes in comparison with other motives has also decreased during the last few decades (Monaco et al. 2013; Fig. 2b).

Importance of each taxonomic group

Of the introduced game species (n = 93), 63.45% were birds and 36.55% were mammals. Species within other taxonomic groups have not been introduced for hunting in Europe. Most of the 34 introduced mammal species were ungulates (Fig. 2a). In this respect, at least 25 species out of 257 existing species of ungulates have been introduced into Europe to be exploited as game species. Another well-represented group among mammals was lagomorphs, with at least eight species introduced for game purposes, representing 23.5% of the introduced mammals (Fig. 2a).

Our results further show that the majority of introduced game bird species belong to three orders: Galliformes, Anseriformes, and Columbiformes, accounting for 44, 42 and 6.7% of the total number of introduced bird game species, respectively (Fig. 2a). The family that encompasses the most frequently introduced species within the order of Galliformes is *Phasianidae*: 26 alien species out of the 177 species of this family (14.7%) have been introduced into Europe for hunting purposes (Blackburn and Duncan 2001). Anseriformes is also a very important taxa with a total of 25 introduced species out of the 162 species within this group (15.4%) (Blackburn and Duncan 2001).

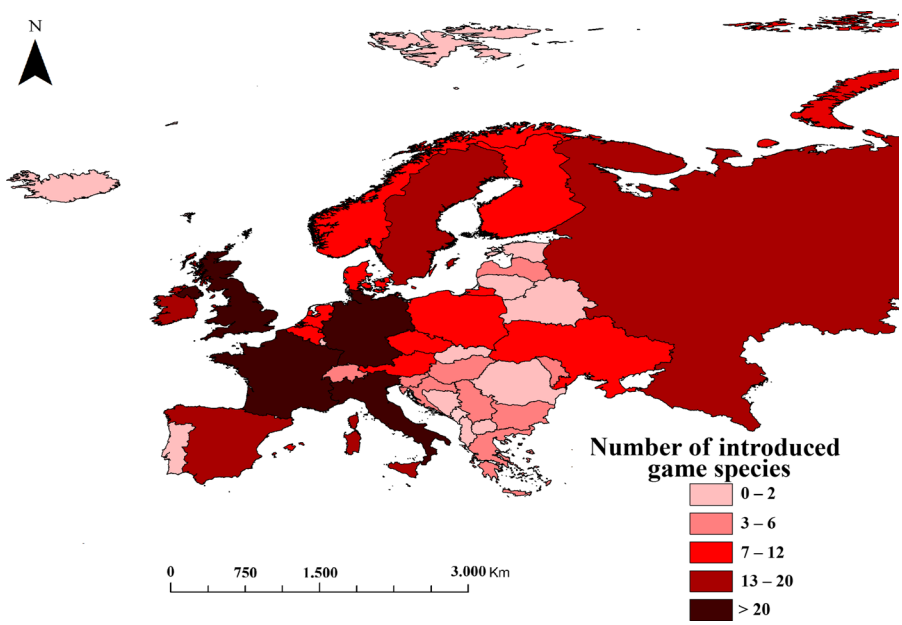


Fig. 1 Map depicting the number of species (mammals and birds) introduced into European countries for hunting purposes

Introduced species composition by country and underlying factors of their diversity

The clustering analyses carried out grouped different countries according to the similarity of the game species introduced into their territories (Fig. 3). Overall, three main clusters of countries and eight sub-clusters were found. Cluster 1 (C1) included a group of countries in Eastern Europe (e.g. Balkan countries) with a low number of introductions (mean = 3.4 species). A second cluster (C2) was composed of most of the Northern countries (Sweden, Norway, Finland) and several Central European countries (Austria, Poland, Czech Republic), together with Russia and other Eastern European countries (Poland and Ukraine), and was characterized by a medium number of species introduced for hunting (mean = 11.7 species). Cluster 3 (C3) was mainly composed of those countries with a larger number of introduced game species (mean = 29.2 species), and it included countries like the UK, Germany, France, Spain or Italy.

Fig. 3 Dendrogram showing three hierarchical clusters and ▶ eight sub-clusters of countries grouped according to the similarity of the composition of game species introduced into their territories

Figure 4 represents the distribution pattern of different taxonomic groups within each sub-cluster. Ungulates, Lagomorphs, Galliformes and Anseriformes were present in all the sub-clusters, whereas Columbiformes were present in all the sub-clusters with the exception of SC1. However, the proportion of each taxonomic group varied between sub-clusters. For instance, the most important taxon in sub-cluster SC1 was Galliformes, while ungulates stood out in sub-clusters SC2, SC3 and SC4, and Anseriformes in sub-clusters SC6 and SC8. In sub-cluster SC5, SC7 and SC8 Ungulates, Anseriformes and Galliformes were represented in similar proportions.

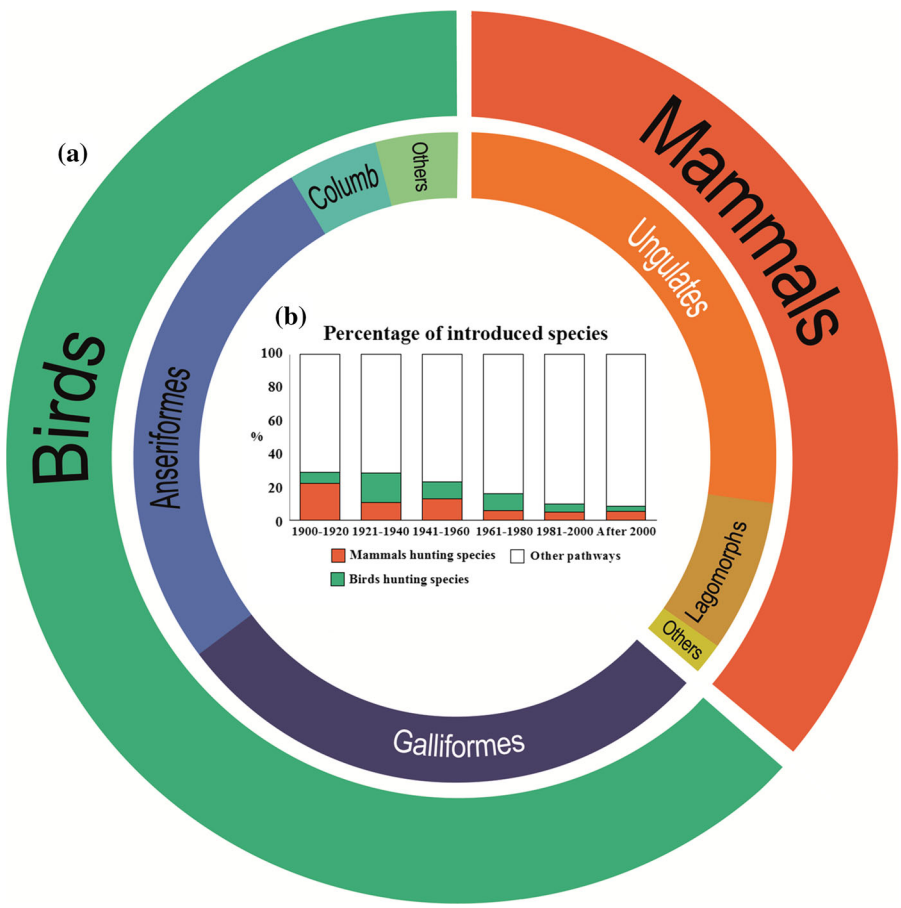
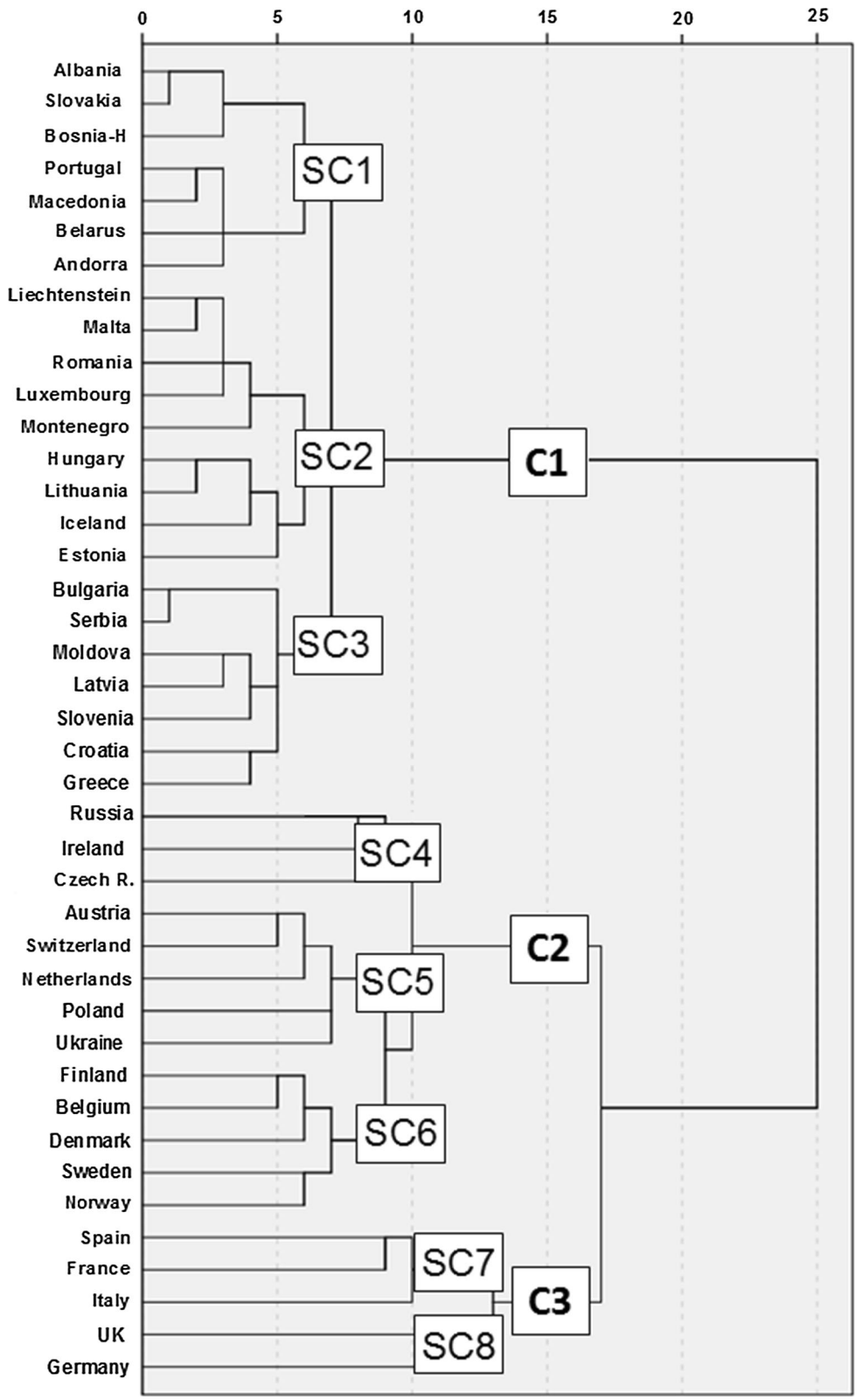


Fig. 2 **a** Proportion of species of different taxonomic groups within birds and mammals that were, according to our review, introduced into Europe during the twentieth century for hunting purposes. Columb. refers to Columbiformes; **b** Trend of the percentage of introductions of mammals and birds for hunting purposes and other pathways of introduction. Change over time is shown in 20 year-periods. Information adapted from Monaco et al. (2013) (original data from DAISIE European Invasive Alien Species Gateway; http://www.europe-aliens.org)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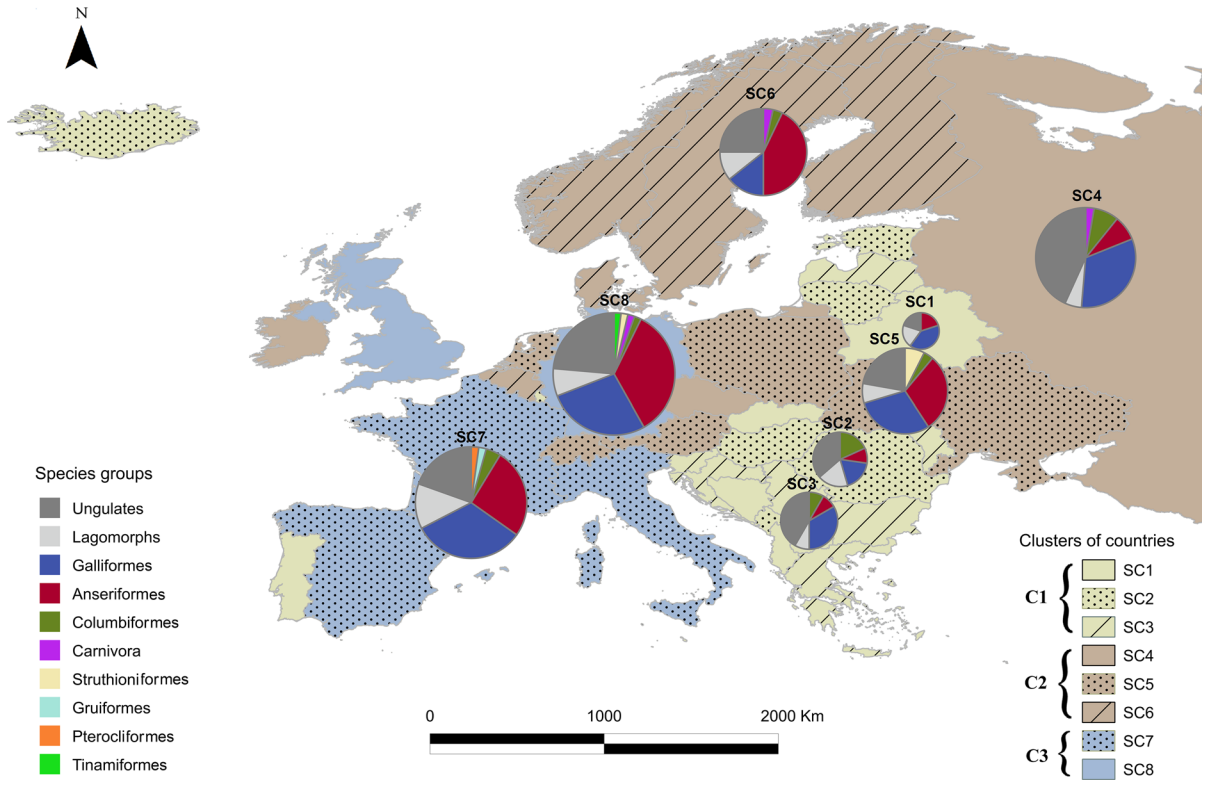

Fig. 4 Map representing the clusters and sub-clusters of grouped countries, showing the frequency distribution of each taxonomic group within each sub-cluster. The size of the diagram is proportional to the number of species within each sub-cluster

Finally, candidate models assessing the effect of countries' characteristics on the total number of alien game species in each country and the proportion of game species with regard to the total number of introduced species in each country are shown in Table 1. The factors retained in the best models (model 1 and 2) are displayed in Table 2. The results show that the country's size, human population density and percentage of hunters were statistically and positively associated with the total number of introduced game species per country (model 1). Furthermore, the proportion of game species relative to the total number of introduced species was positively associated only with the percentage of hunters (model 2).

Discussion

Game species in the context of alien species introductions

Europe has historically been a hotspot of alien species, since several thousands of non-native species have been introduced and have subsequently become established (Vilà et al. 2009; Keller et al. 2011), including several game species, as our results demonstrate. According to our review, 24.3% of alien mammal and 30.2% of alien bird species were released primarily for hunting purposes, revealing that hunting has been a major motivation for the intentional introduction of species into Europe. Indeed, hunting was one of the main pathways by which non-native species were introduced into Europe during the twentieth century (Fig. 5). Although not all species that moved beyond their native range become established in invaded areas (Sala et al. 2000), the introduction of a high proportion of game species has been successful (56% in birds and 60% in mammals), possibly owing to the intensive effort made by humans to establish stable populations (Champagnon et al. 2012) in addition to their high reproductive rate (Thompson and King 1994).

Another point to consider is not only the number of species, but also the total number of individuals released. Although, unfortunately, this information is

Table 1 Candidate models assessing the effect of countries' characteristics on the total number of alien game species in each country (model 1) and the proportion of hunted species relative to the total number of introduced species in each country (model 2)

	k	AICc	ΔAICc	*wi*
Candidate models (model 1)				
Size + density + % of hunters + GDP	4	217.172	0	0.43
Size + density + % of hunters	3	217.329	0.157	0.40
Size + density + % of hunters + % of rural population	4	219.128	1.956	0.16
Candidate models (model 2)				
% of hunters +% of rural population	2	175.476	0	0.38
% of hunters	1	176.299	0.823	0.25
Size + % of hunters + % of rural population	3	176.797	1.321	0.2
Size + % of hunters	2	177.112	1.636	0.17

The number of model parameters (k), the Akaike information criteria for small sample sizes (AICc), the difference between each model and the best model (ΔAICc), and the Akaike weight (*wi*) are shown

Table 2 Best models explaining the number of alien game species in each country (model 1) and the proportion of introduced hunted species relative to the total number of introduced species in each country (model 2), respectively

Variable	Estimate ± SE	Wald	*p* value
Number of alien game species (model 1)			
Intercept	0.421 ± 0.23	3.241	0.07
Country size (Km^2)	**0.003 ± 0.0006**	**30.61**	**<0.001**
Population density (people per km^2)	**0.004 ± 0.001**	**13.96**	**<0.001**
% of hunters	**0.102 ± 0.053**	**3.69**	**0.05**
GDP per capita (€)	0.001 ± 0.007	2..93	0.085
Proportion of hunted species (model 2)			
Intercept	−0.82 ± 0.16	24.65	<0.001
% of hunters	0.093 ± 0.03	**7.66**	**<0.01**
% of rural population	−0.01 ± 0.005	2.8	0.09

Variables that were statistically significant in the models are highlighted in bold type

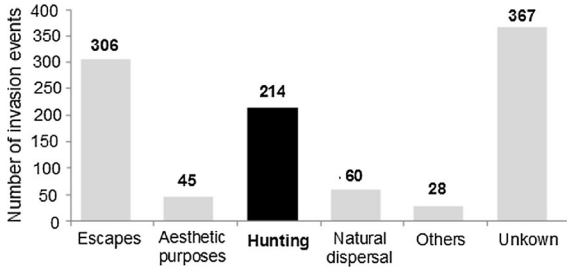

Fig. 5 Number of invasive terrestrial vertebrate events in Europe during the last century, associated with particular pathways of introduction (adapted from DAISIE European Invasive Alien Species Gateway; http://www.europe-aliens.org)

not available in most cases, it is known that massive releases of non-native small game species occur frequently in Europe (Champagnon et al. 2012). For example, it is estimated that 35 million pheasants (*Phasianus colchicus*) and 6.5 million red legged partridge (*Alectoris rufa*) are released annually in the UK (PACEC 2006), while 100–200,000 Japanese quails (*Coturnix japonica*) are released in northwest Spain and other Mediterranean countries such as Italy, Greece, France or Portugal (Puigcerver et al. 2007).

Underlying reasons for game species introductions

Although the eventual goal of hunting introductions is the exploitation of a game species to obtain economic or social benefits, our review stresses the existence of two main motivations behind the introduction of game species: diversifying the number of hunting species and superseding declining native species. Game

species have been introduced in order to diversify the spectrum of huntable species, particularly in the case of new species that are valued for their game trophy, which usually has an associated profit. For example, since ungulates are highly valued in trophy hunting (Coltman et al. 2003), several non-native species of deer (such as, *Cervus nippon or Cervus canadensis*), ibex (*Capra pyrenaica* and *Capra ibex*), bighorn sheep (*Ovis canadensis*), aoudad (*Ammotragus lervia*), mouflon (*Ovis orientalis*) and Himalayan thar (*Hemitragus jemlahicus*), among others, were introduced throughout Europe during the twentieth century. These introductions have generated a considerable income, directly through license fees and indirectly through the purchase of equipment and associated hunting services in general (Long 2003; Arnett and Southwick 2015).

Species substitution may also occur when the species that has been traditionally exploited has undergone a marked decline, and managers introduce a new alien species to supplement the harvest (Clavero 2016). For example, the chukar partridge (*Alectoris chukar*) has been introduced into Spain, France and Italy owing to the fact that the native red-legged partridge has declined, thus reducing opportunities for hunters (Barilani et al. 2007; Blanco-Aguiar et al. 2008). The brown hare (*Lepus europaeus*) has also been introduced to increase hunting opportunities in areas of Sweden and Russia in which mountain hares (*Lepus timidus*) have declined (Thulin 2003).

In addition, it is known that some species (or their hybrids) are more easily farm-reared than others, which may explain why the former have often been used for releasing purposes even when they may be alien species. For example, chukar partridges, along with their hybrids resulting from breeding with red-legged partridges, produce a higher number of chicks in captivity than do red-legged partridges, and are therefore usually released for shooting in Spain (Blanco-Aguiar et al. 2008), although they are not native.

Temporal patterns in game species releases

Although some species are still released in Europe for hunting purposes, the proportion of new species introductions attributed to this activity has declined over the past decades (Fig. 2b). There are several potential reasons for this pattern. First, it is obvious that many alien game species were introduced several decades ago (Grinnell 1925), which reduces the likelihood of introducing new species. Furthermore, the development of more restrictive international regulations in terms of invasive species may also have favoured the reduction in game species introductions. Finally, the increase in regulations for the transportation of wildlife, owing to the risk of disease transmission (e.g. African swine fever, foot and mouth disease, avian influenza or Newcastle disease), with the emergence of organisations such as the World Health Organisation, the World Organisation for Animal Health or the World Trade Organisation (Fèvre et al. 2006), may also have contributed to reducing animals' movements. Interestingly, the proportion of mammals *versus* birds introduced for game has also changed during the twentieth century, with a decline in the importance of the former (Fig. 2b).

Over the past decades, several wild ungulates, such as the red deer (*Cervus elaphus*), the roe deer (*Capreolus capreolus*) or the wild boar (*Sus scrofa*), have expanded their range and increased in abundance throughout Europe, leading to a huge increase in the number of big game animals harvested (Côté et al. 2004; Apollonio et al. 2010; Massei et al. 2015). However, an opposite pattern has occurred in the case of several small game species, many of which have declined dramatically; e.g. the European wild rabbit (*Oryctolagus cuniculus*) and the red-legged partridge in Spain (Blanco-Aguiar et al. 2004; Delibes-Mateos et al. 2009). This may have caused an increase in the release of these species (Champagnon et al. 2012) in addition to a shift from small game to big game species.

There are some other potential explanations for the recent decline in the number of game species introduced into Europe besides those discussed above. For example, previous bad experiences owing to the low efficiency of releases may have prevented some game managers from carrying out new introductions, as has been reported in the case of the chukar partridge (van Wieren 2012). The foundation of different agencies, such as the International Union for Nature Conservation (IUCN) or the International Union of Game Biologists (IUGB), may have played an important role as regards transferring information concerning the risks associated with the introduction of non-native species to hunters. This may have increased their awareness of this issue, probably preventing some of

them from using the release of non-native species as a game management tool (Nentwig 2007; Monaco et al. 2013). Although hunting is currently no longer a 'popular' pathway for the introduction of new alien game species (Fig. 2b), it continues to be an "open gateway" for alien species, and new introductions of alien game species are being reported in different countries. Examples of this are the recent introduction of the cotton-tail rabbit (*Sylvilagus floridanus*) into Italy, or that of the wild boar into Ireland and Sweden (Welander 2000; McDevitt et al. 2013).

Importance of each taxonomic group

Our review shows that the introduction of game species has been biased towards several wildlife orders, mainly Artiodactyls, Anseriformes and Galliformes. Ungulates stand out from the others (with 73.5% of introduced mammals species), probably because of their importance in trophy hunting (Spear and Chown 2009). Ungulate species have been introduced on the whole continent, and this is one of the most important groups everywhere (Fig. 4).

The Lagomorpha constituted the mammal order with the second most introduced game species. For instance, the cotton-tail rabbit was introduced into some European countries for hunting purposes, although wild populations apparently survived only in Italy (Rosin et al. 2008). Other examples are the New England cotton-tail (*Silvilagus transitionalis*) in Germany or the Cape hare (*Lepus capensis*) in Italy (Nentwig et al. 2010).

In the case of birds, Galliformes and Anseriformes were introduced primarily for hunting and ornamental purposes (Long 1981). Examples of Galliformes game species introduced outside their native range include the common pheasant, the red legged partridge and the chukar partridge, the barbary partridge (*Alectoris barbara*) and the rock partridge (*Alectoris graeca*) (Abellán et al. 2015; Barbanera et al. 2015).

The Anseriformes order is an important taxon in countries such as France, the UK, Germany, Sweden or Finland, where examples of species that were introduced for hunting purposes include the Canada goose *(Branta canadensis)* or the ruddy duck *(Oxyura jamaicensis)* (Long 1981; Baker et al. 2014). Another very important order is the Columbiformes, which consists of one single family: *Columbidae*. This family includes 313 species, of which 31 (10%) have been introduced throughout the world (Blackburn and Duncan 2001), and at least 4 of them were introduced into Europe for hunting purposes during the twentieth century.

Uneven distribution of introduced game species in Europe and associated factors

Overall, different countries with similar customs and bioclimatic and geographic ranges were grouped into clusters or sub-clusters on the basis of their similar compositions of introduced game species. Interestingly, those countries characterised by a long-standing hunting tradition, such as the UK, Germany, France, Spain and Italy, were grouped in the same cluster, with the highest number of introduced game species. In addition, our results show that the highest number of introduced game species appears in larger countries with a higher population density, which offer better opportunities for game releases (Cardador et al. 2016). Finally, countries with a higher proportion of hunters within the total population were associated with an increasing number of introduced game species and with the proportion of hunted species introduced relative to the total number of introduced species.

Concluding remarks and future directions

The deliberate introduction of non-native game species should be strongly discouraged by precautionary national and international biosecurity policies and practices. 'Prevention is better than cure', and proposed new introductions need to be thoroughly assessed (Mack et al. 2000; Jeschke and Strayer 2005; Keller et al. 2007). If new management programmes are not brought into force in Europe, it is inevitable that more alien game species will arrive, and that the impacts of these species on the economy, environment, and human and wildlife and livestock health will continue to grow (Keller and Perrings 2011; Blackburn et al. 2014; Schindler et al. 2015). Scientific studies have demonstrated that introduced game species have several negative impacts on those areas into which they have been introduced. These include predation (Barrios-Garcia and Ballari 2012), competition with native wildlife (Bartos et al. 2002; Kumschick et al. 2011; Bertolino et al. 2013), diseases and their related consequences (Kralova-Hromadova

et al. 2010), hybridisation (Barbanera et al. 2009, 2010; Baker et al. 2014), and habitat alteration (Kumschick et al. 2011). These ecological impacts may also have important economic effects, including damage to human infrastructures, human health risk, negative effects on human social life, the spread of disease to livestock, and agricultural damage (Nentwig et al. 2010; Keller et al. 2011; Simberloff et al. 2013; Schindler et al. 2015).

The objective of additional measures should be to boost declining native hunting species populations rather than releasing alien species. Hunting management strategies based on scientific evidence should therefore be carried out in order to ensure sufficient native harvest bags. Another key issue is how to manage certain established alien game species that are already an important hunting resource (e.g. White tailed-deer in Finland; Kekkonen et al. 2016), but cause negative impacts. From a strictly ecological point of view, they should be removed from their non-native range. However, hunters sometimes disagree with this option and it is, therefore, essential for all the stakeholders involved to reach agreements on these measures. Another interesting measure would be that of performing environmental education campaigns targeted towards hunters with the aim of providing information about the negative consequences of alien species. It would also be advisable for these campaigns to provide information regarding the low success of some game species restocking/introduction programmes and how to boost native game species.

The increasing pressure on global biodiversity as the result of invasive alien species, including those introduced for hunting purposes, as stressed in this review, requires considerable additional effort if this target is to be achieved, and strong emphasis should be placed on improving and harmonising legislation targeting biological invasions.

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References

Abellán P, Carrete M, Anadón JD, Cardador L, Tella JL (2015) Non-random patterns and temporal trends (1912–2012) in the transport, introduction and establishment of exotic birds in Spain and Portugal. Divers Distrib 22:263–273

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

Arnett EB, Southwick R (2015) Economic and social benefits of hunting in North America. Int J Environ Stud 72:1–12

Baker J, Harvey KJ, French K (2014) Threats from introduced birds to native birds. Emu 114:1–12

Barbanera F, Guerrini M, Khan AA, Panayides P, Hadjigerou P, Sokos C, Gombobaatar S, Samadi S, Khan BY, Tofanelli S, Pasoli G, Dini F (2009) Human-mediated introgression of exotic chukar (*Alectoris chukar*, Galliformes) genes from East Asia into native mediterranean partridges. Biol Invasions 11:333–348

Barbanera F, Oliver RW, Pergams ORW, Guerrini M, Forcina G, Panayides P, Dini F (2010) Genetic consequences of intensive management in game birds. Biol Conserv 143:1259–1268

Barbanera F, Forcina G, Cappello A, Guerrini M, van Grouw H, Aebischer NJ (2015) Introductions over introductions: the genomic adulteration of an early genetically valuable alien species in the United Kingdom. Biol Invasions 17:409–422

Barilani M, Bernard-Laurent A, Mucci N, Tabarroni C, Kark S, Garrido JAP, Randi E (2007) Hybridisation with introduced chukars (*Alectoris chukar*) threatens the gene pool integrity of native rock *(A. graeca*) and red-legged (*A. rufa*) partridge populations. Biol Conserv 137:57–69

Barnes MA, Deines AM, Gentile RM, Grieneisen LE, Ziska LH, Dukes JS (2014) Adapting to invasions in a changing world: invasive species as an economic resource. In: Lew Z, Duker J (eds) Invasive species and global climate change. CABI Publishing, Oxford

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol Invasions 14:2283–2300

Bartos L, Vankova D, Miller KV, Siler J (2002) Interspecific competition between white-tailed, fallow, red, and roe deer. J Wildl Manag 66:522–527

Beierkuhnlein C (2006) Biogeographie. Ulmer, Stuttgart

Bertolino S, di Montezemolo NC, Perrone A (2013) Habitat use of coexisting introduced eastern cottontail and native European hare. Mamm Biol 78:235–240

Blackburn TM, Duncan RP (2001) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. J Biogeogr 28:927–939

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugala A, Nentwing W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM,

Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12:e1001850

Blanco-Aguiar JA, Virgós E, Villafuerte R (2004) Perdiz roja (*Alectoris rufa*). In: Madroño A, González C, Atienza JC (eds) Libro Rojo de las Aves de España. Dirección General para la Biodiversidad-SEO/BirdLife, Madrid, pp 182–185

Blanco-Aguiar JA, González-Jara P, Ferrero ME, Sánchez-Barbudo I, Virgós E, Villafuerte R, Dávila JA (2008) Assessment of restocking contributions to anthropogenic hybridization: the case of the Iberian red-legged partridge. Anim Conserv 11:535–545

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Cardador L, Carrete M, Gallardo B, Tella JL (2016) Combining trade data and niche modelling improves predictions of the origin and distribution of non-native European populations of a globally invasive species. J Biogeogr. doi:10.1111/jbi.12694

Caro J, Delibes-Mateos M, Vicente J, Arroyo B (2014) A quantitative assessment of the release of farm-reared red-legged partridges (*Alectoris rufa*) for shooting in central Spain. Eur J Wildl Res 60:919–926

Carrete M, Tella J (2008) Wild-bird trade and exotic invasions: a new link of conservation concern? Front Ecol Environ 6:207–211

Champagnon J, Guillemain M, Gauthier-Clerc M, Lebreton JD, Elmberg J (2009) Consequences of massive bird releases for hunting purposes: Mallard *Anas platyrhynchos* in the Camargue, southern France. Wildfowl 2:192–201

Champagnon J, Elmberg Guillemain M, Gauthier-Clerc M, Lebreton JD (2012) Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. J Nat Conserv 20:231–241

Clavero M (2016) Species substitutions driven by anthropogenic positive feedbacks: Spanish crayfish species as a case study. Biol Conserv 193:80–85

Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M (2003) Undesirable evolutionary consequences of trophy hunting. Nature 42:655–658

Convention on Biological Diversity (2014) Pathways of introduction of invasive species, their prioritization and management. https://www.cbd.int/sp

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). https://www.cites.org/eng/disc/text.php

Côté SD, Rooney TP, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Annu Revi Ecol Evol Syst 35:113–147

Delibes R, Delibes-Mateos M (2015) Linking historical ecology and invasion biology: some lessons from European rabbit introductions into the new world before the nineteenth century. Biol Invasions 17:2505–2515

Delibes-Mateos M, Farfán M, Olivero J, Márquez A, Vargas J (2009) Long-term changes in game species over a long period of transformation in the Iberian Mediterranean landscape. Environ Manag 43:1256–1268

Delivering Alien Invasive Species Inventories for Europe (DAISIE). Retrieved from http://www.europe-aliens.org/. Accessed on June 2015

Fèvre EM, Bronsvoort BMC, Hamilton KA, Cleaveland S (2006) Animal movements and the spread of infectious diseases. Trends Microbiol 14:125–131

Fischer J, Lindenmayer DB (2000) An assessment of the published results of animal relocations. Biol Conserv 96:1–11

Genovesi P, Bacher S, Kobelt M, Pascal M, Scalera R (eds) (2009) Alien mammals of Europe. In: Handbook of alien species in Europe. Springer, Amsterdam, pp 119–128

Genovesi P, Carnevali L, Alonzi A, Scalera R (2012) Alien mammals in Europe: updated numbers and trends, and assessment of the effects on biodiversity. Integr Zool 7:247–253

Gertzen E, Familiar O, Leung B (2008) Quantifying invasion pathways: fish introductions from the aquarium trade. Can J Fish Aquat Sci 65:1265–1273

Global Invasive Species Database (GISD). Retrieved from http://www.issg.org/database/welcome/. Accessed on June 2015

Griffith B, Scott JM, Carpenter JW, Reed C (1989) Translocation as a species conservation tool: status and strategy. Science 245:477–480

Grinnell J (1925) Risks incurred in the introduction of alien game birds. Science 61:621–623

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Hulme PE (2015) Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. J Appl Ecol 52:1418–1424

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J Appl Ecol 45:403–414

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. Proc Natl Acad Sci USA 102:7198–7202

Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. Glob Chang Biol 12:1608–1619

Kekkonen J, Wikström M, Ala-Ajos I, Lappalainen V, Brommer JE (2016) Growth and age structure in an introduced and hunted cervid population: white-tailed deer in Finland. Ann Zool Fenn 53:69–80

Keller RP, Perrings C (2011) International policy options for reducing the environmental impacts of invasive species. Bioscience 61:1005–1012

Keller RP, Drake JM, Lodge DM (2007) Fecundity as a basis for risk assessment of non indigenous freshwater molluscs. Conserv Biol 21:191–200

Keller RP, Geist J, Jeschke JM, Kühn I (2011) Invasive species in Europe: ecology, status, and policy. Environ Sci Eur 23:1–17

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236

Kralova-Hromadova I, Bazsalovicsová E, Štefka J, Špakulová M, Vávrová S, Szemes T, Tkach V, Trudgett A, Pybus M (2010) Multiple origins of European populations of the giant liver fluke Fascioloides magna (Trematoda: Fasciolidae), a liver parasite of ruminants. Intern J Parasitol 41:373–383

Kumschick S, Alba C, Hufbauer RA, Nentwig W (2011) Weak or strong invaders? A comparison of impact between the native and invaded ranges of mammals and birds alien to Europe. Divers Distrib 17:663–672

Lambdon PW, Lloret F, Hulme PE (2008) How do introduction characteristics influence the invasion success of Mediterranean alien plants? Perspect Plant Ecol Evol Syst 10:143–159

Long JL (1981) Introduced birds of the world: the worldwide history, distribution and influence of birds introduced to new environments. Universe Books, New York

Long JL (2003) Introduced mammals of the world: their history, distribution and influence. CABI Publishing, Oxford

López-Legentil S, Legentil M, Erwin P, Turon X (2015) Harbor networks as introduction gateways: contrasting distribution patterns of native and introduced ascidians. Biol Invasions 17:1623–1638

Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for current introductions of species for aesthetic purposes present the largest single challenge for predicting which plant immigrants will become future pests. Bioscience 51:95–102

Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Massei G, Kindberg J, Licoppe A, Gačić D, Šprem N, Kamler J, Baubet E, Hohmann U, Monaco A, Ozoliņš J, Cellina S, Podgórski T, Fonseca C, Markov N, Pokorny B, Rosell C, Náhlik A (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest Manag Sci 71:492–500

McDevitt AD, Carden RF, Coscia I, Frantz AC (2013) Are wild boars roaming Ireland once more? Eur J Wildl Res 59:761–764

Mirkin B (2012) Clustering: a data recovery approach. CRC Press, Boca Raton

Monaco MA, Genovesi MP, Middleton A (2013) European code of conduct on hunting and IAS. In: Convention on the conservation of European wildlife and natural habitats. 33rd meeting Strasbourg, 3–6 December 2013

Nentwig W (2007) Pathways in animal invasions. In: Nentwig W (ed) Biological invasions. Springer, Berlin, pp 11–27

Nentwig W, Kühnel E, Bacher S (2010) A generic impact-scoring system applied to alien mammals in Europe. Conserv Biol 24:302–311

Olson LJ (2006) The economics of terrestrial invasive species: a review of the literature. Agric Resour Econ Rev 35:178–194

Oteros J, García-Mozo H, Hervás-Martínez C, Galán C (2013) Year clustering analysis for modelling olive flowering phenology. Int J Biometeorol 57:545–555

PACEC (2006) The economic and environmental impact of sporting shooting. http://www.shootingfacts.co.uk/. Accessed 28 April 2014

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends Ecol Evol 24:497–504

Puigcerver M, Vinyoles D, Rodríguez-Teijeiro JD (2007) Does restocking with Japanese quail or hybrids affect native populations of common quail *Coturnix coturnix*? Biol Conserv 136:628–635

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annu Rev Environ Resour 35:25–55

Rosin A, Gilio N, Meriggi A (2008) Introduced lagomorphs as a threat to "native" lagomorphs: the case of the Eastern cottontail (*Sylvilagus floridanus*) in Northern Italy. In: Alves P, Ferrand N, Hackländer K (eds) Lagomorph biology. Springer, Berlin, pp 153–164

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Sanchirico JN, Albers HJ, Fischer C, Coleman C (2010) Spatial management of invasive species: pathways and policy options. Environ Resour Econ 45:517–535

Savini D, Occhipinti-Ambrogi A, Marchini A, Tricarico E, Gherardi F, Olenin S, Gollasch S (2010) The top 27 animal alien species introduced into Europe for aquaculture and related activities. J Appl Ichthyol 26:1–7

Schindler S, Staska B, Adam M, Rabitsch W, Essl F (2015) Alien species and public health impacts in Europe: a literature review. NeoBiota 27:1–23

Shimono Y, Konuma A (2008) Effects of human-mediated processes on weed species composition in internationally traded grain commodities. Weed Res 48:10–18

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Spear D, Chown SL (2009) The extent and impacts of ungulate translocations: South Africa in a global context. Biol Conserv 142:353–363

Thompson HV, King CM (1994) The European rabbit: the history of a successful colonizer. Oxford University Press, Oxford

Thulin CG (2003) The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? Mamm Rev 33:29–42

van Wieren SE (2012) Reintroductions: learning from successes and failures. In: Van Andel J, Aronson J (eds) Restoration ecology: the new frontier. Wiley, Hoboken, pp 87–100

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Hulme PE (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front Ecol Environ 8:135–144

Welander J (2000) Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. J Zool 252:263–271

Wolf CM, Griffith B, Reed C, Temple SA (1996) Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv Biol 10:1142–1154

Wolfe DH, Patten MA, Shochat E, Pruett CL, Sherrod SK (2007) Causes and patterns of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management. Wildl Biol 13:95–104

Yiming L, Zhengjun W, Duncan RP (2006) Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighbouring mainland China. Oecologia 148:129–136

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York