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REVIEW

The roles of leporid species that have been translocated: a review of their ecosystem effects as native and exotic species

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ABSTRACT

1. Historically, humans have translocated some species of Leporidae (order Lagomorpha) around the world as an introduced food source and as game species. This family is now cosmopolitan and occupies areas where it did not previously exist. With the exception of European rabbits *Oryctolagus cuniculus*, evidence of the effects of these introduced species is scattered and in many cases anecdotal, though they share many biological traits with *Oryctolagus cuniculus*, one of the most harmful invasive species worldwide.
2. We review available studies on the 12 leporid species that have been introduced by humans to areas beyond their native ranges. Our aim is to describe and compare the species' ecological roles in their native geographic ranges and in their exotic ranges. We review the species' effects on the ecosystem at different levels of the trophic chain. We also evaluate the consequences of introductions for animal and human health, and their economic consequences, and we consider control measures.
3. In their native ranges, the 12 leporids are known to provide resources for other species, act as seed dispersers and ecosystem engineers, function as primary prey items for several predator species, and have many other functions. The effects of the leporids in their exotic geographic ranges are also conspicuous, and in many cases strongly negative, due to competition with native fauna and the facilitation of the presence of other invaders. Nonetheless, they constitute a food resource for native and exotic predators. As game species for humans, their hunting may indirectly impact the ecosystems by increasing the amount of lead in the environment. Moreover, they may be carriers of zoonotic diseases.
4. Conservation biologists should carefully consider the contrasting effects of the introduced leporids species in the ecosystem before developing any management strategy including these species.

INTRODUCTION

The Leporidae constitutes the biggest family in the order Lagomorpha; it includes 62 species of small- to medium-sized mammals, the rabbits and hares (Ge et al. 2013, Wilson et al. 2016). The original geographic range of this family before its members were translocated by humans was worldwide with the exception of Oceania, southern South America, and Antarctica (Alves et al. 2008). This geographic range reflected the family's palaeontological origin in Asia from which they began radiating and colonising North America, Europe, and Africa (Lopez-Martinez

Table 1. List of all 12 leporid species (order Lagomorpha) that have been introduced (translocated) by humans to date. We include their original (pre-translocation) geographic range, destination, and the year of first introduction

Species	Original geographic range	Translocated to	Year	References
Lepus americanus	USA, Canada	Within same country and nearby islands	1864	*
Lepus arcticus	Canada, Greenland	Within same country and nearby islands	1969	*
Lepus californicus	USA, Mexico	Within same country	1920	*
Lepus capensis	Africa, Middle East	Nearby island (Sardinia)	300 BC	†
Lepus corsicanus	Italy	Nearby island (Corsica)	1500	†
Lepus europaeus	Europe, Eastern Asia	Europe	300 BC	†
		Oceania	1851	*
		North America	1888	*
		South America	1886	*
Lepus granatensis	Iberian Peninsula	Nearby island (Mallorca)	1400 BC	†
Lepus nigricollis	Southern Asia	Indonesia, Mauritius, several islands in the Indian Ocean	1810	*
Lepus timidus	Asia, Western Europe	Denmark, Norway, Northern UK and nearby islands, Japan	1920	*
Lepus townsendii	USA, Canada	Within same country	1950	*
Oryctolagus cuniculus	Iberian Peninsula	Europe	1400 BC	*,†
		Several remote islands	~1700	*
		Oceania	1788	*
		South America	1756	*
Sylvilagus floridanus	North and Central America	Central Europe	1953	*

*Long 2003, †Masseti & De Marinis 2008.

2008, Ge et al. 2013). The family became cosmopolitan due to the introduction of several species, both in continental areas and on islands (Duff & Lawson 2004). Twelve of the 62 species (20% of the family members) have been introduced; ten of these species belong to the genus *Lepus*, while the remaining two species are *Oryctolagus cuniculus* and *Sylvilagus floridanus* (Table 1; Flux et al. 1990, Long 2003). Unlike some other smaller mammals, whose introductions might be accidental or inadvertent (Atkinson 1985), these leporid species have been deliberately transported and introduced by humans, with the aim of establishing new foreign populations (Long 2003). The history of their introduction goes as far back as 1400 BC (Long 2003, Masseti & De Marinis 2008); however, the most intense period of translocation was four centuries ago (Flux & Fullagar 1992). In this period, travellers released rabbits and hares on remote islands as food resources, and acclimatisation societies released them in continental areas mainly as game species (Flux & Angermann 1990, Flux 1994, Jennings 2017).

The geographical extent of the introduction of each of the 12 leporid species is clearly different. While nine *Lepus* spp. were translocated within the same country or in islands close to their original (pre-translocation) geographic range (Table 1, Fig. 1), the remaining three were successfully introduced in foreign continents: the eastern cottontail *Sylvilagus floridanus* in Europe, the European hare *Lepus europaeus* in Oceania and America, and the European rabbit *Oryctolagus cuniculus* in Europe, Oceania, America, and on more than 800 islands (Fig 1; Wilson et al. 2016). *Lepus europaeus* and *Oryctolagus cuniculus* are the two most successful invaders (i.e. species that overcame every barrier after their introduction, with individuals dispersing and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence; Blackburn et al. 2011) among the leporids (Long 2003, Alves et al. 2008). In fact, *Oryctolagus cuniculus* is included on the '100 of the world's worst invasive alien species' list, and much scientific attention has been paid to this species as it has led to significant economic losses (Lowe et al. 2000, Pimentel et al. 2001).

Reproductive capacity and dispersal rates are two of the biological traits shared by these leporids which make them successful invaders. Their high reproduction rates may be their main strategy to cope with predation, which in some cases can cause juvenile mortality of up to 90% (Soriguer 1981, Chapman & Flux 1990). Most leporids have multiple litters per year with litter sizes varying from 1 to 11 individuals, and each female produces between 10 and 45 young per year (Flux 1965, von Holst et al. 2002, Wilson et al. 2016). Their dispersal rates after introduction are also remarkable. *Lepus europaeus* and *Oryctolagus cuniculus* advanced on average 10–20 km year^{-1} (Grigera & Rapoport 1983, Stodart & Parer 1988), but they reached up to 100 km year^{-1} in some areas, so that they are considered among the most rapid mammal colonisers ever recorded (Jarman 1986, Williams et al. 1995). They also inhabit a wide range of environments, colonising

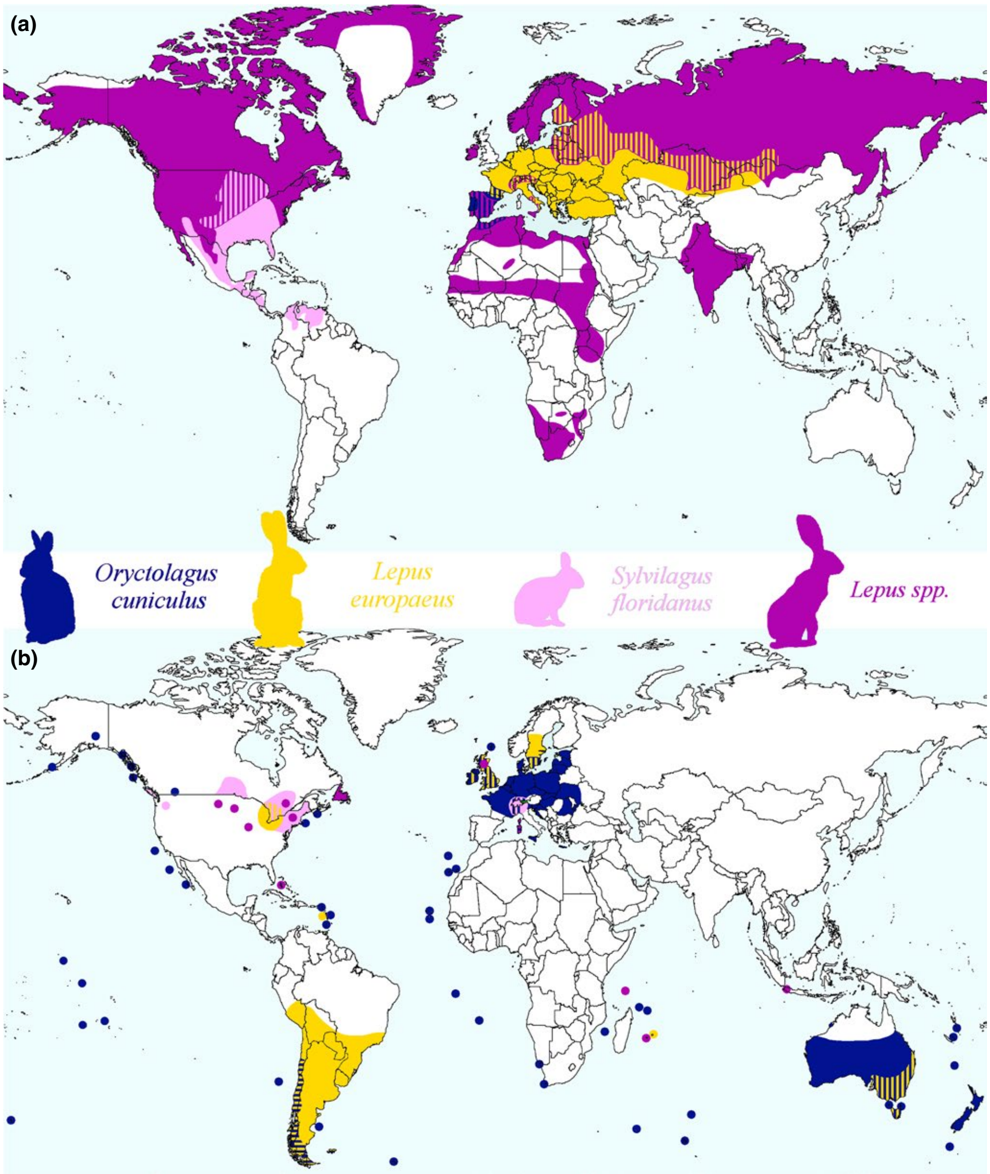

Fig. 1. Map of approximate a) original (pre-translocation) geographic range and b) current exotic range (adapted from Long 2003 and the International Union for Conservation of Nature: www.iucnredlist.org) for *Oryctolagus cuniculus*, *Lepus europaeus*, *Sylvilagus floridanus*, and the other nine species of *Lepus* that have been introduced worldwide. Striped areas contain both of the species indicated by the colour-coding.

forest areas, steppes, and semi-arid deserts, from sea level to 4000 m above sea level (Stodart & Parer 1988, Bonino et al. 2010).

Here, we review the main ecological roles of the 12 species of leporid that have been translocated in their native geographic ranges (Fig. 2) and contrast them with their roles in their exotic ranges (i.e. in the places where they have been introduced; Fig. 3). For this purpose, we performed a bibliographic search on those species that have been recorded as introduced (Long 2003, Table 1). We paid particular attention to the three more widely dispersed species (*Oryctolagus cuniculus, Lepus europaeus,* and *Sylvilagus floridanus*) and included information on the other species whenever data were available and relevant to the subject. We synthetised their ecological roles in both the native and exotic geographic ranges, including the effects of the species on: 1) the environment (nutrients and ecosystem roles), 2) primary producers (through their consumption and grazing effects), 3) other herbivores (species at the same trophic level: by either competing or facilitating), 4) their predators, and 5) other organisms (indirect effects). Finally, we review the potential impacts

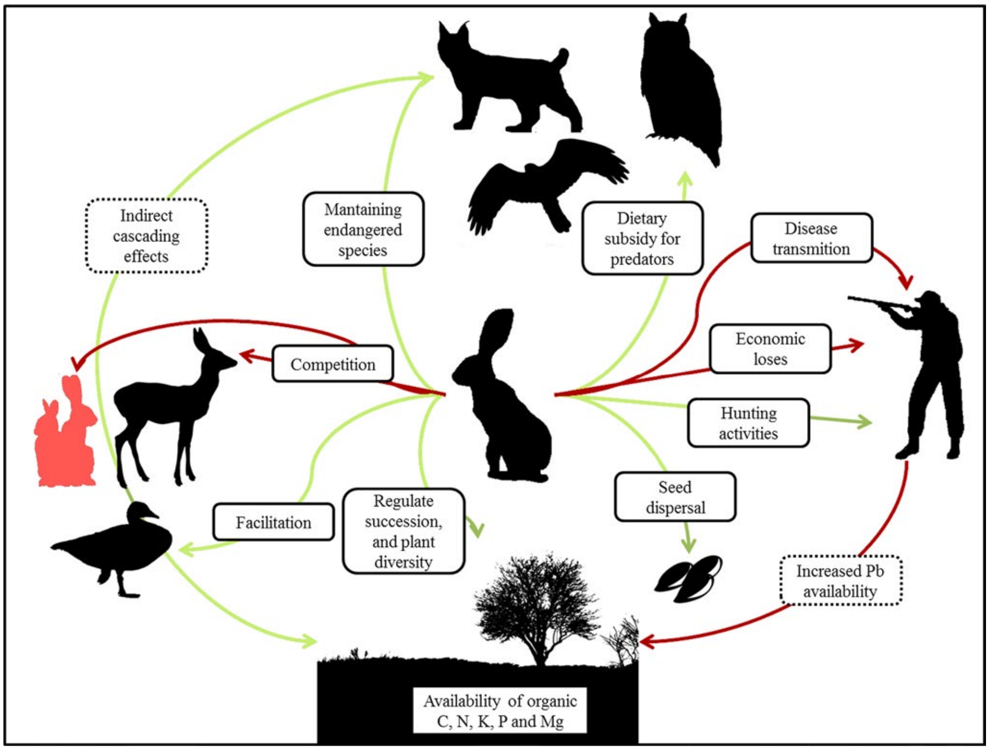

Fig. 2. Principal ecological roles and effects leporids have on biodiversity, the environment and humans in their native geographic ranges. Direct effects are shown in solid-lined boxes; indirect effects are in dotted-lined boxes. Simplified versions of interactions are shown as negative impacts (darker arrows) and positive impacts (lighter arrows). Lighter silhouettes represent the exotic species. Elements are carbon (C), nitrogen (N), potassium (K), phosphorous (P), magnesium (Mg), and lead (Pb).

of the species in their exotic ranges on animal and human health and the economic impacts of their introductions, and consider control measures. For details of the methodology used for the review and the numbers of articles found on each species and study subject, see Appendix S1.

EFFECTS ON THE ENVIRONMENT

Leporids can affect their surroundings by either chemically or physically changing their environment. First, they can significantly change nutrient availability and cycles as they are often abundant herbivores consuming large amounts of resources (De Mazancourt et al. 1998, Bakker et al. 2004). In its native range, *Oryctolagus cuniculus* is known to enhance local availability of organic compounds containing carbon, nitrogen, potassium, phosphorous, and magnesium (Willott et al. 2000). Some of the 12 leporid species produce physical changes in the environment when building refuges. *Lepus* spp. and *Sylvilagus floridanus* use earth depressions or simple burrows as thermal refuges and places to give birth, while *Oryctolagus cuniculus* construct complex warrens (Cowan & Bell 1986, Gibb 1990). These serve as seed pits and casual thermic and anti-predator refuges for other animals (Flux & Angermann 1990, Pike & Mitchell 2013). The complex underground structures constructed by *Oryctolagus cuniculus* are inhabited by many animals and plants adapted to them, and many communities (e.g. Mediterranean shrubs) depend on them to exist, making rabbits ecosystem engineers (Delibes-Mateos et al. 2007, Gálvez et al. 2008, Gálvez Bravo et al. 2009).

In their exotic range, chemical alterations produced by these leporids have proven to be somewhat detrimental. Introduced *Oryctolagus cuniculus* in the United Kingdom may enhance nitrogenated compounds but ultimately have negative long-term effects on nitrogen availability for plants (e.g. Olofsson et al. 2007). In Australian arid environments, a simple behavioural difference between native burrowing mammals and *Oryctolagus cuniculus* is sufficient to affect nutrient availability. There, native burrowing mammals feed and defecate near their burrows, which may enhance nutrient availability (James & Eldridge 2007). Individuals of *Oryctolagus cuniculus* feed on plants near their warrens while using more distant dunghills and urinating sites, so, they ultimately cause nutrient-poor soil patches in the landscape (Bakker et al. 2004, Eldridge & Koen 2008). In South America, behavioural differences

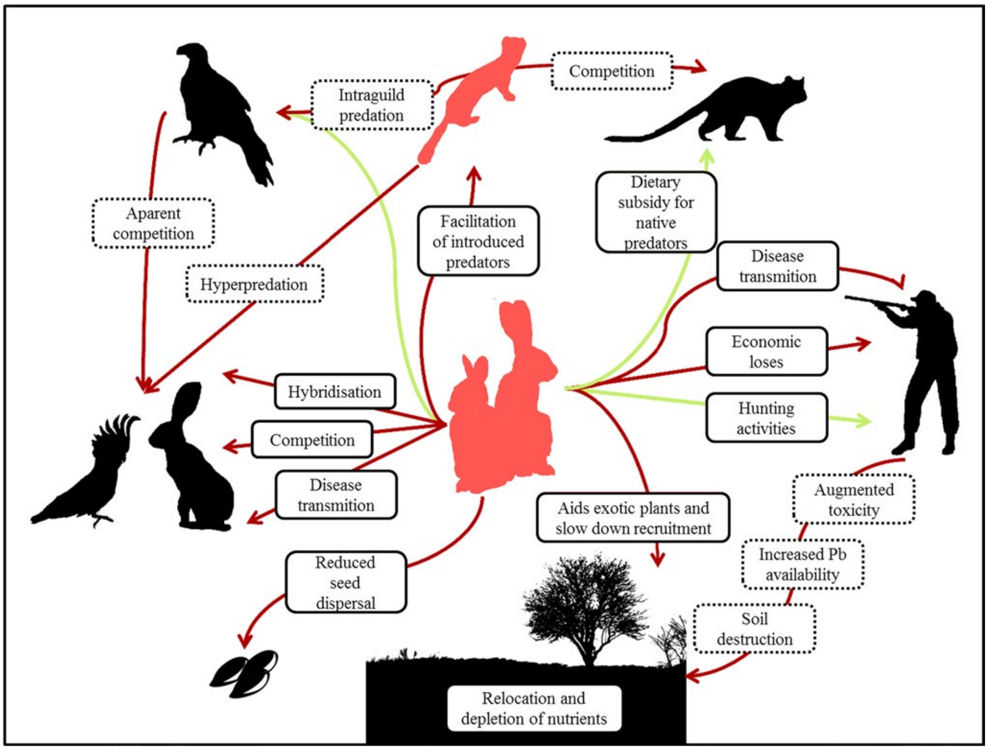

Fig. 3. Principal ecological roles and effects leporids have on biodiversity, the environment, and humans in their exotic geographic ranges. Direct effects are in solid-lined boxes; indirect effects are in dotted-lined boxes. Simplified versions of interactions are shown as negative impacts (darker arrows) and positive impacts (lighter arrows). Lighter silhouettes represent the exotic species. Lead is abbreviated as Pb.

between native herbivores and exotic *Lepus europaeus* could be a source of nutrient relocation: larger native herbivores (e.g. *Lama guanicoe*) choose to feed in meadows due to their productivity and openness, aiding in predator avoidance (Wurstten et al. 2014), and mainly defecate there. In contrast, *Lepus europaeus* also tends to feed in meadows but, given its pattern of movement and microhabitat selection (Galende & Raffaele 2008, Puig et al. 2015), tends to defecate under vegetation cover in the surrounding arid environment (Flux & Angermann 1990, Buono et al. 2010).

Physical alterations to the soil produced by leporid invaders are also conspicuous. In the Australian desert, soil removal rates caused by *Oryctolagus cuniculus* warrens may differ from those caused by burrowing native mammals, and thus above-warren removed bare soils may end up being less suitable for biological decomposition of organic matter (Whitford & Kay 1999, Eldridge & Myers 2001). While the simple burrows and earth depressions of *Sylvilagus floridanus* and *Lepus* spp. do not seem to have major impacts in the regions where they have been introduced, *Oryctolagus cuniculus* warrens are highly impactful. These warrens can be massive (a 5-year-old warren in Canberra, Australia, consisted of over 500 m in tunnels from which more than 10 m^3 of soil had been displaced; Parer et al. 1987) and may change the substrate's configuration, making it less stable. In some islands, *Phocarctos hookeri* pups can become trapped in collapsing warrens, which causes the morality of 10% of pups (Courchamp et al. 2003).

EFFECTS ON PRIMARY PRODUCERS

In their native ranges, leporids are widely known to affect plant community richness, composition, and succession (e.g. Gómez Sal et al. 1999, Kuijper & Bakker 2005, García-Fuentes et al. 2006, Delibes-Mateos et al. 2007, Kuijper et al. 2008). In some cases, their grazing effects are strong enough to slow down invasive grass species, and their browsing prevents recruitment of young trees, slowing forest restoration (D'Antonio 1993, Holl & Quiros-Nietzen 1999, Kuijper et al. 2004, Olnes et al. 2017). Through their soil disturbances and nutrient relocation, they are also recognised as plant diversity enhancers in harsh environments (Gálvez et al. 2008, Gálvez-Bravo et al. 2011). Finally, the ecological role of leporids as seed dispersers, either by endozoochory (seeds transported in the digestive tract and deposited with defecation) or epizoochory (seeds dispersed via being attached to the animals' body), is common and has been well documented, for *Lepus* spp., *Sylvilagus floridanus* (Flux & Angermann 1990, Schupp et al. 1997), and *Oryctolagus cuniculus* (Malo et al. 2000, Delibes-Mateos et al. 2008a).

In their exotic ranges, the effects produced by leporid herbivory pressure may affect native plants (Denyer et al. 2010). In heavily grazed fields in Europe, *Lepus europaeus* maintains plant communities by grazing, preventing the recovery of the native state (Holmgren 2002). Snowshoe hares *Lepus americanus*, introduced to Hay Island, Ontario, Canada, significantly reduced seedling recruitment and changed the morphology of the native trees (Wheelwright 2016). In Australia, *Oryctolagus cuniculus* prevents the recruitment of many *Acacia* trees and other shrubs (e.g. Cooke 2012). With their warrens, *Oryctolagus cuniculus* also provide a recruitment place for seeds in their pits; however, there is evidence that they do not do so as efficiently as native semi-fossorial mammals (James et al. 2009b). They are less efficient than native species as seed dispersers. For instance, in the UK, *Oryctolagus cuniculus* and *Lepus europaeus* faeces contain fewer seeds from fewer species than the faeces of other mammalian seed dispersers (Eycott et al. 2007, Panter & Dolman 2012). The facilitation of exotic plants is another possible interaction that occurs. For instance, in Chilean grasslands, *Oryctolagus cuniculus* has a predilection for feeding on native grasses, which facilitates exotic grass invasions (Meserve et al. 2011). Moreover, soil disturbance in warrens may favour the establishment of exotic plants (Holmgren et al. 2000, Eldridge & Simpson 2002), producing different ecosystem structuring (James & Eldridge 2007, James et al. 2009a).

EFFECTS ON OTHER HERBIVORES

In their native range, leporids commonly compete with several other mammal species, varying from similarly sized mammals such as *Cynomys ludovicianus* competing with *Sylvilagus floridanus* (Eads et al. 2016), to medium-sized mammals such as deer and wild sheep competing with *Lepus americanus*, *Lepus californicus,* and *Lepus europaeus* (Wilmshurst et al. 2006, Sangiuliano et al. 2016, Guo et al. 2017), and even larger mammals such as African ungulates competing with *Lepus capensis* (French 1985). However, leporids may also facilitate the presence of other herbivores. For instance, grazing by *Lepus europaeus* limits the growth of some plants and maintains short consumable grasses for *Branta bernicla* (Van der Wal et al. 2000).

In their exotic ranges, the leporid species have negative interactions with native herbivores as well. Not surprisingly, exotic leporid species tend to compete directly with their native counterparts from the area (e.g. Flux 2008, Rosin et al. 2008, Reid 2011). They also compete with many other herbivores in invaded regions where native leporids are not present. In Oceania, *Oryctolagus cuniculus* competes with many small native mammals such as plain rats *Pseudomys* spp. and *Notomys* spp., and with medium-sized mammals such as kangaroos, wallabies, and wombats *Macropus* spp. and *Vombatus ursinus* (Dawson & Ellis 1994, Cooke 1998, 2012). In South America, the interactions of *Lepus europaeus* with native herbivores are not well understood. However, dietary overlap exists with medium-sized rodents such as maras and viscachas *Dolichotis patagonum*, *Lagidium viscacia* and *Lagostomus maximus*, small deer *Mazama gouazoubira*, and more loosely with rheas *Rhea pennata* (Bonino et al. 1997, Puig et al. 2006, Kufner et al. 2008).

Aside from competition, exotic leporids may also affect their native counterpart populations by hybridisation. This interaction between different *Lepus* spp. is probably common throughout their native ranges. There is evidence suggesting that hybridisation was common during Pleistocene glaciations between *Lepus timidus*, *Lepus granatensis*, *Lepus europaeus,* and *Lepus castroviejo* (Melo-Ferreira et al. 2007, Alves et al. 2008), and it continues in the present. For instance, genetic evidence shows that *Lepus corsicanus* is suffering from the effects of hybridisation due to the introduction of *Lepus europaeus* and *Lepus granatensis*, which are deteriorating the gene pool of this Vulnerable species (Pietri et al. 2011). In Sweden, introduced *Lepus europaeus* hybridise with *Lepus timidus,* and, even when gene introgression appears to be low, behavioural differences between the males (where *Lepus europaeus* males guard females, preventing mating with their conspecifics) may cause the loss of species-specific litters (Thulin 2003, Jansson et al. 2007). Hybridisation in Ireland is particularly concerning, where the endemic subspecies *Lepus timidus hibernicus* has undergone long-term population declines. The presence of the introduced *Lepus europaeus*, through their interspecific interactions including hybridisation, is one of the causes of this decline (Reid 2011).

EFFECTS ON PREDATORS

In their native geographic ranges, one of the most well-known and strongest effects of leporids is their key role in predator–prey systems (Wilson et al. 2016). They are consumed by various predators. Large to medium-sized mammals such as pumas *Puma concolor*, Canadian lynx *Lynx lynx,* and coyotes *Canis latrans* consume *Lepus californicus* and *Lepus americanus*; smaller ones such as the fisher *Martes pennati* consume these species and also *Sylvilagus floridanus* (Ackerman et al. 1984, O'Donoghue et al. 1997, Bowman et al. 2006, Arias-Del Razo et al. 2011). Leporids are also important prey items for diurnal raptors, such as golden eagles *Aquila chrysaetos,* that consume *Lepus californicus* and *Sylvilagus floridanus*, and for nocturnal raptors such as great horned owls *Bubo* *virginianus*, that consume *Lepus americanus* (Collopy 1983, Donázar et al. 1989). They are even preyed upon by very unusual predators, from light-weight terrestrial birds, such as the greater roadrunner *Geococcyx californianus* (Anticona et al. 2013), to American red squirrels *Tamiasciurus hudsonicus* which scavenge on *Lepus americanus* and also hunt younglings (O'Donoghue 1994).

In the Iberian Peninsula, native *Oryctolagus cuniculus* are key food sources for predator species, since they are consumed by more than 30 carnivore species and are the primary prey item for many of them (Delibes & Hiraldo 1981, Moreno et al. 2004, Delibes-Mateos et al. 2007, Delibes-Mateos et al. 2008). During the Pleistocene glaciations, which isolated this peninsula from the rest of Europe, the occurrence of *Oryctolagus cuniculus* may have led to the evolution of two super-specialist species for which rabbits make up more than 90% of the diets: the Iberian lynx *Lynx pardinus* and the Spanish imperial eagle *Aquila adalberti* (Ferrer & Negro 2004). In North America, *Lepus americanus* is a very important food source for other predators. Its population cycle, with peaks of extreme abundances every 10 years, is known to affect predator populations directly and to have indirect effects on the whole community (e.g. Keith & Cary 1991, Boutin et al. 1995, O'Donoghue et al. 1997).

Introduced leporid species are consumed in great numbers by both native and exotic predators, which quickly became adapted to the new prey after translocation (Barbar et al. 2016). In Oceania, *Oryctolagus cuniculus* became the primary prey item of native predators that switched from diets previously composed mainly of birds and reptiles (Baker-Gabb 1984, Aumann 2001). This not only occurred with large eagles, similar to those that would consume leporids in their native ranges (e.g. the wedge-tailed eagle *Aquila audax*), but also with much smaller species that would not normally consume prey of that size (e.g. the brown falcon *Falco berigora*; Barbar et al. 2016). Similarly, native predators in South America consume large numbers of *Lepus europaeus*. They became primary prey for large predators such as *Puma concolor*, large to medium-sized raptors such as red-backed hawks *Buteo polyosoma*, and even for obligate scavengers such as the Andean condor *Vultur gryphus* (Vázquez 2002, Monserrat et al. 2005, Lambertucci et al. 2009, Elbroch & Wittmer 2013, Buenavista & Palomares 2017).

Introduced leporids may strongly affect their predators, both native and exotic. *Lepus europaeus* and *Oryctolagus cuniculus* now make up 90% of the diet of the black-chested buzzard-eagle *Geranoaetus melanoleucus* and *Aquila audax* (Olsen et al. 2010, Arriagada et al. 2011). Therefore, the feeding behaviour of these eagles is now similar to that of those super-specialists that consume leporids in their native range (e.g. *Aquila adalberti*; Ferrer & Negro 2004). The effects of *Oryctolagus cuniculus* on exotic predators are a concerning conservation issue. Red foxes *Vulpes vulpes*, domestic cats *Felis catus,* and stoats *Mustela erminea* are examples of the many predators that consume *Oryctolagus cuniculus* as their main prey in its exotic range (Gillies 1998, Glen et al. 2006, Cooke 2012, Doherty et al. 2015). The predators are some of the most harmful mammals: alongside *Oryctolagus cuniculus*, the predators are on the '100 of the world's worst invasive alien species' list (Lowe et al. 2000); leporids, particularly *Oryctolagus cuniculus*, may play a role in facilitating their invasion processes.

INDIRECT EFFECTS ON OTHER ORGANISMS

In its native geographic range, the partial recovery of *Oryctolagus cuniculus* after the outbreak of Rabbit Haemorrhagic Disease (RHD; Abrantes et al. 2012) was followed by the recovery of the Eurasian eagle-owl *Bubo bubo*. This bird preys heavily on *Oryctolagus cuniculus* and frequently attacks and kills diurnal raptors (Donázar & Ceballos 1989, Serrano 2000), leading to intraguild predation (Sergio & Hiraldo 2008). High abundances of *Oryctolagus cuniculus* may also have cascading effects by promoting the presence of top predators, such as the Iberian lynx, which regulate mesopredators, such as the Egyptian mongoose *Herpestes ichneumon*, either via intraguild predation or by consuming their main prey (Palomares et al. 1995).

In their exotic geographic ranges, leporids may also have some indirect effects, since their strong influence on predators may be similar to that described in their native range. In fact, in Oceania, *Oryctolagus cuniculus* supports populations of dingoes *Canis lupus dingo*, which act as large top predators and regulate populations of native predators like quolls (*Dasyurus* sp.). Rabbits also support other more recently introduced predators such as red foxes and domestic cats (Glen & Dickman 2005, Kennedy et al. 2012). In South America, the ways in which predators interact with each other in response to the presence of these new and very abundant food sources are not well understood. However, in some areas of this continent, functional responses to the presence of *Lepus europaeus* have been recorded for at least two large raptors (*Geranoaetus melanoleucus* and *Geranoaetus polyosoma*) that prey upon and eventually control mesopredators such as the chimango caracara *Milvago chimango* and the American kestrel *Falco sparverius* (Pavez et al. 1992, Hiraldo et al. 1995, Monserrat et al. 2005). Other evidence of these indirect effects in South America is provided by the observation that high numbers of *Lepus europaeus* are negatively correlated with high levels of predation of livestock by pumas and foxes. This could be related to the fact that hares, where they are present in sufficient numbers, may supply enough food for those predators (Novaro et al. 2000, Kissling et al. 2009).

Enhanced predator populations affect not only intraguild interactions, but also the interactions of predators with their prey. A new source of food for predators does not necessarily lead to less predation on their native prey; instead, augmented numbers of predators may place much more hunting pressure on native prey species (Courchamp et al. 2000, Norbury 2001, Oliver et al. 2009). Both exotic and native predators pose a very serious threat to native prey, and may lead to cases of hyperpredation and apparent competition (Courchamp et al. 2000, 2003, Lees & Bell 2008). Thus, even when leporids do not compete directly with other herbivores, they may be affecting them indirectly.

EFFECTS ON ECOSYSTEMS AND ON HUMAN AND ANIMAL HEALTH

Leporids may influence the health of ecosystems by accumulating pollutants or introducing zoonotic diseases. In their native geographic ranges, many studies have shown the capacity of leporids to accumulate different concentrations of heavy metals present in the environment (arsenic, cadmium, mercury, lead, and zinc) in their tissues and internal organs. These toxins are found in leporids in heavily polluted areas such as gas treatment plants, old lead or zinc mines, and even highways (Massányi et al. 2003, Kramárová et al. 2005, Špirić et al. 2012, Petrović et al. 2014, Tota et al. 2015, Amuno et al. 2016). Moreover, millions of leporids are hunted by humans each year. The ammunition used produces an increase in lead availability in the environment that affects several species. For instance, just in Spain, up to 6 million leporids are harvested annually (Delibes-Mateos et al. 2008), representing at least that amount of ammunition shot.

In their exotic geographic ranges, hunting pressure is similar or sometimes higher than in their native ranges, as leporids were introduced as game animals. In Argentina, 6 million individuals of *Lepus europaeus* are hunted per year, 2.5 million of which are exported as food to Europe (Bonino et al. 2010). During hunting activities, a high percentage of wounded animals are not retrieved and die shortly after the hunt in the field (Lambertucci et al. 2010, Pain et al. 2010). The use of lead ammunition and the current lack of regulation in many countries could be inadvertently increasing lead availability for many species in the environment, in particular for scavenger species (Watson et al. 2009, Lambertucci et al. 2010). In fact, hunting activities have been shown to cause accumulation of lead in the environment and in the predators and humans that consume the leporids (Fisher et al. 2006, Wiemeyer et al. 2017). Therefore, leporids may be an important source of this problem for carnivores and humans (which is particularly concerning for children and pregnant women; Watson et al. 2009); however, this relationship has been poorly evaluated in both native and exotic ranges.

The presence of leporid species can also present a human-wildlife health hazard, as they act as natural reservoirs of many zoonotic diseases including, among many others, tularaemia, Lyme borreoliosis, and Crimean-Congo haemorrhagic fever (Fontanesi et al. 2016). The roles of leporids as vectors or reservoirs in their exotic geographic ranges have been well documented. In Argentinean Patagonia, the prevalence of *Fasciola hepatica* in *Lepus europaeus* is sufficient to maintain a viable wild reservoir of this disease (Fuentes et al. 1997, Kleiman et al. 2004). *Sylvilagus floridanus* is an effective vector of the West Nile virus, a threat to several vertebrate species (Tiawsirisup et al. 2005), and carries dermatophyte fungi that affect humans (Gallo et al. 2005). In its exotic geographic range in Italy, *Sylvilagus floridanus* hosts many transmittable parasites and is an asymptomatic carrier of myxomatosis and pseudo-tuberculosis, directly affecting native leporids (Tizzani et al. 2002). Therefore, even when these roles are not exclusive to this group, all exotic leporid species could be a source of various threats to the ecosystem health, both for wild fauna (including species within their same family) and for humans.

ECONOMIC CONSEQUENCES OF INTRODUCTIONS

All introduced leporids are or were treated as pests in their native ranges, due to their history of crop and forestry damage (Long 2003). Not surprisingly, they have the same effects and are considered similarly in their exotic ranges. *Oryctolagus cuniculus* has caused incalculable economic losses since the 1800s, when most of its exotic populations originated. In the UK alone, crop damage caused by rabbits added up to US$ 1.2 billion in annual losses (Pimentel et al. 2001). In Australia, economic losses reached a similar figure when the effects on livestock production, environmental degradation, and private and public expenditures for control were included (Williams et al. 1995, Cooke 2012, Cooke et al. 2013). In all of these heavily impacted regions, the economic benefits of harvesting wild populations of *Oryctolagus cuniculus* are not even close to matching the economic losses in agricultural production and the environment (Williams et al. 1995).

Hunting activities can provide economic profit in the native ranges of leporids. In Spain alone, 1 million hunters take part each year, and hunting states cover around

70% of the land (Delibes-Mateos et al. 2009). Hunting produces an economic profit via the sale of meat, but also via business around the activity (around 4.5 billon US$ annually and 54000 jobs; Oficina Nacional de Caza 2017). *Oryctolagus cuniculus* is one of the main species hunted in Spain: on average, there are five rabbits per hunting bag, and over 4 million individuals are harvested annually (Virgós et al. 2007, Delibes-Mateos et al. 2008a). Strict hunting restrictions for *Oryctolagus cuniculus* are desirable, although rarely implemented, to ensure the conservation of the species and its sustainable long-term use (Angulo & Villafuerte 2004). Profit from hunting and reduced rabbit numbers due to uncontrolled hunting and disease outbreaks has resulted in translocations for restocking populations. However, uncontrolled restocking can have negative conservation outcomes, as it may affect the genetics of the native Iberian Peninsula populations (Delibes-Mateos et al. 2008b).

The economic losses caused by *Lepus* spp. and *Sylvilagus floridanus* are not as well documented as those caused by *Oryctolagus cuniculus*. Nevertheless, all 12 species are known to feed on crops and browse young coniferous tree plantations, thus generating economic loss (Long 2003). In their exotic ranges, *Lepus europaeus* have overlapping diets with livestock, so that they may compete with them and reduce per hectare productivity (Bonino 2006, Puig et al. 2006). For instance, current *Lepus europaeus* densities in northern Patagonia, reaching up to 250 individuals per km^2 (Barbar et al. 2018), reduce the carrying capacity of agricultural land by one sheep every two hectares (Bonino 1995, 1999). Other estimates are even worse, suggesting that, at this density, *Lepus europaeus* may consume nearly 15% of the palatable plants available for livestock in meadows (Amaya 1978).

CONTROL MEASURES

The measures to control exotic leporid species are almost invariably driven by the need to mitigate economic losses rather than an effort to protect biological diversity (but see: Thulin 2003, Reddiex et al. 2007, Reid 2011). This is clearly evident in South America, where *Lepus europaeus* control was limited to declaring it as a pest, while its actual effects were almost ignored (Grigera & Rapoport 1983). This species continues to increase in abundance and distribution in South America (Jaksic et al. 2002, Bonino et al. 2010).

The measures applied to control leporids, which include direct methods (hunting and poisoning) and diverse biological controls, have often been detrimental to the environment. Direct measures implemented as warren destruction in Australia ended up having negative long-term impacts on soil composition and structure (Mutze 1991, Eldridge & Myers 2001, McPhee & Butler 2010). Moreover, the use of baits to kill *Oryctolagus cuniculus* is surely changing the chemical burden of many compounds in the environment, but its effect is not actually being quantified (McLeod & Saunders 2013). Among the biological controls used is the introduction of voracious mustelid predators, which are now out of control and pose a serious threat to many native organisms (Alterio & Moller 1997, Gillies 1998). Diseases such as myxomatosis and viral haemorrhagic disease have been introduced for control, but though this method may be effective, there has not been a complete evaluation of its ultimate effect on the environment (Mutze et al. 2002, Saunders et al. 2010). In mid-2016 in Australia, a newly synthetised variant of the RHD virus (RHDV-K5) was released to eradicate the remaining individuals of *Oryctolagus cuniculus* (APVMA 2015). However, this could be dangerous, as the virus may accidentally reach wild populations of native *Oryctolagus cuniculus* on the Iberian Peninsula, as occurred with other strains of the same virus (Abrantes et al. 2012).

CONCLUSION

This review highlights the importance of the 12 introduced leporids, both in their native ranges (Fig. 2) and in their exotic ranges (Fig. 3). Leporid translocations appear to have been governed by poor judgement and irresponsible decisions (Baker 1986, Long 2003), and the effects produced have been mainly negative for all the regions in which the leporids were introduced. In the 1800s, there was little awareness about or care given to the possible effects of translocations, and in fact, leporids were intentionally introduced in many places, leading to a widespread distribution of these species globally (Table 1, Fig. 1). Nevertheless, and surprisingly, documented introductions continued until the early 1970s, when *Sylvilagus floridanus* was introduced in Europe, even after the catastrophic effects of *Oryctolagus cuniculus* were well-documented worldwide (Long 2003). These misplaced efforts to diversify game species only led to competition among species and the possible risk of disease dispersion, which has the potential to decimate entire populations (Tizzani et al. 2002, Rosin et al. 2008).

Several information gaps still exist and should be filled with further research. For instance, although leporids can reach high densities and consume huge amounts of resources, few studies have actually reported their effects on nutrient allocation and availability. Moreover, current competition interactions are not properly recorded, especially for *Lepus europaeus* in South America, even though the species is widely distributed there and interacts with many herbivore species. The effects of *Lepus europaeus* on predators have been better studied, but in general, the literature available describes their diets, but rarely goes further to relate this to population-level or community-level impacts. This is particularly concerning since exotic leporids may generate significant bottom-up effects, affecting predator and scavenger species and, therefore, generating cascading effects in the invaded ecosystems (Fig. 3). The effects on environmental health have also been overlooked and merit special attention. Given the number of individual leporids hunted each year either for sport or for human consumption, it is surprising that the effects of the leporids on lead deposition, chemical toxicity due to poisoning, and the possible zoonotic transmission of diseases (e.g. *Fasciola hepatica*) have not been studied in more detail.

In their native geographic ranges, the 12 leporid species are important elements of the ecological community that should be conserved (e.g. *Oryctolagus cuniculus* and *Lepus americanus*). Moreover, many of their populations suffer the consequences of poor management (e.g. Delibes-Mateos et al. 2011). However, in this review, we highlight the important roles of leporids in the environment and the various and severe impacts they may produce when they are introduced (Fig. 3). We call special attention to the need to study the effects of all introduced lagomorph species. Economic losses should not be the only driver of decisions about control and eradication, as leporids are now playing key ecological roles in the invaded ecosystems by interacting with many species at different trophic levels (Cooke 2012, Barbar et al. 2016). The exotic species should be removed in order to protect biodiversity (Parker et al. 1999, Myers et al. 2000, Simberloff 2009). However, this review shows the depth to which leporids are involved in the native and invaded ecosystems, such that any changes in their abundance and distribution will impact the entire ecosystem. Conservation biologists should be aware of all of these direct and indirect effects in order to plan adequate conservation actions.

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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. Bibliographic search methodology and number of studies found for each of the 12 species of introduced lagomorphs using as keywords each of the scientific names combined with (AND connector) the keyword on the first row.