Occupancy, abundance, potential dislribution and spatial competitíon of the critically endangered European mink (*Mustela lutreola*) and the invasive non-native American mink (*Neovison vison*) in the Iberian Peninsula

Giulla Santulli Sanzo

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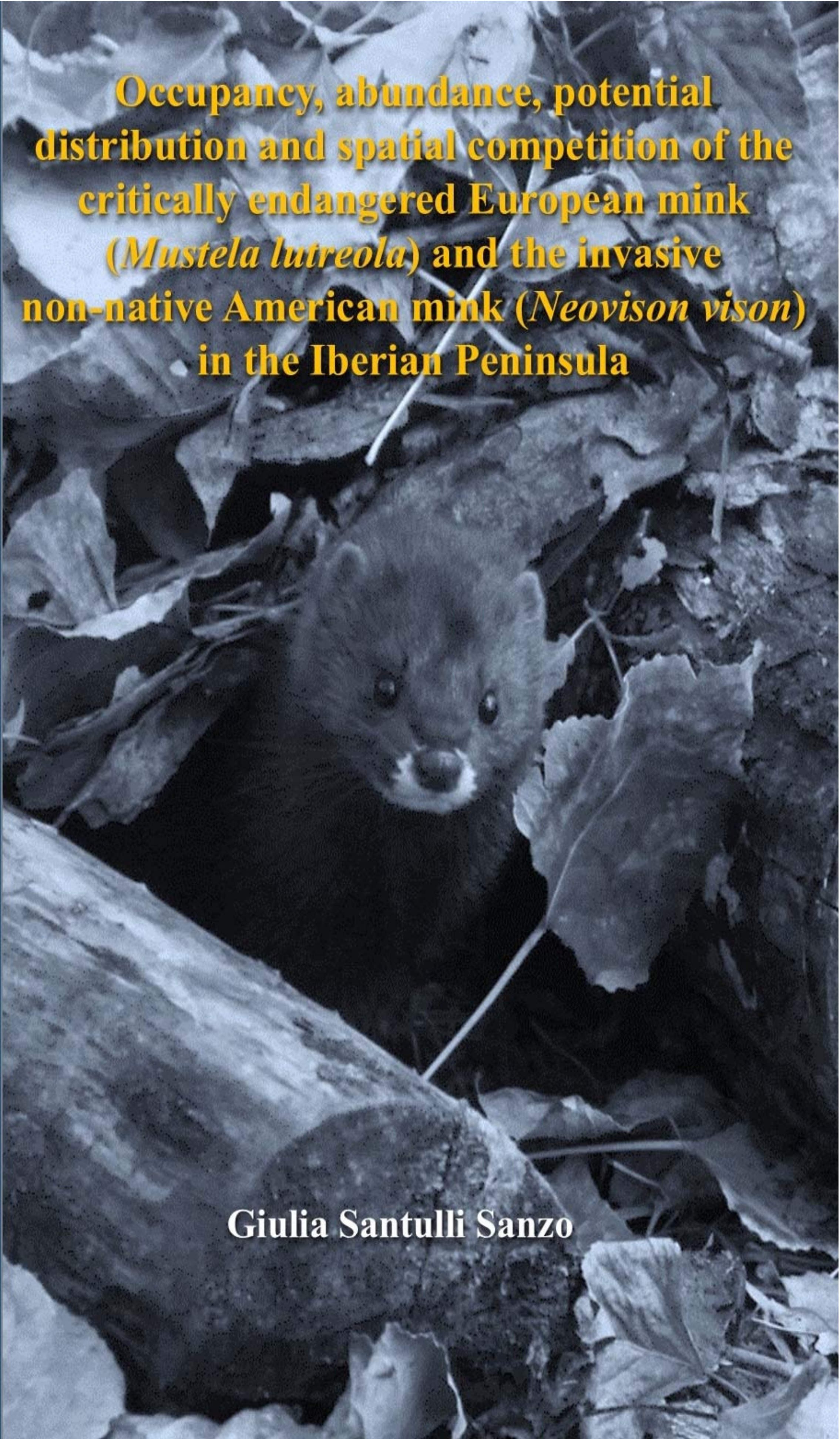

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Facultad de Biología
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OCCUPANCY, ABUNDANCE, POTENTIAL DISTRIBUTION AND SPATIAL COMPETITION OF THE CRITICALLY ENDANGERED EUROPEAN MINK (*Mustela lutreola*) AND THE INVASIVE NON-NATIVE AMERICAN MINK (*Neovison vison*) IN THE IBERIAN PENINSULA

Ocupación, abundancia, distribución potencial y competencia espacial de una especie en peligro crítico de extinción, el visón europeo (*Mustela lutreola*) y de una especie exótica invasora, el visón americano (*Neovison vison*), en la Península Ibérica

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Introduction

INTRODUCTION

The last IUCN Red-list analysis on extinction worldwide (Baillie *et al.*, 2004) concluded that the most pervasive threats that mammals are currently facing are habitat destruction and fragmentation, over-exploitation, disease, pollution and contaminants, incidental mortality and biological invasions.

Most of these threats are believed to act on target species at the landscape scale (Boyd *et al.*, 2008) (commonly perceived as a human-defined area ranging in size from few to few hundreds of km^2, Forman and Godron, 1986), which is the scale by which most studies are carried out.

The two most important component of the spatial scale are the “grain”, defined as the minimum spatial resolution of the data or the size of the individual units of observation, and the “extent”, the scope or domain of the data, which typically corresponds to the study area.

Understanding species’ status and distribution over large extents (i.e. at country or regional level) can be critical in determining species conservation priorities. At country level, regulations can be put into place, protected areas can be designated, and other broad reaching conservation actions can be carried out, and thus they can be scale-down to a smaller extent or a finer grain to implement effective management of the species or the area of interest (Turner, 2005).

Moreover, the capacity of correctly interpreting biotic interactions depends on the spatial scale of the analysis. In order to detect the influence of one species on the other, grain size i.e. should be large enough to include home ranges of several individuals, and the extent of the study should embrace an area where the dynamic patterns of populations’ interaction are significant.

This can be particularly important to understand the effect of invasive non-native species (INNS hereafter) on native biodiversity. An INNS has been defined as “an alien species, which becomes established in natural or semi-natural ecosystems or habitat, which could not occupy without direct or indirect introduction or care by humans and which becomes an agent of change and threat of native biological diversity” (DAISIE, 2009; IUCN, 2000).

INNS are widely recognized as the second most important cause of biodiversity decline, after habitat loss and alteration, and their environmental, economic and ecological impacts has been largely explored (Hoffmann *et al.*, 2010; Gurevitch and Padilla, 2004; Mack *et al.*, 2000; Parker *et al.*, 1999).

INNS may have a destructive impact especially on critically endangered species, which are already facing an extremely high risk of extinction due to a dramatic reduction in population size and geographic range (IUCN, 2000).

The target species of this thesis, the European mink (*Mustela lutreola*) and the American mink (*Neovison vison*), are considered respectively as one of the most threatened carnivores (Maran *et al.*, 2011) and as one of the worst invaders in Europe (DAISIE, European Invasive Alien Species Gateway (http://www.europe-aliens.org). Their interaction, occupancy, abundance and potential distribution were analyzed in this thesis over their range of distribution in the Iberian Peninsula.

The European mink is endemic of the European continent and its historical range extended from the east of Urals Mountains to the Atlantic French coast and from Finland to Caucasian Mountains (Maran, 2007; Youngman, 1982).

The native range of distribution of the American mink occupies almost all of North America, excluding the north of the Arctic Circle and the most Southern part of the United States (Larivière, 1999), but the species has now established in twenty-one European countries (Bonesi and Palazon, 2007) and it has been introduced in Argentina, Chile, Russia, China, Japan, Kazakhstan and New Zealand (Ibarra *et al.*, 2009; Reid and Helgen, 2008; Bonesi and Palazón, 2007; Previtali and Cassini, 1993).

The European mink and the American mink: biological and ecological traits

Both mink species are semi-aquatic mustelid inhabiting fresh water and costal ecosystems, which have near identical morphologies and very similar habitat requirements (Sidorovich *et al.*, 2009; Maran *et al.*, 1998a;).

European mink is found primarily along small streams, occurs infrequently on large rivers and selects the mouths of small tributaries (Youngman, 1990), whilst the American mink can be found in a wider spectrum of habitats unusual for a semiaquatic predator (i.e. swampy meadows and even non-swampy forests located far from river bank or shores) (Sidorovich and Macdonald, 2001). The two mink use similar resting sites along riverbanks, usually located under roots of trees, rock piles and dense brambles patches (Yamaguchi *et al.*, 2003; Zabala *et al.*, 2003).

Both mink are solitary and territorial, showing no overlap between home ranges of resident males, although temporal overlap with transient mink has been observed in some cases (Melero, 2008a; Yamaguchi *et al.*, 2003), and smaller females' home ranges overlapping with the males' territories (Dunstone, 1993).

The European mink's mean linear home range is larger than the one of the American mink: studies carried out in the Iberian Peninsula reported values of 13.1 ± 2.8 sd km for males and 3.4 ± 2.8 km for females in the case of the endemic mink (Palazón and Ruiz-Olmo, 1998a) and for the INNS species ranges were 0.89 – 6.8 km for males and 0.21 - 2.9 6 km for males and 4.92 ± 3.79 km for females (Melero *et al.*, 2008a).

The American mink is substantially bigger than the European mink: mean weight of males is 1500 g in the case of the invader and 700-900 g in the case of the native mink, while females' average weight is 900 g compared to the 450-600 g of the European mink females (Melero *et al.,* 2012b; Palazón *et al.,* 2006b; Sidorovich, 1997; Palazón and Ruiz-Olmo, 1995; Birks and Dunstone, 1985).

In the Iberian Peninsula reproduction of the American mink occurs between February and April (Melero and Palazón, 2011), while the European mink estrus occurs between the end of March and June (Youngman, 1990). Results of studies conducted in captivity showed that American mink had greater fecundity than the endemic mink, with 5.4 *versus* 4.3 offspring per litter respectively (Amstislavsky *et al.*, 2008).

The analogies in the ecology and appearance of the two species (Fig. 1) are so strong that for a long time they were distinguished only as subspecies (Maran *et al.*, 1998a; Novikov, 1939), whilst recent phylogenetic studies assigned the American mink to a distinct New World lineage and to the ad-hoc genera *Neovison* (Harding and Smith, 2009; Kurose *et al.*, 2008).

Figure 1. European mink (left) and American mink (right) captured in the Spanish Regions of La Rioja and Catalonia respectively. (G. Santulli Sanzo)

The European mink: historical decline and current threats

The European mink conservation status changed from endangered to critically endangered in 2011 (Maran *et al.*, 2011). It is also included in the Catalogue of Directive Habitat (Directive 92/43/CEE, modified by Directive 97/62/CE).

The decline and local extinction of the species was first recorded in central Europe in the 19th century. Before the 1950s it became extinct in most of the Western European countries and thereafter the species disappeared progressively from almost 85% of its original range (Maran *et al.*, 2011). Currently only three populations remain in isolated and fragmented enclaves: one in Western Europe (northern Spain and south-western France), one in the Danube delta in Romania, and one in Ukraine and Russia (divided into several subpopulations) (Maran, 2007; Michaux, 2004; Palazón *et al.*, 2002, 2003; Sidorovich, 2001), and they are in decline and at low densities (Maran *et al.*, 2011).

Multiple causes are thought to be implied in the local extinction and the disappearance of the European mink all over its original range. Large-scale human alteration of landscapes had a substantial impact in most countries, and it likely acted in concert with others factor to exacerbate and accelerate the species' decline (Maran, 2007). Although a different combination of the causes of decline is believed to act in each region, the key factors considered to have had the strongest impact on the European mink are: over-hunting, degradation and loss of habitats, water pollution and the invasion of the American mink (Lodé *et al.*, 2001; Maran *et al.*, 1998a; Maran and Henttonen, 1995).

The Western population (France and Spain) of the European mink received a particular attention in the last decades for its conservational value and for its unique history.

First records of the species in France are surprisingly recent (from the year 1839, Youngman, 1982) and even more in Spain (1951), (Palazón and Ruiz-Olmo, 1992; Rodríguez de Ondarra, 1955). It is not clear if in this region the species has been introduced by humans or if its spread has been a natural colonization, but there are strong evidences that the Western population has a reduced genetic variability likely caused by a “bottleneck” during its establishment (Michaux *et al.*, 2005; Michaux, 2004). This led some authors to suggest the consideration of the Western population of the European mink as a distinct unit of management regarding the Eastern European populations, mainly as a precautionary measure to avoid outbreeding depression in potential reintroductions programs (Michaux, 2004).

The situation of the Western population is indeed object of concern. In France, the European mink suffered a rapid decline: in a few decades, at the end of the 20th century, it disappeared from the Northern half of its range, and it is now restricted to the south-western part of the country (Maizeret *et al.*, 2002).

The decline has been attributed mainly to the conjunction of intensive trapping, alteration of water quality and habitat modification, while competition with the American mink couldn’t have been the decisive cause, because in this area the European mink disappeared several years before its introduction (Lodé *et al.*, 2001).

The Spanish population of the European mink likely derived from the expansion of the French one, which firstly colonized the Atlantic basins in the 1950s (where now is found in small and fragmented populations), and then expanded along the river basins of La Rioja and Navarra, Basque Country, Castilla and León (Burgos and Soria Provinces) and Aragón (in the Zaragoza Province) (Gómez *et al.*, 2011; Palazón *et al.*, 2003) (Fig. 2).

Despite recent evidences of expansion of the population’s range southward along the Aragón and Ebro rivers (Gómez *et al.*, 2011), in Spain the European mink is threatened by several factors which are putting at risk its persistence in the short-medium term.

The spread of the invasive competitor, the American mink, around and inside the area of distribution of the endangered mink is considered one of the most important menaces (Põdra *et al.*, 2013; Bonesi and Palazon, 2007; Maran, 2007;

Zabala, 2006; Palazón *et al.*, 2003), as discussed in detail in the following sections.

Habitat loss, fragmentation and deterioration have been pointed out as mayor threats for the European mink in Spain, especially for the alteration of the riparian habitat by removing the vegetation which is essential as shelter and to maintain preys diversity (Palazón *et al.*, 2006c). Evidences that habitat fragmentation reduces the persistence of the European mink has been reported in the Basque Country (Zuberogoitia *et al.*, 2013), and the impact on the gene flow between isolated sub-population, which likely are already affected by a low genetic variability, may be catastrophic.

Moreover, water pollution can strongly affect the European mink, and organchlorine compounds (PCBs) and heavy metals can seriously damage its reproduction and growth (Lopez-Martin *et al.*, 1994), an effect observed also in the American mink and other semiaquatic mammals (Zwiernik *et al.*, 2009; Harding *et al.*, 1999; Aulerich *et al.*, 1990).

Road kills are the main cause of direct human-induced mortality of the European mink in the last two decades, and they especially affect males during the mating season (Palazón *et al.*, 2012a), while the Aleutian Mink Disease (ADV) parvovirus, probably introduced by the American mink, has a very high prevalence in the Spanish population of the European mink (Mañas *et al.*, 2001).

There is a growing evidence that in Spain the European mink suffered a decline since the decade of the 90s (Palazón and Melero, in press; Palazón *et al.*, 2003). Several studies carried out since 1992 lead to an estimate of the current population size of European mink in Spain on approximately 500 individuals and to state that its total distribution covers 2300 km of watercourses (Palazón *et al.*, 2013; Palazón *et al.*, 2012b).

A Spanish European mink National Conservation Strategy has been carried out under the direction of the Ministry of Natural, Rural and Marine Environment since 2005, and previously or concurrently a series of European LIFE projects for the conservation of the mink have been realized by the autonomic governments of La Rioja (LIFE 00/NAT/ E/7331: 2001-2004), Álava (LIFE 00/NAT/E/7335: 2001-2004), Castilla and León (LIFE 00/NAT/7299: 2001-2004), Catalonia (LIFE 02/NAT/E/8604: 2002-2005) and Navarra (2005-2008 and 2010-2014). A new LIFE Plus project (2014-2018) has been recently approved to conserve the European mink in La Rioja, Aragón, Basque Country and Valencia (LIFE 13 NAT/ES/001171).

These projects are focused mainly in monitoring the population of the native mink, in regenerate its habitat, in carrying on a captive breeding program and in the control of the invasive population of the American mink.

The American mink invasion

The American mink has been introduced in Europe at the beginning of the 20th century for fur farming and as a result of escapes and intentional releases, occurred wherever farms were settled, is currently present in at least 21 European countries, though there is great variability in terms of its abundance between countries (Bonesi and Palazon, 2007).

Several studies all over Europe showed that the American mink can have a significant impact on ground-nesting birds, rodents and amphibians, as well as on the European mink and the European polecat (*Mustela putorius*) (Põdra *et al.*, 2013; Melero *et al.*, 2012a; Brzezinski *et al.*, 2010; Banks *et al.*, 2008; Bonesi *et al.*, 2007; Bartoszewicz and Zalewski, 2003; Macdonald and Harrington, 2003; Nordström *et al.*, 2002; Aars *et al.*, 2001; Sidorovich *et al.*, 1999).

In Spain, mink farming started at the end of the 1950s, and by the beginning of the 1990s almost 220 farms were present in the country (Bonesi and Palazon, 2007; Ruiz-Olmo *et al.*, 1997). Massive escapes and intentional liberations from farms resulted in the establishment of six different populations: one in Central Spain (from the center of the Burgos province to Portugal, in the entire Castilla and León, Madrid, Castilla-La Mancha and North of Extremadura), one in Galicia, one in Catalonia, one in Teruel, Zaragoza and Castellón, one in Álava and one in the North of the Basque Country (Melero and Palazón, 2011; Ruiz-Olmo *et al.*, 1997) (Fig. 2). The latter two populations are currently merging (Palazón, pers. comm.).

At the moment 37 farms are present in the Spanish territory (MAGRAMA, 2013), and 2 farms are still active inside or very close to the range of distribution of the European mink (Palazón, pers. obs.).

The total population size is estimated to be of 30.000 individuals occupying approximately 12.500 km of rivers only in the Spanish territory (MAGRAMA, 2013).

In Portugal, the first reported sighting of the American mink occurred in 1985 in the border between northwest Portugal and Galicia (Vidal-Figueroa and Delibes, 1987) and since then, only sporadic references of mink presence were reported in the northwest of the country (Santos-Reis and Petrucci-Fonseca, 1999). However the spread of the species southward up to the Duero river basin has been recently described, although the expansion seems to proceed relatively slowly (about 55 km in 20 years) (Rodrigues *et al.*, 2014).

Several evidences exist on the impact of the American mink on native species through predation or competition in the Iberian territory.

This INNS can prey on and cause the decrease and local extinction of endangered species such as the with-clawed crayfish (*Austropotamobius pallipes*), the Iberian desman (*Galemys pyrenaicus*) and the southwestern water vole (*Arvicola sapidus*) (Palomo and Gisbert, 2002; Palazón and Ruiz-Olmo, 1998b).

Moreover, the American mink can affect the population structure of other riparian predators such as the Eurasian polecat, the Eurasian otter (*Lutra lutra*) and the European mink due to competition and disease transmission (Melero *et al.*, 2012a; Mañas *et al.*, 2001; Ruiz-Olmo and Palazón, 1991).

Intensive control campaigns are carried out in Spain since 2001 mainly as a part of the European mink National Conservation Strategy. Initially, the program has been implemented through live-trapping surveys in Alava, Burgos and Teruel and Castellón, and then it expanded to all the six existing populations.

The effectiveness of culling campaigns has been tested only locally and whilst there are evidences that the main effect of the control is to locally reduce the density of the invader, it has been suggested that the eradication at a moderate-low costs is feasible only in restricted areas (Melero *et al.*, 2010; Zabala *et al.*, 2010; Zuberogoitia *et al.*, 2010).

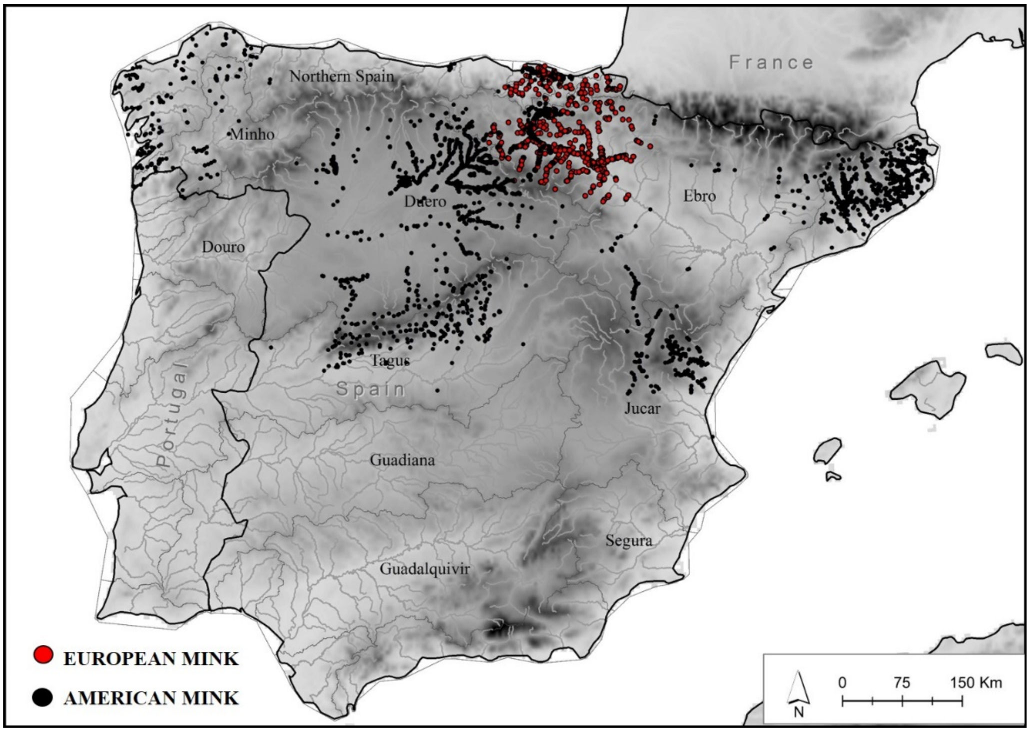


Figure 2. European mink and American mink distribution in the Iberian Peninsula: points represent captures and observations collected between 1999 and 2012 (See Material and Methods).

The reasons of the conflict

The conflict between the American mink and the European mink arise from to the strong ecological competition between both species. The three main mechanisms by which the American mink may cause the decline of the European mink are considered to be competition for resources, interspecific aggression and transmission of diseases (Macdonald and Harrington, 2003).

A considerable overlap in the diet of the two species exists, and even though the European mink has a slightly more specialized diet than the American mink, both feed on a wide spectrum of preys such as small mammals, amphibians, fish and other prey (Palazón *et al.*, 2004; Sidorovich, 2001; Maran *et al.*, 1998b).

Moreover the European mink has narrower habitat requirement than the invasive counterpart, and it selects territories with non-polluted slow-flowing watercourses, high fish biomass, dense riparian vegetation and low human-disturbance (Zuberogoitia *et al.*, 2013; Zabala, 2003; Lodé, 2002; Lodé *et al.*, 2001), which are likely highly attractive also for the American mink (Maran *et al.*, 1998a).

The American mink can be 40% larger in body size than the European mink (Maran, 2007; Sidorovich *et al.*, 1999), shows delayed implantation of embryos which can increase the survival probability of the new-borns (Thom *et al.*, 2004; Maran *et al.*, 1998a) and have larger litters which facilitate a rapid spread (Bonesi *et al.*, 2006; Sidorovich *et al.*, 1997).

Additionally, the American mink shows smaller home ranges than the European mink and it can hence be found at higher densities, while the endemic mink has greater spatial requirements. Overall, the higher ecological plasticity of the invasive mink enable it to outcompete the native one.

In Estonia the American mink has been reported to aggressively ousted the European mink from high quality territories (Maran *et al.*, 1998a); in Belarus the native mink rapidly disappeared from previously inhabited watercourses during the expansion of the INNS mink (Sidorovich, 2001); and in the Basque Country the local replacement of the native mink has been observed after a short period of co-existence of the two mink species (Carreras *et al.*, 2006; Ceña *et al.*, 2003).

The presence of the American mink even at low densities can be detrimental for the native mink as demonstrated by Põdra *et al.* (2013), who reported evidences of killing of the European mink by the competitor in a protected area in the Vitoria Province (Basque Country).

In Spain the American mink is considered the main vector of spread of the Aleutian Mink Disease (ADV) parvovirus in the European mink population (Mañas *et al.*, 2003). Besides, direct mortality this virus, which had a high prevalence in fur farms in the Iberian territory, can cause a decrease in fertility and spontaneous abortions, physiological malfunctions and immunological problems (Palazón and Melero, in press; Mañas *et al.*, 2001), factors that can have a deleterious effect on the threatened population of European mink.

The American mink is rapidly surrounding the current range of distribution of the European mink from the Southwest and the North (MAGRAMA, 2013). A great threat is posed by three expanding populations in the Basque country (in Alava, right in the centre of the endangered mink distribution area, Northern Biscay and Western Guipúzcoa), which can potentially merge in the next future and rapidly ousted the endemic mink (Palazón and Melero, in press; Carreras *et al.*, 2006; Zabala *et al.*, 2006; Ceña *et al.*, 2003; Zuberogoitia and Zabala, 2003).

Which information is needed in the Iberian Peninsula?

A great amount of high quality data and knowledge on the two mink species has been generated in the last decades in the Iberian Peninsula thanks to the efforts of researchers, managers and technicians who worked for, or collaborated with Spanish and Portuguese Academies, Regional Governments and the Environment Ministry.

Many research studies and technical reports have been produced to shed light on the ecology, the distribution, the habitat, the causes of decline and expansion, the competitive interaction of the European mink and the American mink, and most of the conservation policies and management actions carried out until now have been guided by this valuable work.

Reasonably, most of these studies are focused on part of the area of distribution of both species, exploring biological features, ecological processes and management options mainly at a local scale.

Several studies have been carried out in Biscay (Basque Country) to explore the environmental and biotic factors affecting the occupancy of the European mink, revealing that in this area water quality, riverbanks alteration and habitat fragmentation may have a stronger effect on the endemic mink than the presence of the invasive counterpart (Zuberogoitia *et al.*, 2013; Zabala *et al.*, 2006, 2003).

In Vitoria (Basque Country) the spread of the American mink inside the range of distribution of the European mink has been related to the disappearance of the native species from the area (Carreras *et al.*, 2006; Ceña *et al.*, 2003).

In Catalonia, Melero *et al.* (2012a) revealed a negative effect of the abundance of the American mink on two competitors, the spotted genet (*Genetta genetta*) and the European polecat, and on three native fish species.

In 2007, first records of the European mink in Aragón were reported, leading to suggest an expansion of the species' range southeastward (Gómez *et al.*, 2011).

While all together these works contribute to delineate the picture of the status of the native and the invasive mink in the Iberian Peninsula, a global view of the interaction, potential distribution and spatial dynamic of the two species over the entire Iberian range has not emerged clearly so far.

This kind of sight is crucial to understand which processes are going on at the population level for both mink species and it may provide essential information for their conservation and management.

Objectives

OBJECTIVES

Main objective

The goal of this thesis is to contribute to the knowledge of the status of the critically endangered European mink and the invasive non-native American mink in the Iberian Peninsula through the analysis of their potential distribution, occupancy, abundance and spatial competition over their entire Iberian range. This contribution aims to provide sound basis in order to guide conservation and management actions of both species' populations in the Iberian territory.

Specific objectives

To achieve this goal, this thesis has been structured in four Chapters and a global discussion that address the following specific objectives:

1. Test for changes in the occupancy of the two mink species inside the range of distribution of the European mink since the 2000, and for evidences of a large-scale competitive exclusion of the native species by the invasive mink. (Chapter 1)
2. Evaluate the spatial and temporal trend in the abundance of the European mink since 2000 and identify the environmental factors with the strongest influence on this parameter. (Chapter 2)
3. Predict the potential expansion of the American mink in the Iberian Peninsula by testing a multi-scale hierarchical approach to species distribution modeling. (Chapter 3)
4. Identify priority conservation areas for the European mink through the spatial analysis of the overlap of the two mink species' potential distribution in the Iberian Peninsula.(Chapter 4)
5. Provide a global analysis of the status of the two mink species in the Iberian Peninsula and suggest practical guidelines for their management based on the results obtained in the thesis. (Results and Discussion)

Materials and Methods

MATERIAL AND METHODS

Species surveys and data processing

Since 1992 the methodology to monitoring the European and American mink populations in Spain follows a protocol developed by the managers and technicians involved in the European mink National Conservation Strategy.

The procedure is based on live-trapping with at least one trapping station per 10x10km Universal Transverse Mercator (U.T.M.) cells in Navarra, Aragón (Zaragoza and Huesca), La Rioja, Basque Country (Biscay, Guipúzcoa and Alava), Castilla and León (Burgos and Soria), Cantabria and Catalonia (Palazón and Melero, in press) carried out by administrative officers, technicians and forest rangers of regional governments coordinated by the Spanish Ministry of Agriculture, Food and Environment.

Trapping stations are composed by ten baited cage traps (15 cm x 15 cm x 60 cm) suitable for the live capture of both mink species (Fig. 3), placed along riverbanks sections of 1 to 5 km at a distance of 100 – 300 m from each other, and operated for 10 consecutive nights.

The endemic mink is marked with a subcutaneous passive transponder and released once the individual had fully recovered from anesthesia (Fig. 3), whilst the invasive mink is euthanized, following the Spanish Animal Welfare Law (Royal Act n. 32/2007). Traps geolocation are collected with GPS generally with a precision of 10 m.

Moreover biometric parameters (sex, age, length of the body, of the front and hind leg and of the ear) are measured for each trapped individual of both species, although these data were not used in this thesis.

This protocol allows detecting the presence or absence of the two mink species with high precision, capturing animals safely, collecting biometric parameters and is highly selective (the great majority of trapped animals are European and American mink).

Inside the area of distribution of the European mink trapping surveys are carried out twice per year in the species' pre-breeding period (from January to mid-March) and in the post-breeding period (from September to December), although the effort can vary depending on funding and on regional government policy.

Where the European mink is absent, trapping session can be realized all year long to control and monitoring the American mink population. Generally, once the invader is detected at one site, the number of trapping stations is increased in that and in the closest sites to maximize the number of individuals removed (Palazón, pers. comm.).

In this thesis we transformed European mink and American mink records collected in the Iberian Peninsula between the 1999 and the 2012 in three type of data, depending on the analysis performed and on the objective of the study: (1) detection / non-detection data for the occupancy analysis (Chapter 1), (2) count data for the abundance analysis (Chapter 2) and (3) geolocation of individuals for the distribution modeling (Chapters 3 and 4) (Table. 1).

For both species, detection histories and count data were elaborated at the resolution of the 10x10 km U.T.M. cells (one value per cell), whilst geolocation in the Iberian territory were up-scaled to the resolution of 2,5 km and used as presence-only data to predict species potential distribution.

In the analysis of occupancy and abundance, only data from the Spanish range of the two mink species were used. Instead, to model the species' potential distribution in the Iberian Peninsula, data from the European mink historical range and from the native (North America) and invaded (Europe) range of the American mink were collected (apart from the presence-only data elaborated as mentioned above).

These data were partly extracted from the Global Biodiversity Information Facility database (http://www.gbif.org) and in part geo-referenced from several different studies conducted in Europe and in North America.

Geographic coordinates of the historical distribution of the European mink were gathered from Maran (2007), Maizeret *et al.* (2002), Lodé *et al.* (2001) and Youngman (1982). Data on the distribution of the American mink in North America were obtained from Kay and Wilson (2009), Bluett *et al.* (2006), Viljugrein *et al.* (2001), and Ensor (1991).

Figure 3. Cage trap (left) used in the live-trapping surveys carried out in the study area and an anesthetized individual of European mink (right) in the vet clinic for the application of the subcutaneous transponder. (G. Santulli Sanzo)

Study area

The study area was the entire Iberian Peninsula (Fig 4) although two of the studies of this thesis, the occupancy and abundance analysis (Chapter 1 and 2), focused respectively on nine and eight Spanish Provinces.

The Iberian Peninsula is located between 36º00’N - 43º47’ N and 9º29’W and 3º19’E, occupies an area of approximately 582.000 km^2 and is composed by three countries: Portugal, Spain and Andorra.

Between the most significant environmental features affecting the presence and the spread of the European mink and the American mink, there are the hydrological system (both mink are semi-aquatic species) and the climate, especially for its influence on water balance.

In the most recent revision of the Köppen-Geiger climate classification (Peel *et al.*, 2007) three general categories of climate are reported to be dominant in the Peninsula (Fig. 4):

1. Arid: in the Southeast of the Peninsula in the provinces of Almeria, Murcia and Alicante (desert), and in the Ebro valley and in Extremadura (steppe).
2. Temperate: in the Southern part of the Peninsula and in the Mediterranean coastal zones this type of climate shows dry and hot summers is the most frequent type of climate covering about 40% of the Peninsula, while in the North (Cantabria, Iberian System, Pyrenees) the dry season is absent.
3. Cold: in general with dry winter in the Cantabrian Mountains, Iberian System, Central System and Sierra Nevada.

Precipitation and river flow regimes are characterized by large values of inter-annual variability, with great disparities between wet and dry years, especially in Southern Iberia (Trigo *et al.*, 2004).

Highest values of mean annual precipitation (2200 mm) are recorded in forested mountain areas in Northwest Portugal, in Northeast Navarra and in some areas in Southwestern Galicia. Lowest values are observed in Southeast Spain, in the Murcia and Almeria provinces, with a mean annual precipitation of 200 - 300mm. Moreover mean monthly precipitation indicate a strong seasonality, especially in the Southern half of the Peninsula, and a clear decrease of rainfall during summer, whilst the wettest month is in general December (AEMET, 2011).

About three quarters of the Peninsula are occupied by the “Meseta Central”, a vast plateau ranging from 610 to 760 m of altitude ringed by mountains, which hold the sources of most of the rivers finding their way through gaps in the mountain barriers on all sides. The major rivers are the Ebro, Duero, Tajo, Guadiana and

Guadalquivir. The Tajo is the longest river in the Peninsula and the Ebro is the biggest river by discharge volume, its source is in Cantabria and it flows eastward to the Mediterranean basin.

Apart from the Northeastern areas and the big rivers, in the Iberian rivers are subject to seasonal variations in flow and, especially in the Southeast, to droughts and low regimes.

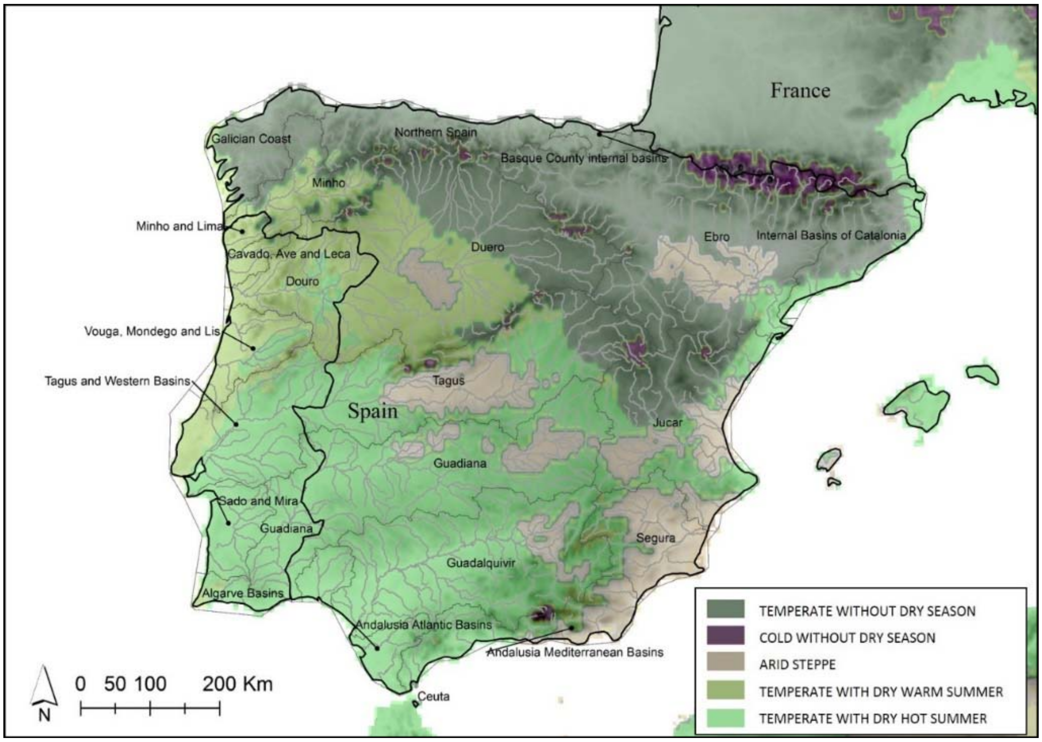


Figure 4. The Iberian Peninsula is the study area of this thesis: major river basins and climates are represented.

Statistical analysis

Three different statistical techniques were used to analyze the data: Occupancy Models, N-mixture Models and Species Distribution Models (SDMs). In this section, the principal characteristics of each technique are reported, whereas in each Chapter details on the application of the methods are provided.

Occupancy Models

Estimating and interpreting patterns of occupancy lie at the heart of many questions in ecology and problems in conservation (Rota *et al.*, 2009; MacKenzie *et al.*, 2006;).

Occupancy models aim to estimate the fraction of sites occupied by a species that is imperfectly detected (MacKenzie, 2005) and they can be useful in both long-term monitoring programs and metapopulation studies. For example in a monitoring context, site occupancy probabilities may be used as a metric reflecting the current state of a population.

There is a growing literature on occupancy modelling and many apparently successful applications. The methodology seems to be widely viewed as having achieved the status of a ''gold standard'' for analyzing ecological data which are subject to detection error (Welsh *et al.*, 2013).

The classical multi-season occupancy model implemented by MacKenzie and colleagues (2003) is based on the estimation of four fundamental parameters: occupancy (φ), detection (p), colonization (γ) and extinction (ε).

Occupancy probability can be interpreted as the proportion of sites that are occupied; extinction probability as the proportion of occupied sites at time *t* not occupied at time *t+1*; and colonization probability as the proportion of sites not occupied at time *t* occupied at time *t+1*. Commonly the standard maximum likelihood techniques are used to obtain estimates of the model parameters.

MacKenzie *et al.* (2006) indicated that the initial occupancy state before the first survey of the first season is conveniently represented as

$$\varphi_0 = [\varphi_1 \quad 1 - \varphi_1]$$

And the matrix that determines the probability of a site transitioning between occupancy states between season *t* and *t+1* is (for $t \geq 1$)

$$\varphi_t = \begin{bmatrix} 1 - \varepsilon_t & \varepsilon_t \\ \gamma_t & 1 - \gamma_t \end{bmatrix}$$

So that the seasonal occupancy probability is calculated using the relationship

$$\varphi_t = \varphi_t - 1(1 - \varepsilon_t - 1) + (1 - \varphi_t - 1)\gamma_t - 1$$

Site-specific or sampling-specific covariates can be incorporated in these models using a logistic model in which the probability of interest Θ is:

$$\Theta = \exp\,(Y\beta) \,/\, 1 + \exp\,(Y\beta)$$

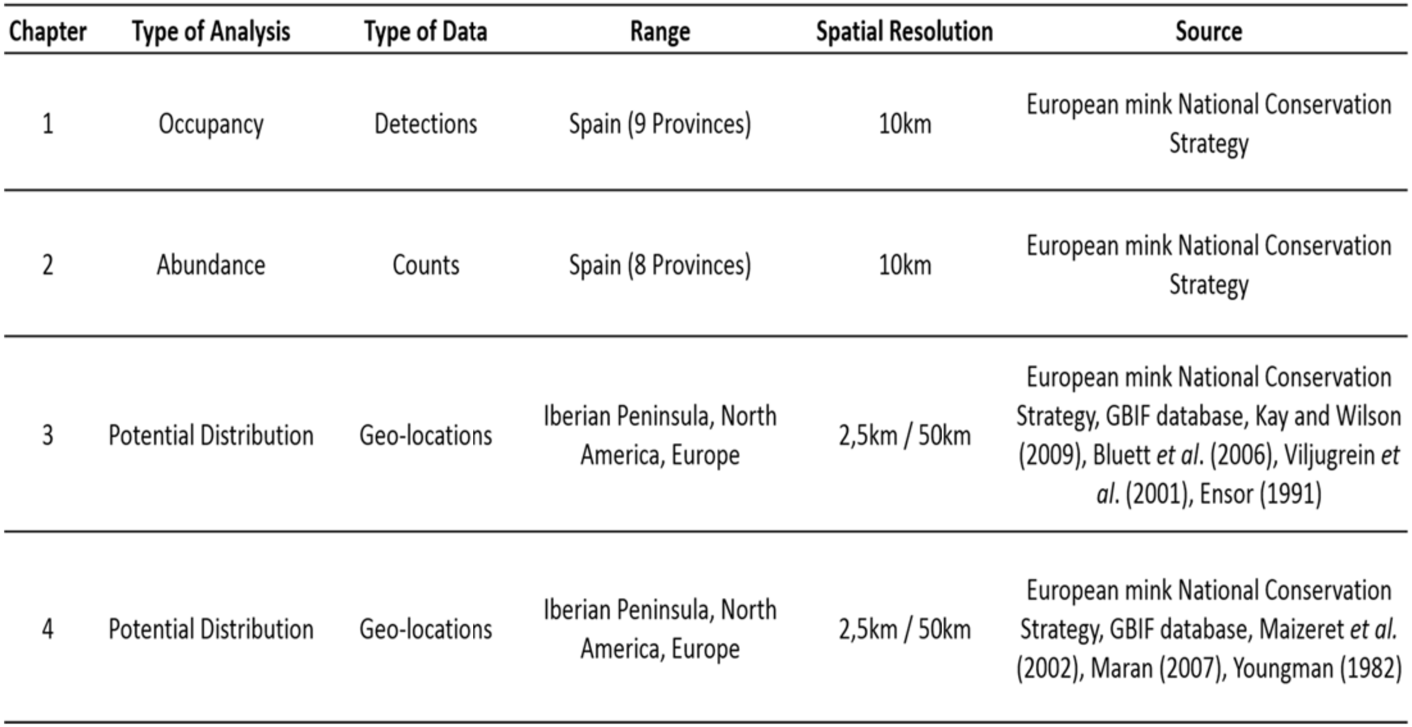
where Y is the matrix of covariates information, and β is the vector of logistic model coefficients to be estimated.

Underlying assumptions in estimating occupancy are that: 1) surveyed sites are occupied by the species of interest throughout the duration of the study, with no sites becoming occupied or unoccupied during the survey period (closure assumption); 2) models parameters are constant across sites (e.g. there is not heterogeneity in detection probability over the study area); 3) species are not falsely detected, but can remain undetected if present; 4) species detection at a site is assumed to be independent of species detection at other sites.

A further development of the occupancy models is represented by its application in investigating the pattern of co-occurrence of two or more species from repeated detection-non detection data (Richmond *et al.*, 2010; MacKenzie *et al.*, 2004). These models, commonly named “two-species occupancy models”, directly estimate a species interaction factor (SIF) that is a ratio of how likely two (or more) species are to co-occur compared to what would be expected under a hypothesis of independence of occurrence.

Besides the parameters mentioned above, a two-species multi-season occupancy model estimates occupancy, detection, colonization and extinction as a function of the presence or the absence of the coexisting species, and hence can be very useful to detect the impact of one species upon the other.

For example, is possible to detect competitive exclusion by demonstrating that increase or decrease in the occupancy probability of the species of interest are linked to each other through the influence of occupancy of one species on local extinction and colonization of the other (MacKenzie *et al.*, 2006), as has been done in Chapter 1.



Chapter	Type of Analysis	Type of Data	Range	Spatial Resolution	Source
1	Occupancy	Detections	Spain (9 Provinces)	10km	European mink National Conservation Strategy
2	Abundance	Counts	Spain (8 Provinces)	10km	European mink National Conservation Strategy
3	Potential Distribution	Geo-locations	Iberian Peninsula, North America, Europe	2,5km / 50km	European mink National Conservation Strategy, GBIF database, Kay and Wilson (2009), Bluett *et al*. (2006), Viljugrein *et al*. (2001), Ensor (1991)
4	Potential Distribution	Geo-locations	Iberian Peninsula, North America, Europe	2,5km / 50km	European mink National Conservation Strategy, GBIF database, Maizeret *et al.* (2002), Maran (2007), Youngman (1982)

TABLE 1. Summary of the type of analysis, data, spatial range of the analysis and source of the data used in each chapter of the thesis

While single species or single season occupancy studies abound, few studies reached the level of evidence to detect asymmetrical interactions between species through a multi season co-occurrence analysis (Lazenby and Dickman, 2013; Bailey *et al.*, 2009).

N-mixture Models

Between the models proposed in the last decades to estimate organisms total abundance from repeated counts, the one implemented by Royle (2004) has been shown to have the best performance, especially in presence of sparse counts (Dail and Madsen, 2011).

This model is classified as an N-mixture model, a class of hierarchical models for estimating animal abundance and probability of detection from count data, which assumes that the distribution of organisms across survey sites follows a Poisson distribution and the probability of detecting n organisms at a site represents a Binomial trial ("mixture" refers to the combination of two statistical distributions).

This model requires a set of temporally replicated counts at a number of sample locations or sites i in time t that are considered as independent realizations of a binomial random variable with index parameter N_i (local abundance) and outcome probability p of detection.

$$y_{it} \sim \text{Binomial}(N_i, p)$$

$$N_i \sim \text{Poisson}(\lambda_i)$$

Where y_{it} is the number of distinct individuals counted at location i in time t and λ_i is the expected population size at site i. This analytic framework is extremely flexible: it is possible to model both abundance and detection as a function of spatially and temporally varying covariates (e.g. habitat variables, survey effort), and even to model simultaneous effects of a single covariate on both abundance and detection (Kéry *et al.*, 2009).

However, the main limit to this model is the assumption that each site has a closed population, which cannot experience births, deaths or migrations and so remain constant throughout the course of the study. While this statement can be valid for e.g. a single breeding season, it is easily violated in annual count studies. Moreover, the trend in a population abundance, which is commonly a parameter of great interest in conservation studies, cannot be directly estimated with this model.

A dynamic N-mixture model, which is a generalization of the single season N-mixture model, has been recent proposed by Dail and Madsen (2011). It relaxes the closure assumption by describing population change between seasons. Specifically, it includes parameters of initial population state (abundance in first year of sampling, k) and vital rates, namely recruitment rate including births and immigrations (γ) and apparent survival (1 – deaths and emigrations, ω). The model also describes the observation process underlying data collection (p).

Estimates of population size at each time period can be derived from these parameters using a recursive equation of the type

$$N_{it} = N_{i,t-1}\, \omega^{t-1} + \gamma(1 - \omega^{t-1})/(1-\omega)$$

The models assumed that: 1) there is no change in abundance at the sites between the first and last visit in a given season; 2) covariates can account for detection heterogeneity across time *t* and sites *i*; 3) detections within each site are independent across visits; and 4) abundance can be modeled by covariates with an appropriate distribution model (e.g. Poisson, negative binomial, zero-inflated Poisson).

In Chapter 2 the objective was to assess the trend in the abundance of the Spanish population of the European mink, so the “exponential growth” version of the Dail and Madsen model has been applied, which allows to estimate the tendency of a population by setting the dependence of the recruitment rate γ on the population abundance at site *i* during the previous sampling period

$$N_{it} = N_{i,t-1}\, \gamma$$

Hence, in this case γ is the finite rate of increase (commonly named lambda). Specifically, the selected option can be summarize as:

$$N_{i1} \sim \text{Poisson}(\lambda)$$

$$N_{it} \sim \text{Poisson}(\gamma N_{it-1})$$

$$y_{ijt} \sim \text{Binomial}(N_{it}, p)$$

In the very last years since it has been proposed, the model has been successfully applied e.g. to test the effect of cavity availability on flying squirrel (*Glaucomys sabrinus*) population dynamics in Canada (Priol *et al.*, 2014), to evaluate its reliability in estimating the abundance of the red-legged partridge (*Alectoris rufa*) in the French Mediterranean region (Jakob *et al.*, 2014) or to examine the effects of recreational hiking on bird communities in New Hampshire, USA (Deluca and King, 2014).

One of the greatest advantages of this modeling approach, according to these studies' results, is that it turns out to be more cost-effective for species monitoring than capture–recapture methods, and more reliable than indices of relative abundances, which are commonly used to inform many management actions.

Species Distribution Models

Predicting species' distributions has become an important component of conservation planning in recent years, and a wide variety of modeling techniques has been developed for this purpose (Guisan and Thuiller, 2005).

Species Distribution Models (SDMs) are correlative models aimed to estimate the environmental conditions that are suitable for a species by associating known species' occurrence records with suites of environmental variables that can reasonably be expected to affect the species' ecology and probability of persistence.

The use of SDMs in supporting spatial conservation decision making has grown exponentially in the last decade i.e. for reserve design and selection (Carvalho *et al.,* 2010; Loiselle *et al.,* 2003), assessing reserves adequacy (Marini *et al.,* 2009;

Catullo *et al.,* 2008), locating hotspots of biodiversity and priority areas for conservation (Rodríguez-Soto *et al.,* 2011; Rondinini *et al.,* 2011; Peralvo *et al.*, 2006) and identifying conflict areas between native and invasive species (Gallardo and Aldridge, 2013; Vicente *et al.*, 2011).

The species' occurrence records and the environmental variables are entered into an algorithm that aims to identify environmental conditions that are associated with species occurrence. Having run the modeling algorithm, a map can be drawn showing the predicted species' distribution. The ability of the model to predict the independent data is assessed using a suitable test statistic. Commonly the modeling algorithms predict a continuous distribution of environmental suitability (i.e. a prediction between 0 and 1), whilst it is sometimes a necessary step to apply test statistics to convert model output into a prediction of suitable (1) or unsuitable (0) environmental space (which is a conceptual space defined by the environmental variables to which the species responds).

A striking characteristic of SDMs is indeed their reliance on the niche concept (Guisan and Zimmermann, 2000). It has been noted that the relevant niche definition in the case of SDMs is the Hutchinson's "realized niche" (Hutchinson, 1957) in which species are excluded from part of their fundamental niche (*sensu* Grinnell, 1917) by biotic interactions and dispersal limitations, resulting in the realized niche that is actually observed in nature (Guisan and Thuiller, 2005). As SDMs are founded on the observed distribution of species, they are thought to quantify the Hutchinson's realized niche, although for dominant species experiencing little exclusion and with total range filling, the realized niche may be close to the fundamental niche (Araújo and Pearson, 2005).

There are two major assumption behind SDMs: 1) the equilibrium (or pseudo-equilibrium) state of species with their environment, which postulates that a species occupies all suitable areas while being absent from the unsuitable ones and 2) the niche conservatisms which states that the niche occupied by a species do not change over time and space.

The first postulates can be both violated in the case of a critically endangered species which disappeared from most of its range and of an INNS which may have not invaded all its potential range due i.e. to lack of dispersal and invasion history (Václavík and Meentemeyer, 2012; Araújo and Guisan, 2006).

Moreover, evidences that an INNS can occupy distinct niche spaces in the area of introduction has been recently reported (Petitpierre *et al.,* 2012; Broennimann *et al.,* 2007), which potentially may lead to the violation of the niche conservatisms assumption.

The main consequences of this violations are: 1) models calibration with non-equilibrium data may lead to the exclusion of sets of conditions potentially suitable for the species and hence to underestimate potential distribution range (Guisan and Thuiller, 2005); and 2) if the niche occupied by an INNS in the new range is very different from the native one, the model calibrated with data from the species native area will likely predict erroneous potential ranges (Gallien *et al.,* 2010).

Although SDMs seem not to be suitable to the case of endangered species and INNS they have been largely applied to conservation planning. Different strategies has been proposed in the last decade to mitigate the effect of the assumptions' violation on potential distribution prediction and in this thesis, three of those strategies has been applied and tested (Chapters 3 and 4):

1. the *ensemble forecasting*, which by combining predictions from different modelling techniques aim to adjust for the inherent uncertainty from the each technique (Araújo and New, 2007).
2. a *multi-scale hierarchical framework* (Pearson and Dawson, 2003; Mackey and Lindenmayer, 2001) based on the combination of models calibrated at different spatial scales. This scheme allows to account for species adaptation to local conditions while considering their climatic limitations on a global scale, and helps to refine predictions and make them more informative (Guisan *et al.*, 2006).

3. in the case of INNS, the *models' calibration with data from both the native and the invaded range* and for the endangered species with data from *distribution before local extinction*. By including the largest possible amount of available information on the range of conditions occupied by the species of interest, this strategy provides more reliable predictions (Broennimann and Guisan, 2008; Peterson and Vieglais, 2001).

Chapters

CHAPTER 1

MULTI-SEASON OCCUPANCY ANALYSIS REVEALS LARGE SCALE COMPETITIVE EXCLUSION OF THE CRITICALLY ENDANGERED EUROPEAN MINK BY THE INVASIVE NON-NATIVE AMERICAN MINK IN SPAIN

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ABSTRACT

Understanding changes over time in the distribution of interacting native and invasive species that may be symptomatic of competitive exclusion is critical to identify the need for and effectiveness of management interventions. Occupancy models greatly increase the robustness of inference that can be made from presence/absence data when species are imperfectly detected, and recent novel developments allow for the quantification of the strength of interaction between pairs of species.

We used a two-species multi-season occupancy model to quantify the impact of the invasive American mink on the native European mink in Spain through the analysis of their co-occurrence pattern over twelve years (2000 – 2011) in the entire Spanish range of European mink distribution, where both species were detected by live trapping but American mink were culled. We detected a negative temporal trend in the rate of occupancy of European mink and a simultaneous positive trend in the occupancy of American mink. The species co-occurred less often than expected and the native mink was more likely to become extinct from sites occupied by the invasive species. Removal of American mink resulted in a high probability of local extinction where it co-occurred with the endemic mink, but the overall increase in the probability of occupancy over the last decade indicates that the ongoing management is failing to halt its spread. More intensive culling effort where both species co-exist as well as in adjacent areas where the invasive American mink is found at high densities is required in order to stop the decline of European mink.

RESUMEN

Para planificar y evaluar la eficacia de las intervenciones de gestión de especies autóctonas e invasoras que interactúan es fundamental entender si los cambios en el tiempo en su distribución puedan relacionarse a una exclusión competitiva.

Los modelos de ocupación incrementan la robustez de la inferencia que puede derivarse de datos de presencia / ausencia cuando las especies se detectan de forma imperfecta, y los recientes avances de estos modelos permiten cuantificar la fuerza de la interacción entre dos especies.

En el presente estudio hemos utilizado un modelo multi-estación para dos especies para cuantificar el impacto del visón americano, una especie exótica invasora, sobre el visón europeo, una especie autóctona, a través del análisis del patrón de su co-ocurrencia durante doce años (2000 – 2011) en la totalidad del área de distribución de la especie autóctona en España, en la que ambas especies son capturadas en vivo y la invasora es sacrificada.

Se ha observado una tendencia negativa en la tasa de ocupación del visón europeo, y una simultanea tendencia positiva en la ocupación del visón americano. Las dos especies co-ocurren con menor frecuencia de lo esperado y la especie autóctona tiene una probabilidad mayor de desaparecer en sitios colonizados por la especie invasora. El control del visón americano ha dado como resultado una elevada probabilidad de extinción en las áreas de co-ocurrencia con la especie autóctona, pero el general aumento de su capacidad de ocupación en la última década indica que la actual política de gestión no consigue frenar su expansión. Para parar el declive del visón europeo se necesita un esfuerzo mayor en el control de la especie invasora especialmente en las áreas en las que los dos visones coexisten y en las áreas adyacentes donde el visón americano se encuentra en elevadas densidades.

INTRODUCTION

Species ranges tend to respond to biotic changes, expanding or contracting in response to interactions with other species (Burton *et al.*, 2010; Case and Taper, 2000). The spread of invasive non-native species (INNS) is one process known to lead to range contraction of native species that are either outcompeted or preyed upon (Mack *et al.*, 2000). INNS interact strongly with native species having similar ecological requirements, owing to their morphology or foraging specialization. This may lead to competitive exclusion through range expansion and contraction of non-native and native species respectively occurring simultaneously (Case *et al.*, 2005; MacKenzie *et al.*, 2004). A classic example is the replacement of the European red squirrel (*Sciurus vulgaris*) by the invasive non-native American Grey squirrel (*Sciurus carolinensis*) in England (Tompkins *et al.*, 2003; Reynolds, 1985). While small scale, behavioral or demographic studies of competitive exclusion abound (Olson *et al.*, 2005; Usio *et al.*, 2002; Holway, 1999), the distributional consequences of interactions between INNS and native species have been rarely documented (but see Vicente *et al.*, 2011; Anderson *et al.*, 2002).

Because few survey techniques detect a species with 100 % certainty, characterizing the dynamics of the range of interacting species requires multiple years of detection of invasive and native species and, where possible, the use of occupancy modelling techniques. Establishing causality in patterns consistent with competitive exclusion requires demonstrating that increase and decrease in the occupancy of the invasive and native species, respectively, are linked to each other through the influence of occupancy of one species on local extinction and colonization of the other (MacKenzie *et al.*, 2006). This level of evidence has only been met by a small number of studies using spatial or temporal patterns of species co-occurrence to detect asymmetrical interactions (Lazenby and Dickman, 2013; Bailey *et al.*, 2009).

In this study, we used the multi-season extension of a two-species occupancy model developed by MacKenzie *et al.* (2004) to quantify the distributional changes and test the interaction between the invasive American mink (*Neovison vison*, AM hereafter) and the native European mink (*Mustela lutreola*, EM hereafter) in its entire Spanish range through the analysis of their co-occurrence pattern over twelve years (2000 – 2011).

AM is a generalist carnivore introduced in Europe for fur farming during the 20th century and is now naturalized in fresh water and coastal ecosystems throughout Europe (Bonesi and Palazon, 2007), where it depresses the abundance of many native prey and competitor species of conservation concern (Melero *et al.*, 2012; Bartoszewicz and Zalewski, 2003; Macdonald and Harrington, 2003; Aars *et al.*, 2001; Sidorovich *et al.*, 1999). Recurrent AM escapes from fur farms in the Iberian Peninsula since the late 1950s have given rise to six independent established populations, three of which are located close to or inside the range of EM (Ruiz-Olmo *et al.*, 1997). Despite intensive control campaigns carried out in Spain since 2001, the number of AM captured inside the range of EM has increased at an alarming rate over the last decade (Tragsatec-Magrama, 2012).

The critically endangered status of the endemic EM s due to the ongoing contraction and fragmentation of its range, now restricted to few isolated enclaves in northern Spain and western France, in the Danube delta in Romania, and in Ukraine and Russia (Maran, 2007) . The most detrimental factors causing the decline and local extinction of EM throughout the European continent are habitat loss, river water pollution, over-hunting and the impact of AM (Lodé *et al.*, 2001; Maran *et al.*, 1998b; Maran and Henttonen, 1995). The Europe-wide decline of EM started before the invasion of AM (Lodé *et al.*, 2001; Rozhnov, 1993), although where the species co-occur, AM is considered the main threat to the viability of EM (Palazón *et al.*, 2003; Sidorovich, 2001).

Both mink species are territorial, have near identical morphologies, similar habitat requirements and potentially compete for the same resources (Sidorovich *et al.*, 2009; Maran *et al.*, 1998a). AM, however, can be 40 % larger in body size, have larger litters and a higher ecological plasticity (Maran, 2007). The negative effects of AM on EM are thought to be mediated by inter-specific aggression (Põdra *et al.*, 2013; Maran *et al.*, 1998b), competition for food (Sidorovich *et al.*, 2009), and introduced diseases (Mañas *et al.*, 2001). Despite a contracting range in much of Europe, Gómez *et al.* (2011) presented intriguing evidence that EM has been undergoing a southward range expansion in Spain, where it has only been discovered in 1951 after entering from South-western France in the late 1940's (Palazón *et al.*, 2003; Camby, 1990).

In this conservation context, characterizing the speed and ubiquity of the replacement of the native EM by the non-native invasive AM is crucial to evaluate the effectiveness of ongoing management interventions.

We analyzed trapping data collected as part of a management program aiming to halt the decline of EM through live trapping followed by removal of AM. We investigated the dynamic of the two mink species occupancy with the aim of quantifying the impact of AM on EM through the analysis of detection, colonization and extinction probabilities of both species. We expected the rate of colonization of AM to be higher than extinction and the probability of occupancy of the invader to increase over the study period. Moreover, we expected to detect competitive exclusion of the native EM through the analysis of the differences in the rate of its colonization and extinction in presence or absence of the invasive mink.

MATERIAL AND METHODS

Study area

The study was conducted in nine provinces in Northern Spain (Fig.1a), an area of almost 70 000 km^2. Rivers of three main basins were sampled: the Ebro river basin, the northeastern part of the Duero river basin and the Atlantic basin. The study area includes both Mediterranean and Atlantic bioclimatic regions. At the beginning of the 1990s, almost seventy fur farms were thought to be present inside the study area (Ruiz-Olmo *et al.*, 1997) and three farms are still active (Palazón, pers. obs.).

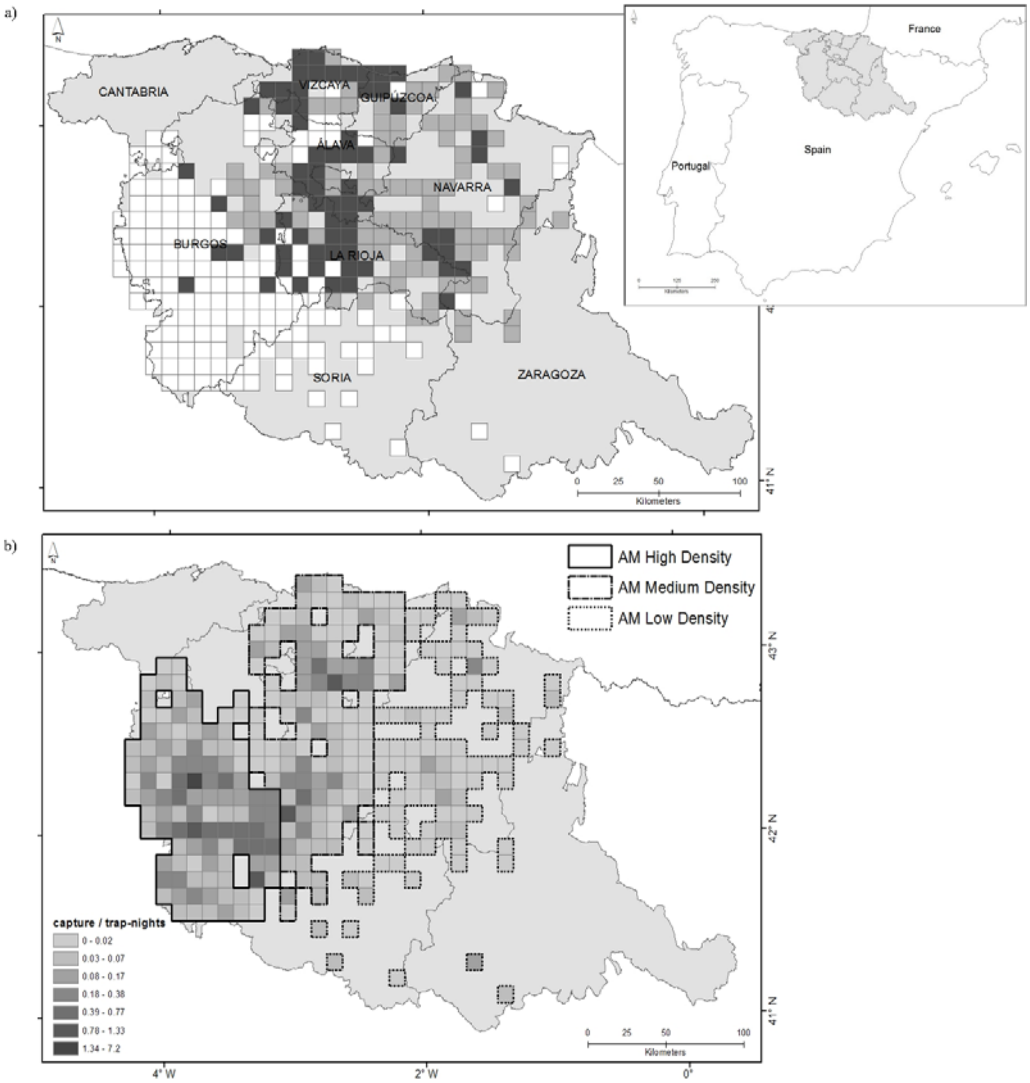


Figure 1. **a**) Study area in Northern Spain covering 70 000 km^2 and 9 provinces. Dark grey squares show the 10 km x 10 km cells where both the American mink and the European mink were detected between 2000 and 2011, light grey squares and white squares show cells were respectively only the European mink and only the American mink was detected. **b**) Map showing the three sub-areas with high, medium, low density of American mink used to establish whether detection probability is a function of AM density. Equal number of cells was assigned to each sub-area, and density was taken as the mean number of AM captured/trap-nights over the entire study period.

Species surveys and sampling design

EM and AM site occupancy data were gathered from live-trapping surveys conducted between 2000 and 2011 as part of EM conservation plan and AM control plan implemented by technicians of regional governments coordinated by the Spanish Ministry of Agriculture, Food and Environment. Trapping surveys took place according to an ad-hoc sampling design whereby river sections of 5 km (trapping stations hereafter) were selected inside 318 cells of 10 km x10 km (sites hereafter) based on the Universal Transverse Mercator grid reference system. Trapping stations were selected in areas where signs of presence of EM or AM were detected. Sampling was concentrated on the range of EM and on its periphery in order to detect potential range expansion and on the area of sympatry with AM. Within each site, ten baited cage traps (15 cm x 15 cm x 60 cm) suitable for the live capture of both species were placed along the river banks at a distance of 100 – 300 m from each other, and were operated for 10 consecutive nights (a survey hereafter). The endemic species was marked with a subcutaneous passive transponder and released once the individual had fully recovered from anesthesia, whilst invasive mink individuals were euthanized, following the Spanish Animal Welfare Law (Royal Act n. 32/2007). Following the trapping of AM, the number of trapping stations at a site, and its closest neighboring sites, was increased to maximize the number of AM removed.

Even though the data were not collected with an analytical framework in mind, we chose to analyze the trapping data using “multi-season occupancy models” to explicitly model potential changes in the occupancy state of a site over time through colonization and local extinction probabilities which are based upon species-specific detection histories for each surveyed site (MacKenzie *et al.*, 2006). Trapping was used to inform the occupancy status of both species.

The site resolution of 10 km x10 km permitted the assumption that at least one individual of each species could be detected at the same site, based upon both species mean linear home range values in the studied area (EM: 13.1 ± 2.8 SD km for males and 3.4 ± 2.8 km for females, Palazón and Ruiz-Olmo, 1998b; AM: 7.05 ± 7.78 km for males and 4.92 ± 3.79 km for females (Zabala *et al.*, 2007)).

Occupancy modelling requires that, within each primary period in which occupancy is estimated, sites are visited multiple times (secondary periods) to allow the estimation of detection probabilities (MacKenzie *et al.*, 2006). Thus, we grouped trapping events into annual primary sampling occasions (each year from 2000 to 2011) that included two secondary surveys (January - March and September - December). Logistical constraints due the intensive trapping effort and the large spatial extent of the study area restricted our number of secondary sampling periods to just two, the minimum number required for parameter estimation. Only cells surveyed in both secondary period in at least one primary period over the study (64 % of the total), entered in the analysis, as trapping histories with no repetitions were not suitable for detection probability estimation. Information on trapping success at a daily timescale was not available and such that we could not use these as secondary survey occasions.

Of the 204 sites that entered the modelling, an average of 43.6 ± 9.7 SD % were surveyed at least in one secondary period every year. Of these, 17.7 ± 9.5 % sites/year were surveyed in both secondary periods, 12.7 ± 4.4 % were surveyed only in the first secondary period (January – March), and 13.2 ± 4.2 % were surveyed only in the second secondary period (September – December).

Supplementary data of AM and EM detection histories at each site are available at http://dx.doi.org/10.1594/PANGAEA.831490 and in the Appendix.

Two species multi-season occupancy model

We used a two species multi-season occupancy model to quantify the occupancy dynamics of AM and EM and any interactions between the species. The original model parameterization proposed by MacKenzie *et al.*, (2006) and implemented by Hines (2006) in software PRESENCE (version 5.9) estimates 4 groups of variables (Table 1): occupancy (*psi*), the probability that a site is occupied by one species; the probability of detecting one species at a site in the presence (*r*) or absence (*p*) of the competitor; colonization (*gam*), the probability that an unoccupied site in year t is occupied in year t+1; extinction (*eps*), the probability that a site occupied in year t becomes unoccupied in year t+1. For each group, we also estimated the parameters describing species interaction showed in Table 1.

Because we aimed to detect and quantify species interaction in occupancy and detection, we used the *phi/delta* parameterization of the model. Parameter *phi*, the "species interaction factor" (SIF), is a ratio of how likely the two species are to co-occur compared to what would be expected under the hypothesis of independence, defined by the following equation:

$$Phi = PsiAM.EM \,/\, PsiAM \times PsiEM$$

Where *psiAM.EM* is the probability of both species being present. Values < 1 indicate that the two species co-occur less often than expected, suggesting avoidance or competitive exclusion, while values > 1 indicate positive association. In a similar way, the detection interaction factor, *delta,* denotes whether the two species are detected independently of each other at survey sites. Delta < 1 indicates that one species was less likely to be detected during a survey period if the other species was detected, whilst the reverse is the case for values >1.

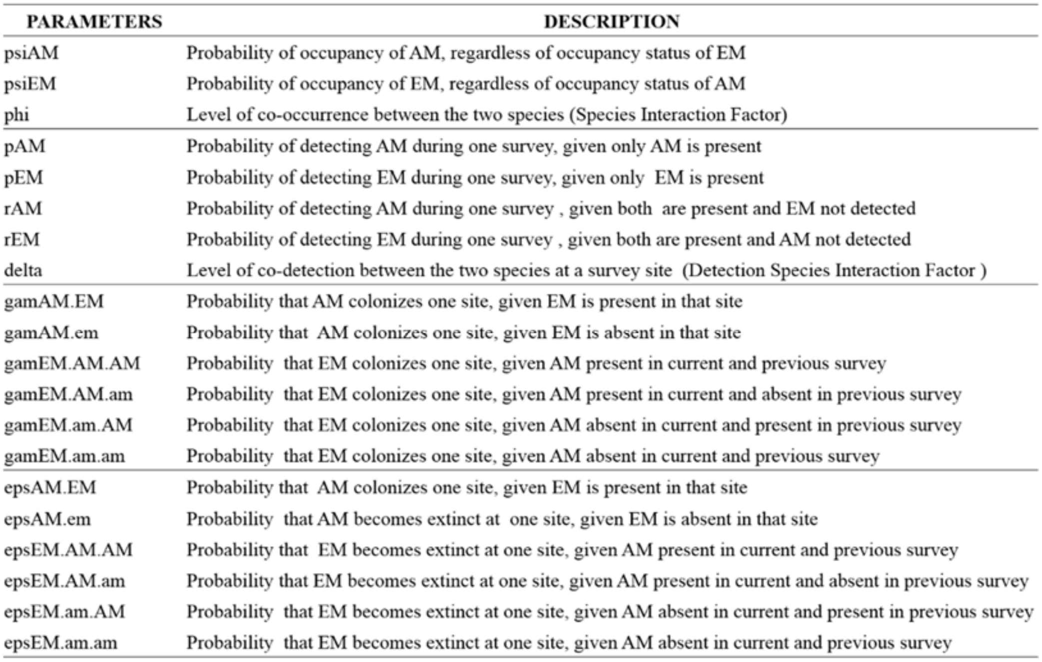
Models were ranked using the Akaike Information Criterion (AIC). Models with a $\Delta AIC \leq 4$ were considered good descriptors of the data, and models with $4 \leq \Delta AIC \leq 7$ had lower empirical support (Burnham and Anderson, 2002).

One critical assumption of occupancy models is that of "closure" meaning that the occupancy status does not change over the primary period at each site, in order not to introduce bias in detection probability estimation.

While this assumption was readily applicable to the European mink, removal of AM could violate it if all AM present at a site were caught. If removal trapping changed true AM occupancy, an excess of detection histories "10" (detected in first secondary session, not detected in the second) inside one primary period would be expected and this could lead to underestimating AM detection probability.

However, according to MacKenzie *et al.* (2006) if individuals exhibit random movement in and out of surveyed sites, then the closure assumption may be relaxed, although the occupancy estimation would then reflect the probability that the species was present at a site at least in one of the surveyed occasions. A "nonparametric multiple test procedure for many-to-one and all pairs comparisons" (Gao *et al.*, 2008) was applied to compare "10" , "01" and "11" histories frequencies for both species.

A second source of bias in occupancy estimation can be heterogeneity in detection probability due to differing species abundance at different site (MacKenzie, 2005). In our study, area the number of AM trapped was highly variable. In the southwestern part AM is found at the highest density (on average 0.22 ± 0.71 captures/trap-nights over the study period), possibly because an earlier establishment of feral populations in the area (Palazón, pers. comm.). In the central and Atlantic part of the study area, the core area of EM distribution, lower numbers of individual AM were captured per sampling event (0.08 ± 0.18), whilst in the easternmost part AM was only rarely captured (0.01 ± 0.03). We thus modelled detection probabilities as a function of AM density, by selecting three sub-areas representing high, medium and low density of AM (Fig.1b). The same number of cells was assigned to each sub-area.



PARAMETERS	DESCRIPTION
psiAM	Probability of occupancy of AM, regardless of occupancy status of EM
psiEM	Probability of occupancy of EM, regardless of occupancy status of AM
phi	Level of co-occurrence between the two species (Species Interaction Factor)
pAM	Probability of detecting AM during one survey, given only AM is present
pEM	Probability of detecting EM during one survey, given only EM is present
rAM	Probability of detecting AM during one survey , given both are present and EM not detected
rEM	Probability of detecting EM during one survey , given both are present and AM not detected
delta	Level of co-detection between the two species at a survey site (Detection Species Interaction Factor)
gamAM.EM	Probability that AM colonizes one site, given EM is present in that site
gamAM.em	Probability that AM colonizes one site, given EM is absent in that site
gamEM.AM.AM	Probability that EM colonizes one site, given AM present in current and previous survey
gamEM.AM.am	Probability that EM colonizes one site, given AM present in current and absent in previous survey
gamEM.am.AM	Probability that EM colonizes one site, given AM absent in current and present in previous survey
gamEM.am.am	Probability that EM colonizes one site, given AM absent in current and previous survey
epsAM.EM	Probability that AM colonizes one site, given EM is present in that site
epsAM.em	Probability that AM becomes extinct at one site, given EM is absent in that site
epsEM.AM.AM	Probability that EM becomes extinct at one site, given AM present in current and previous survey
epsEM.AM.am	Probability that EM becomes extinct at one site, given AM present in current and absent in previous survey
epsEM.am.AM	Probability that EM becomes extinct at one site, given AM absent in current and present in previous survey
epsEM.am.am	Probability that EM becomes extinct at one site, given AM absent in current and previous survey

Table 1 Parameters estimated by the two-species multi-season occupancy model proposed by MacKenzie et.al (2006). AM is the invasive American mink and EM is the native European mink.

Model setting

We first addressed whether the species occurred independently or whether there was an evidence of competitive exclusion of EM from the areas occupied by AM. To analyze the dynamical processes of occupancy, we multiplied the vector of the probabilities of a cell being in four possible states (both species present, only AM, only EM, both absent) at time t = 1 by a transition probability matrix as defined in MacKenzie *et al* (2006). Each element within the transition matrix represents the probability of a site changing from one occupancy state to another between seasons. The state vector and the transition probability matrix were defined from the estimations obtained from the best ranked model.

We hypothesized that detection of the two mink species was not independent and that they were less likely to be detected when occurring at the same time at a site (*delta* < 1). As a consequence of the higher abundance, smaller home ranges and inter-specific aggressive behavior of AM (Põdra *et al.*, 2013; Sidorovich *et al.*, 1999), we expected EM to be less detectable when in sympatry with AM. Moreover, we expected detection probabilities of both species to change in function of AM density.

We aimed to detect the effect of AM on colonization and extinction probabilities of EM. We expected EM colonizing success of sites occupied by AM to be lower and the extinction rate to be higher than in its absence. We predicted that the probability of colonization of AM in presence of EM should be lower than the colonization in absence of the competitor. On the other hand, AM could be attracted by territories occupied by the native species because of their qualities (i.e. availability of prey and shelter, higher water quality). In addition, we expected the removal of AM inside the range of EM to translate into higher estimations of extinction probability in sympatry with EM, because this is where the strongest effort in AM removal was focused. As we were interested in detecting changes in the probability of colonization and extinction of both species, we allowed for *gam* and *eps* to vary between years.

RESULTS

Sufficient data was available from 204/318 sites, surveyed 1905 times between 2000 and 2011. EM was detected 497 times over the study period, and AM was detected 820 times.

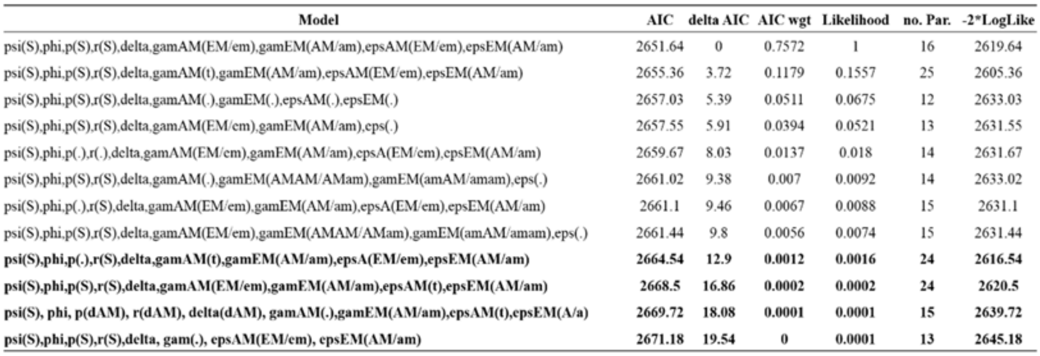
Closure assumption and detection histories frequencies

The analysis of detection histories of AM supported our assumption that true occupancy varied little within primary periods despite the removal of trapped AM. Indeed, there was no excess in the frequency of “10” occupancy histories (AM detected in the first secondary period – non detected in the second secondary period) relative to histories “01” or “11” over the 204 sites analyzed. Histories frequencies “10” and “01” were not significantly different (p-value= 0.3175, alpha=0.05, two-tailed), whilst “10” and “11” comparison gave different frequencies (p-value=0,009) being “11” the most recurrent detection history. In the case of EM, the only detection histories frequencies that resulted to be significantly different were “10” and “11” (p-value=0.0016), where again the “11” history showed the highest occurrence.

Interaction, occupancy and detection

Model selection results (Table 2) and parameter estimations (Fig.3) provided evidence of competitive exclusion of EM from the areas invaded by AM and revealed the impact of AM on native species’ probability of colonization and extinction. In the parameterization of the best ranked model, occupancy probabilities of each species (*psiAM* and *psiEM*) and their interaction factor (*phi*) were estimated; detection probabilities depended on the presence or absence of the counterpart ($pAM \neq rAM$ and $pEM \neq rEM$); colonization and extinction probabilities of EM were dependent upon the occupancy status of AM in the current year (i.e. $gamEM.AM \neq gamEM.am$) but independent from it in the previous year (i.e. $gamEM.AM.AM = gamEM.AM.am$ and $gamEM.am.AM = gamEM.am.am$) (see Table 1 for parameter descriptions).

The Species Interaction Factor estimated by this model (*phi* = 0.46 ± 0.17 SE) indicated that the species co-occurred less often than expected under the assumption of independence, which suggests species avoidance or competitive exclusion. More interestingly, when projected over the entire study period (as described in section 2.4.1), the SIF tended to be constant, suggesting that the magnitude of competitive exclusion did not change over time (Fig.2, solid line).



Model	AIC	delta AIC	AIC wgt	Likelihood	no. Par.	-2*LogLike
psi(S),phi,p(S),r(S),delta,gamAM(EM/em),gamEM(AM/am),epsAM(EM/em),epsEM(AM/am)	2651.64	0	0.7572	1	16	2619.64
psi(S),phi,p(S),r(S),delta,gamAM(t),gamEM(AM/am),epsAM(EM/em),epsEM(AM/am)	2655.36	3.72	0.1179	0.1557	25	2605.36
psi(S),phi,p(S),r(S),delta,gamAM(.),gamEM(.),epsAM(.),epsEM(.)	2657.03	5.39	0.0511	0.0675	12	2633.03
psi(S),phi,p(S),r(S),delta,gamAM(EM/em),gamEM(AM/am),eps(.)	2657.55	5.91	0.0394	0.0521	13	2631.55
psi(S),phi,p(.),r(.),delta,gamAM(EM/em),gamEM(AM/am),epsA(EM/em),epsEM(AM/am)	2659.67	8.03	0.0137	0.018	14	2631.67
psi(S),phi,p(S),r(S),delta,gamAM(.),gamEM(AMAM/AMam),gamEM(amAM/amam),eps(.)	2661.02	9.38	0.007	0.0092	14	2633.02
psi(S),phi,p(.),r(S),delta,gamAM(EM/em),gamEM(AM/am),epsA(EM/em),epsEM(AM/am)	2661.1	9.46	0.0067	0.0088	15	2631.1
psi(S),phi,p(S),r(S),delta,gamAM(EM/em),gamEM(AMAM/AMam),gamEM(amAM/amam),eps(.)	2661.44	9.8	0.0056	0.0074	15	2631.44
psi(S),phi,p(.),r(S),delta,gamAM(t),gamEM(AM/am),epsA(EM/em),epsEM(AM/am)	**2664.54**	**12.9**	**0.0012**	**0.0016**	**24**	**2616.54**
psi(S),phi,p(S),r(S),delta,gamAM(EM/em),gamEM(AM/am),epsAM(t),epsEM(AM/am)	**2668.5**	**16.86**	**0.0002**	**0.0002**	**24**	**2620.5**
psi(S), phi, p(dAM), r(dAM), delta(dAM), gamAM(.),gamEM(AM/am),epsAM(t),epsEM(A/a)	**2669.72**	**18.08**	**0.0001**	**0.0001**	**15**	**2639.72**
psi(S),phi,p(S),r(S),delta, gam(.), epsAM(EM/em), epsEM(AM/am)	**2671.18**	**19.54**	**0**	**0.0001**	**13**	**2645.18**

Table 2. The eight most supported multi-season two-species occupancy models based on AIC (Akaike's Information Criterion). Models with a delta AIC ≥10 (less empirical support) are shown in bold below the top eight. The models were fitted to detection data of the invasive American mink (AM) and the critically endangered European mink (EM) in the study area between 2000 and 2011. The terms in parentheses represent the source of variation in model parameters. 'S' denotes species – specific differences, 'AM/am' means in presence/absence of AM, 'EM/em' means in presence/absence of EM. 't' denotes time dependence and '.' indicates a parameter set equal across species and seasons, 'dAM' refers to the 3 sub-areas with different American mink density. Delta AIC = difference in AIC values between each model and the first ranked model. AICwgt = model weight. no.Par = number of parameters in the model. -2*LogLike = twice the negative log-likelihood.

Initial probability of occupancy of AM and EM regardless the occupancy status of the competitor were comparable (*psiAM* = 0.467 ± 0.062, *psiEM* = 0.523 ± 0.054), but over the study period the probability of a site being occupied only by EM decreased substantially (from 0.407 ± 0.062 in 2000 to 0.195± 0.062 in 2011), whilst AM occupancy probability increased (from 0.351 ± 0.054 in 2000 to 0.480 ± 0.054 in 2011) (Fig.2). Site transition probabilities from one occupancy state to the other are based on colonization and extinction rates, and the observed reduction of EM occupancy means that the species became extinct in more sites that it colonized. The fact that the probability of a site being occupied by both species at the same time was roughly constant (dotted line in Fig.2) is indicative of AM continuously colonizing sites occupied by EM.

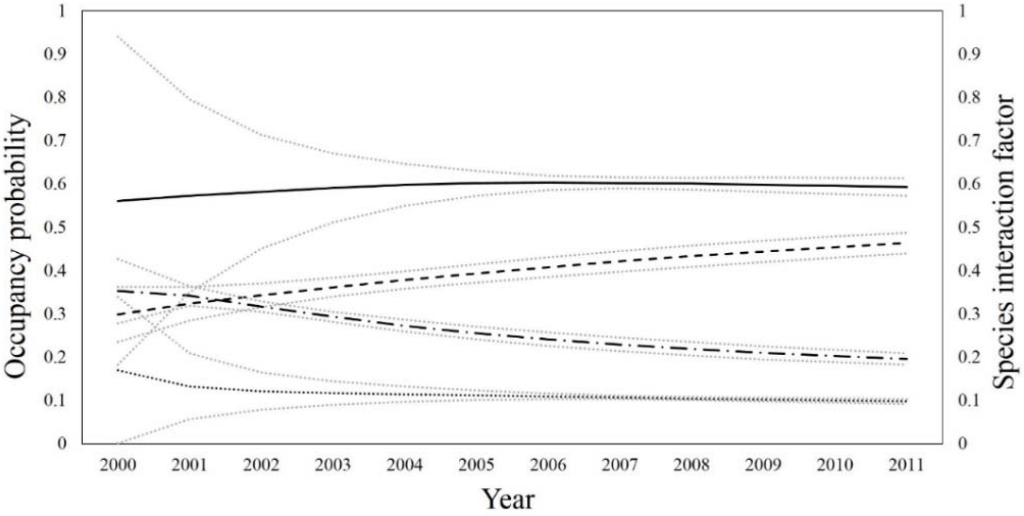


Figure 2. Seasonal probability of occupancy (left vertical axis) obtained from the best AIC ranked model of three possible states: only American mink present (dashed line), only the European mink present (dash-dotted line) and both species present (dotted line). On the right vertical axis: seasonal Species Interaction Factor (SIF) represented by the solid line. Standard errors in light grey dotted line.

Delta value of 0.717 (± 0.063) indicated that when the two mink co-occurred at a site, they were less likely to be detected than when one competitor was absent (Fig.3a). AM had a significantly higher probability of being detected than EM when only one species was present (*pAM* = 0.826 ± 0.019; *pEM*= 0.690 ± 0.038) which is consistent with higher abundance and smaller home ranges of AM (Fig.3a). When the mink species co-occurred, detectability of EM was almost unchanged but that of AM was significantly lowered (*rAM* = 0.517 ± 0.068; *rEM* = 0.665 ± 0.056), the latter likely being the effect of more intensive culling effort and lower density in the area of co-occurrence with EM. On the other hand, AIC did not support the model of dependence of both species detectability on AM density (Table 2).

Colonization and extinction

The probability that an unoccupied site was colonized in the next year was significantly higher for AM than for EM, independent of the occupancy status of the competitor species (Fig.3b). AM preferentially colonized sites already occupied by EM (*gammaAM.EM* = 0.129 ± 0.033; *gammaAM.em* = 0.090 ± 0.026), whilst EM had a small probability of colonizing areas already occupied by AM (*gamEM.AM* = 0.014±0.007) and a slightly higher probability of colonizing an unoccupied site (*gamEM.am* = 0.042±0.019).

Interestingly, the highest estimated probability of extinction was for AM in sympatry with EM (*epsAM.EM* = 0.254 ± 0.081) (Fig.3b), consistent with the local impact of AM culling not being compensated by re-colonization, at least in the next year. In the absence of EM, the extinction rate of AM was the lowest of the four estimated extinction parameters (*epsAM.em* = 0.032 ± 0.012), even though AM were culled irrespective of the known presence of EM. Extinction rate of EM was nearly twice as high when it co-occurred with AM than in its absence (*epsEM.AM* = 0.130 ± 0.045; *epsEM.am* = 0.072 ± 0.024) which again supported the hypothesis of competitive exclusion of EM from territories occupied by AM.

The second best ranked model (Delta AIC 3.72) only differed from the first by the fact that colonization probability of AM was fully time dependent. The estimation of AM probability over the study period (Fig.3c) shows a pattern of values oscillating between a maximum of 0.314 to a minimum of 0, independently from the presence of EM. Model where AM probability of extinction was time constrained was not supported by AIC. None of the models where colonization and extinction probability of EM varied with time were supported.

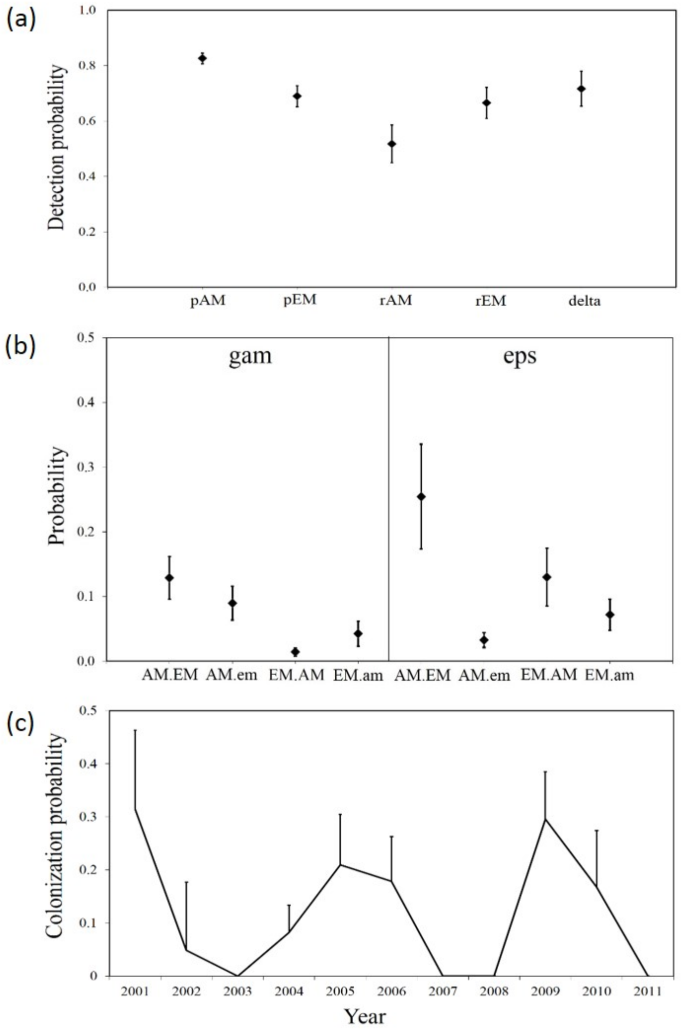


Figure 3. Results of detection (a), colonization (b and c) and extinction (b) probabilities estimations obtained in the study. a) Detection probabilities estimated by the best-ranked model. AM = American mink and EM = European mink. pAM= probability of detecting AM, given only AM present, pEM = probability of detecting EM, given only EM present, rAM = probability of detecting AM, given both species are present and EM not detected, rEM = probability of detecting EM, given both are present and AM not detected, delta = detection species interaction factor. b) Colonization (gam) and extinction (eps) probabilities from the best-ranked model. AM.EM = probability of AM colonizing / becoming extinct at one site, given EM present. AM.em = probability of AM colonizing / becoming extinct at one site, given EM absent. EM.AM = probability of EM colonizing / becoming extinct at one site, given AM present. EM.am = probability of EM colonizing / becoming extinct at one site, given AM absent. c) Time varying American mink colonization probability derived from the second best ranked model.

DISCUSSION

Our analysis on the pattern of co-occurrence of the invasive non-native American mink and the critically endangered European mink at a large spatial scale over multiple seasons using a two-species multi-season occupancy model revealed their asymmetrical competitive interaction. Methodologically, it is likely that the high number of sampling events (seasons) and sites surveyed compensated for the high frequency of missing values resulting from inconsistent survey effort. As a result, fairly precise estimations of model parameters were obtained and formed the basis for our inference.

Even though occupancy models do not allow direct deductions on mechanisms underlying the observed occurrence (MacKenzie *et al.*, 2006), the inverse tendencies in the occupancy of the two mink species over the last decade strongly indicated a substantial effect of the range expansion of the invasive species on the decline of the native one. In spite of earlier claims to the contrary, we support the hypothesis that the competitive exclusion operated by the invasion of AM is leading to the overall range contraction of the critically endangered EM in Spain. Indeed the species co-occurred less often than expected if they did not interact, the native mink was more likely to become extinct from sites occupied by the invasive species than from sites where the competitor was absent, and had scarce probability of colonizing areas already invaded by AM.

On the contrary, AM tended to preferentially colonize sites occupied by the native mink, a further evidence of competitive exclusion. EM has narrower habitat requirements than AM, selecting territories with non-polluted watercourses, high fish biomass (Lodé, 2002), dense riparian vegetation and low human disturbance (Zabala *et al.*, 2006). These habitat features are likely to be highly attractive to AM and aggressive displacement from territories (Maran, 2007; Sidorovich *et al.*, 1999), as well as inter-specific killing (Põdra *et al.*, 2013) are likely to be facilitated by the larger size of AM. There is some existing evidence that scenario of competitive displacement similar to the one we documented here plays out wherever AM and EM coexist. While previous studies documented the displacement of EM by AM from slow-flowing rivers, which represent the highest quality habitat for both species, to the upper reaches of catchment and very small streams (Sidorovich, 2001; Maran *et al.* 1998a), local replacement of EM by AM after a short period of co-existence has been previously reported in a two year study in the Basque Country in Spain (Ceña *et al.*, 2003).

The elevated AM extinction probability when it co-occurred with EM indicated that culling of AM had at least a short term local impact even though the increasing overall AM occupancy imply that management efforts were ineffective at a larger scale. Locally, AM removal suppressed density and slowed down the process of replacement of EM by AM. Indeed, the colonization probability of 10 km x10 km cell by AM in the presence of EM was lower than its extinction probability. In contrast, the detection probability of EM was unaffected by the detection of its competitor ($pEM \approx rEM$), whilst trapping and culling reduced AM detectability when in sympatry with EM, which again reflected depressed density and hence detection probability. The main effect of this heterogeneity in AM density could be the underestimation of occupancy probability in the area of co-occurrence with EM (see MacKenzie, 2005), which would translate in a worse scenario than the one we depict here. On the other hand, the lack of excess of '10' AM detection histories likely compensated for this 'spatial bias' in the overall occupancy estimation.

Overall, our analyses depict a situation where there is no scope for long-term coexistence of the two mink species such that the replacement of EM by AM seems unavoidable unless the effectiveness of ongoing management actions is substantially improved. While many AM culling programs have failed to overcome the compensatory mechanisms involving changes in reproduction and immigration (Melero *et al.*, 2010b; Bonesi *et al.*, 2006) succeses highlighted the paramount importance of stemming the flow of dispersers that readily recolonise control areas.

Nordström *et al* (2002) achieved this by working on the outer edge of an island archipelago while Bryce *et al.* (2011) and Zalewski *et al.* (2009) combined topography, a dense spatial coverage of mink detection raft operated nearly year round so as to rapidly detect and deal with instances of recolonisations and a continuously expanding front of control that intercepted potential recolonists.

Recolonization was well predicted by connectivity including both mink abundance with a one year lag and the distance between controlled areas and sources of recolonists. Crucially, mink more than 30 km away were predicted to effectively reinvade controlled areas.

Accordingly, the fluctuating trend in AM colonization probability (Fig.3c) could reflect not only a pattern regarding AM that was trapped in a given site and in a given year, but also the influence of AM born further afield yet able to travel long distance to re-colonise suitable habitat. Furthermore, year-to-year variation in culling effort reflecting variable funding probably contributed to re-colonisation and the failure of efforts to protect EM.

In conclusion, our study unambiguously documented a contracting distribution of EM resulting from the expansion of AM in Northern Spain.

Our use of the two species occupancy modelling framework applied to data collected with an ad hoc design proved highly informative in revealing a pattern of gradual replacement of the native by the invasive mink species.

Current management efforts aimed at averting the eventual extinction of the European mink are inadequate and failing. Given the high recolonisation ability of American mink, much more intensive efforts are required to provide a comprehensive spatial coverage to remove mink from the whole of EM range and a suitably large buffer area.

It is also necessary to verify the continuing absence of AM from previously controlled areas using an appropriate sampling design so as to obtain evidence that management efforts succeed.

This is likely to be challenging due to the extent of the area invaded by AM, even though low-cost non-invasive genetic methods have proved to be effective in detecting and identifing mustelid species (Gómez-Moliner *et al.*, 2004).

It remains however that without decisive action funded over a sufficiently long time scale, there is no ground for optimism regarding the future of European mink in Spain, and indeed, in the remainder of its range invaded by American mink.

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CHAPTER 2

USING A DYNAMIC N-MIXTURE MODEL TO DETECT LARGE-SCALE TEMPORAL AND SPATIAL TRENDS IN THE ABUNDANCE OF THE CRITICALLY ENDANGERED EUROPEAN MINK IN SPAIN: IS THE POPULATION DECLINING?

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ABSTRACT

Assessing temporal and spatial trends in the abundance of a critically endangered species may give valuable information on the effectiveness of management programs and on how to improve conservation strategies.

Recently developed analytical approaches, named N-mixture models, enable the estimate of abundance, detection probability and population dynamic parameters by assuming a population open between surveyed periods.

The Spanish population of the European mink is thought to be in decline, although population assessments have been based only on density estimates over small areas so far.

In this study, we explored the temporal and spatial changes of the European mink abundance, using count data from a large-scale monitoring program carried out between 2000 and 2010 in its entire range of distribution in Northern Spain.

We detected a slow decrease of the population, as well as a spatially variable abundance, with the higher parameter's values associated with the central part of the range: the upper part of the Ebro river basin.

Abundance was positively correlated to small and, secondarily, medium-size rivers, whilst precipitation of the driest and wettest month, natural vegetation cover and human disturbance had little impact on population size at the spatial resolution and the extent of the analysis.

Although the causes of the decline did not emerged clearly, the negative trend in the population abundance indicated that stronger efforts are required to protect the European mink in Spain. Conservation actions should focus on the area most closely related to rivers and riverbanks and special attention should be paid to the largest central sub-population of the European mink.

RESUMEN

El análisis de la tendencia espacial y temporal en la abundancia de una especie en peligro crítico de extinción puede dar valiosas informaciones sobre la eficacia de los programas de gestión y sobre cómo mejorar las estrategias de conservación.

Los modelos N-mixture, una técnica de análisis recientemente desarrollada, permiten estimar la abundancia, la probabilidad de detección y parámetros de dinámica poblacional asumiendo una población abierta (a través de nacimientos y migraciones) entre los diferentes periodos muestreados.

La población española del visón europeo parece haber disminuido en los últimos años, si bien las evaluaciones del estado de la población hasta el momento han sido basadas en estimaciones de densidad en pequeñas áreas.

En el presente estudio se ha analizado los cambios espaciales y temporales en la abundancia de la población de visón europeo, usando recuentos de individuos entre los años 2000 y 2010 llevados al cabo en un programa de monitoreo a amplia escala en la totalidad del área de distribución de la especie en el Norte de España.

Se ha detectado un lento declive de la población de visón europeo, así como una variabilidad espacial en su abundancia, cuyo valores más altos se encuentran asociados a la parte central del área de distribución: la parte alta del rio Ebro y sus afluentes.

El visón europeo es más abundante en los ríos de dimensiones pequeñas y medianas que en los ríos grandes. Se ha detectado que la precipitación del mes más seco y más húmedo, la cobertura de vegetación natural y el impacto humano tienen un efecto mínimo en la densidad poblacional a la escala espacial del análisis.

Aunque en el análisis realizado no se han detectado las causas directas del declive, la tendencia negativa en la población indica que se requiere un esfuerzo mayor para proteger el visón europeo en España.

Las medidas de conservación deberían estar centradas en el área más estrictamente relacionada con los ríos y las riberas, y se debería prestar una atención especial a la sub-población que se encuentra en la parte central del área de distribución.

INTRODUCTION

Estimate changes over time in the abundance of a critically endangered species is a crucial issue to determine the population status and viability, to assess management programs efficiency and to implement effective conservation actions.

An accurate measure of abundance though can be difficult to obtain, mainly because of the imperfect detection of individuals present in the study area (Thompson, 1992). Population size will be under-stated when simple counts are regarded as true abundance due to the fact that while detection of a species at a location may be unambiguous, non-detection may be due either to a real absence or to a failure to detect its presence (Martin *et al.*, 2011; Stanley and Royle, 2005; MacKenzie, 2005; Royle and Nichols, 2003).

The spatial scale at which we observe a group of individuals is also important to determine population trend: local patterns may not be representative of processes occurring at the population level, because the effect of environmental factors on observed abundance is scale-dependent (Holland *et al.*, 2004; Lundberg *et al.*, 2000). For example, at micro-scale the number of individuals may be limited by the availability of suitable breeding site, at macro-scale the temperature or precipitation may be the most important predictors (Bevers and Flather, 1999).

One of the most reliable sampling design to estimate the probability that an animal present in the area of interest appears in count statistics is the capture-recapture method (William *et al.*, 2002). This design though can be difficult to implement because typically requires an intense and constant effort (Jakob *et al.*, 2014;

Stanley and Royle, 2005; Royle and Nichols, 2003), and hence it may be too expensive, especially in large-scale monitoring programs.

Recently developed analytical approaches enable the estimate of abundance and detection probability using spatially and temporally repeated counts of unmarked individuals (Dail and Madsen 2011; Royle 2004). They are named N-mixture models for combining a simple Poisson generalized linear model, for the unobserved abundances, with a simple Binomial generalized linear model, used to describe the detection process (Kéry, 2010).

The dynamic formulation of these models (Dail and Madsen 2011) relaxed the typical 'close population assumption' (as in Royle, 2004) by including dynamic parameters (births - immigrations and death - emigrations) which can be used to estimate spatial and temporal changes in population size in studies conducted over several years.

Even though these models are becoming increasingly popular for providing a simple and cost-effective way to estimate abundance and account for imperfect detection (Martin *et al.*, 2011), few applications of the dynamic models have been proposed so far, and they focused mainly on avian and game species (Jakob *et al.*, 2014; Hua *et al.*, 2013; Roberts *et al.*, 2013).

In this study, we applied a dynamic N-mixture model to estimate spatial and temporal trend in the abundance of the critically endangered European mink over its Spanish range of distribution.

The European mink is one of the most threatened carnivores in Europe, disappeared from 85% of its range over the last century, and categorized as "critically endangered" by the IUCN since 2011 (Maran *et al.* 2011). However, the species entered in Spain surprisingly recently: the first record was in 1951 (Rodríguez de Ondarra, 1955), and since then the species expanded south- and eastward, following the main river basins in the Northern part of the country (Zabala *et al.*, 2004; Palazón *et al.*, 2003).

Currently, the largest sub-population of the European mink is believed to be located along 250 km of the upper Ebro and tributaries, an area included in the Provinces of Álava, La Rioja and North Burgos (Palazón and Melero, in press). The species inhabits non-polluted slow-flowing watercourses with dense riparian vegetation and low human-disturbance (Zabala *et al.*, 2003; Lodé, 2002; Lodé *et al.*, 2001).

In Spain the European mink is exposed to habitat loss and fragmentation (Zuberogoitia *et al.*, 2013; Zabala and Zuberogoitia, 2006), high human-induce mortality rate (Palazón *et al.*, 2012), low genetic variability (Michaux *et al.*, 2005) and the spread of an invasive non-native competitor, the American mink (*Neovison vison*) (Palazón *et al.*, 2013; Palazón *et al.*, 2003). This latter threat is seen as one of the most alarming, as the invader is expanding inside the area of distribution of the European mink and evidences of an ongoing replacement (Santulli *et al.*, 2014) and direct aggressions (Põdra *et al.*, 2013) have been recently reported.

Determining patterns of the European mink's abundance in Spain is hence crucial to evaluate the effectiveness of the ongoing management programs and improve conservation strategies. Although the population is believed to be in decline (Palazón and Melero, in press), only local estimates of its density based on capture-recapture methods were carried out (Palazón *et al.*, 2006a), and in general its reduction has been explored through changes in its distribution (i.e. disappearance from some areas) rather than in its abundance (MAGRAMA, 2009; Palazón *et al.*, 2006b).

In this study we aimed to asses changes in the population's abundance over the last years using count data from a large-scale monitoring program carried out between 2000 and 2010 in the entire range of distribution in Northern Spain. Moreover, we explored the effect of several environmental factors potentially involved in population changes (namely water availability, human disturbance and proportion of natural habitat, river dimension and the presence of the

American mink) on the parameters of abundance, detection probability and the rate of increase of the population.

Detected spatial and temporal trends were used to make inference on the status of the population and to provide sound basis to guide management actions for the species' conservation.

MATERIAL AND METHODS

Study area

The study was conducted in eight Provinces of Northern Spain: Burgos, Alava, La Rioja, Biscay, Guipúzcoa, North Soria, South Navarre, North, and Western Zaragoza (Fig.1), an area included between 41.8 º N - 43.4 º N and 3.8 º W and 0.9 º W.

Major tributaries of three main river basins were sampled: the Ebro basin, the northeastern part of the Duero basin (mainly along the Alarzón River) and the Atlantic basin. The study area includes both Mediterranean and Atlantic bioclimatic regions, and areas of transition between both.

The Ebro and the Duero are two of the largest rivers of the Iberian Peninsula and they are located in the Mediterranean region. Seasonal low flows and extreme flush effects characterize rivers of these basins. Mean temperature in this area ranges between 2ºC and 19ªC, and average precipitation between 350mm and 1600mm (AEMET, 2011).

Rivers of the Atlantic region flow northward, and generally they are short, narrow, with steep gradients and they are characterized by a torrential regime, with the highest flow in the wet season. In this area, average annual temperatures are between 1ºC and 16ºC and average annual rainfall between 700 and 2700 mm (AEMET, 2011).

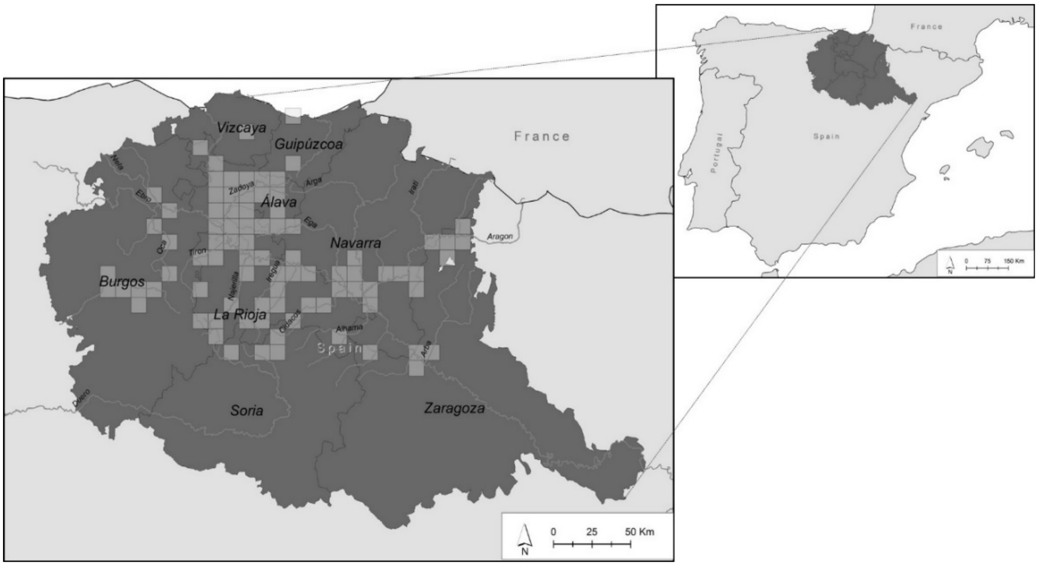


Figure 1. The study area covered eight Provinces in Northern Spain. Grey squares show the 10x10 km U.T.M. cells surveyed between 2000 and 2010 during the European mink monitoring program.

Species surveys and sampling design

European mink count data were gathered from live trapping surveys conducted between 2000 and 2010 following a protocol developed by managers and technicians involved in the European mink National Conservation Strategy coordinated by the Spanish Ministry of Agriculture, Food and Environment.

The procedure involved at least one trapping station per 10x10km Universal Transverse Mercator (U.T.M.) cell, and it included ten baited cage-traps (15 cm x 15 cm x 60 cm) placed along riverbanks sections of 1 to 5 km at a distance of 100 – 300 m from each other, and operated for 10 consecutive nights. Captured individuals were marked with a subcutaneous passive transponder and released once recovered from the anesthesia.

Although capture-recapture data were available, we decided not to use them mainly for the very low recapture rate observed in the study area (4.6%, Palazón *et al.*, 2006a), which may results in very low detectability and hence biased abundance estimation.

In theory, trapping surveys were carried out twice a year during the species pre-breeding season (from January to mid-March) and in the post-breeding season (from September to December) in order not to interfere with species reproduction. In practice, trapping effort and number of visits varied largely between years and Provinces, depending on funding availability and regional government policies.

Counts of captured individuals were extrapolated in the surveyed 10x10km U.T.M. cells for each pre and post-breeding period (secondary periods hereafter) each year between 2000 and 2010 (primary periods hereafter).

Only sites where at least two consecutive secondary periods were sampled in one primary period over the study were selected. Over 22 secondary periods, on average 6.03 ± 3.01 SD visits per site were carried out, being 3 the minimum and 19 the maximum.

We assumed the spatial resolution of the analysis (10x10km) to be suitable to observe independently several individuals, based on species' mean linear home range in the study area (Males 13.1 ± 2.8 SD km and females: 3.4 ± 2.8 km, Palazón and Ruiz-Olmo, 1998).

We used a robust sampling design, made of two count repetitions in one year, which is essential to estimate detection probability, to obtain more precise and accurate parameters estimates and to compensate for missing value in count data (Dail and Madsen, 2011; MacKenzie *et al.*, 2006).

There was a high variability in the number of trap-nights at each site and between secondary periods: mean number of trap-nights over secondary periods was 264.22 ± 114.79 and over the 86 sampled sites was 212.10 ± 166.44.

This variability could have introduce a bias in in count data, because a more intense trapping effort would produce higher count values even if a site is not inhabited by a higher number of individuals.

To overcome this limitation we first tested for the linear relationship between number of captured individual and number of trap-nights: linear regression analysis gave significant results ($R = 0.626$, p-value < 2.26 e-16). The fact that number of captured individual was significantly and positively correlated to number of trap-nights allowed us to use weighted count data obtained by dividing observed values by number of trap-nights.

Dynamic N-mixture abundance modeling

The temporal and spatial trend in the abundance of the European mink in the decade 2000 – 2010 was modeled using a dynamic N-mixture model (Dail and Madsen, 2011).

This model is a generalization of original formulation by Royle (2004) which uses both spatial and temporal replication of count data to jointly estimate local abundance at site *i* in time *t* (N_{it}) and the probability of detection (p). Conditional on p and N_{it}, the observed count n_{it} is a binomial random variable $n_{it} \sim \text{Bin}(N_{it}, p)$.

Royle's model is based on the assumption that population at each site cannot experience births, deaths or migrations and is hence constant over the studied period. While this statement can be valid for i.e. a single breeding season, it is easily violated in annual counts studies.

Dail and Madsen (2011) relaxed the closure assumption including the parameters of the initial population state (λ, the abundance in the first year of sampling), the recruitment rate (γ, births and immigrations), and the apparent survival rate (ω, deaths and emigrations).

This generalization assumes that abundance can change between primary periods, but not over one secondary period. Moreover detection heterogeneity can be estimated across time *t* and sites *i* and is assumed to be independent between sites.

We performed the Dail and Madsen model using the R software package *unmarked* version 0.10 – 4 (Fiske and Chandler, 2011). To assess changes in abundance of the European mink population we chose the "trend" population dynamic option which allows estimating the tendency in model's parameters by setting the dependence of the recruitment rate γ on the population abundance at site *i* during the previous sampling period

$$N_{it} = N_{i,t-1}\,\gamma$$

So that γ actually represents the finite rate of increase of the population, which can be seen as the ratio of population size at the end of one interval to population size at the end of the previous interval. This option of the model can be summarize as:

$$N_{i1} \sim \text{Poisson}\ (\lambda_i)$$

$$N_{it} \sim \text{Poisson}\ (\gamma\, N_{it-1})$$

$$n_{ijt} \sim \text{Binomial}\ (N_{it}, p)$$

where n_{ijt} is the number of distinct individuals counted at location *i* in secondary period *j* in year *t* and λ_i is the expected population size at site *i*.

Models selection was performed using the Akaike Information Criterion (AIC) Models with a ΔAIC ≤ 4 were considered good descriptors of the data, and models with 4 ≤ ΔAIC ≤ 7 had lower empirical support (Burnham and Anderson, 2002). Moreover we assessed the goodness of fit of the top ranked models using a parametric bootstrap based on Pearson chi-square test statistic (number of simulation = 1000).

To draw the inference from the best ranked models we computed model-averaged parameters estimates and their unconditional standard errors for model whit ΔAIC ≤ 4 using the AICmodavg R package version 2.00 (Mazerolle, 2014).

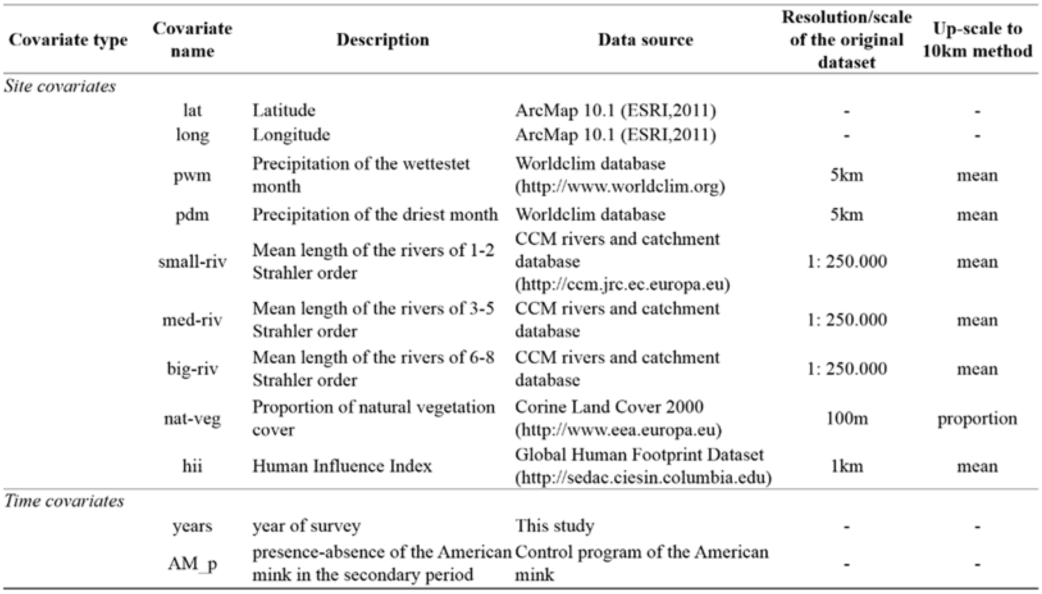
Environmental covariates and biological hypotheses

Environmental covariates that may influence temporal and spatial variation in the abundance, the rate of increase and detection probability of the European mink population were characterized based on the species known ecology, on conservational problems and on the spatial resolution of the analysis (10km).

We used latitude and longitude as covariates to detect geographic variability in models parameters, and to identify potential areas of higher or lower abundance. In particular, we were interested in testing if the largest sub-population is actually found in the upper Ebro and major tributaries, as stated by Palazón *et al.*, (2013).

As water availability is a crucial parameter for the species we modeled the parameters as function of five covariates related to water: mean precipitation of the driest and the wettest month, mean length of rivers of small (Strahler order 1 and 2) medium (Strahler order 3-5) and big (Strahler order 6 - 8) dimensions.

To represent land cover features that can influence species abundance we used the proportion of natural vegetation cover and a "Human Influence Index", and index proposed by the Socioeconomic Data and Application Center (SEDAC), which combines various elements: human population distribution, urban areas, roads, and various agricultural land uses.



Covariate type	Covariate name	Description	Data source	Resolution/scale of the original dataset	Up-scale to 10km method
Site covariates					
	lat	Latitude	ArcMap 10.1 (ESRI,2011)	-	-
	long	Longitude	ArcMap 10.1 (ESRI,2011)	-	-
	pwm	Precipitation of the wettestet month	Worldclim database (http://www.worldclim.org)	5km	mean
	pdm	Precipitation of the driest month	Worldclim database	5km	mean
	small-riv	Mean length of the rivers of 1-2 Strahler order	CCM rivers and catchment database (http://ccm.jrc.ec.europa.eu)	1: 250.000	mean
	med-riv	Mean length of the rivers of 3-5 Strahler order	CCM rivers and catchment database	1: 250.000	mean
	big-riv	Mean length of the rivers of 6-8 Strahler order	CCM rivers and catchment database	1: 250.000	mean
	nat-veg	Proportion of natural vegetation cover	Corine Land Cover 2000 (http://www.eea.europa.eu)	100m	proportion
	hii	Human Influence Index	Global Human Footprint Dataset (http://sedac.ciesin.columbia.edu)	1km	mean
Time covariates					
	years	year of survey	This study	-	-
	AM_p	presence-absence of the American mink in the secondary period	Control program of the American mink	-	-

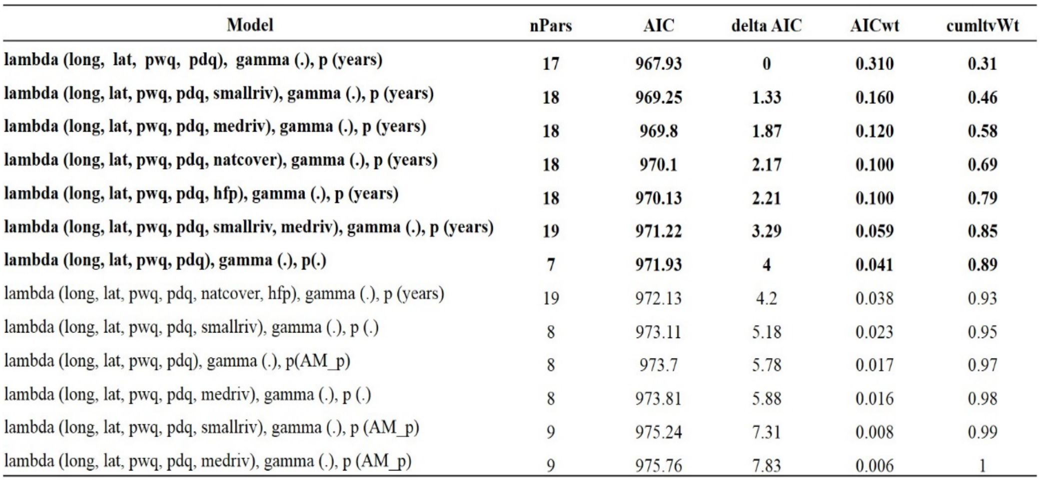
Table 1. Site and time covariates used to estimate abundance (lambda), the finite rate of increase (gamma) and detection probability (p) using the dynamic N-mixture model of Dail and Madsen (2011).

These variables were classified as "site covariates" as they reflected the characteristics of each 10km^2 cell and they were extracted from several databases and processed in ArcMap 10.1 (ESRI, 2012) to upscale them to the spatial resolution of the analysis (Table 1).

Moreover, we tested the effect on detection probability of two “time covariates” represented by 1) the year of survey and 2) the presence / absence of the invasive competitor the American mink at each site in each secondary period (Table 1). This latter covariate was based on live-trapping data collected in the study area with the same method and at the same time of the European mink data, and was used to test if the presence of the competitor had a negative effect on the native species’ detectability.

RESULTS

In total 753 individuals have been captured over 133.508 trap-nights in the 86 sites included in the study between 2000 and 2010, whilst weighted counts resulted in 309 captures. The maximum and the mean number of observation per site were 22 and of 6.03 individuals respectively.



Model	nPars	AIC	delta AIC	AICwt	cumltvWt
lambda (long, lat, pwq, pdq), gamma (.), p (years)	**17**	**967.93**	**0**	**0.310**	**0.31**
lambda (long, lat, pwq, pdq, smallriv), gamma (.), p (years)	**18**	**969.25**	**1.33**	**0.160**	**0.46**
lambda (long, lat, pwq, pdq, medriv), gamma (.), p (years)	**18**	**969.8**	**1.87**	**0.120**	**0.58**
lambda (long, lat, pwq, pdq, natcover), gamma (.), p (years)	**18**	**970.1**	**2.17**	**0.100**	**0.69**
lambda (long, lat, pwq, pdq, hfp), gamma (.), p (years)	**18**	**970.13**	**2.21**	**0.100**	**0.79**
lambda (long, lat, pwq, pdq, smallriv, medriv), gamma (.), p (years)	**19**	**971.22**	**3.29**	**0.059**	**0.85**
lambda (long, lat, pwq, pdq), gamma (.), p(.)	**7**	**971.93**	**4**	**0.041**	**0.89**
lambda (long, lat, pwq, pdq, natcover, hfp), gamma (.), p (years)	19	972.13	4.2	0.038	0.93
lambda (long, lat, pwq, pdq, smallriv), gamma (.), p (.)	8	973.11	5.18	0.023	0.95
lambda (long, lat, pwq, pdq), gamma (.), p(AM_p)	8	973.7	5.78	0.017	0.97
lambda (long, lat, pwq, pdq, medriv), gamma (.), p (.)	8	973.81	5.88	0.016	0.98
lambda (long, lat, pwq, pdq, smallriv), gamma (.), p (AM_p)	9	975.24	7.31	0.008	0.99
lambda (long, lat, pwq, pdq, medriv), gamma (.), p (AM_p)	9	975.76	7.83	0.006	1

Table 2. Top seven dynamic N-mixture models based on the Akaike information criterion (AIC), showing the distance between each model and the top-ranked model (delta AIC). nPars = number of parameters estimated; AICwt = model weight; cumltvWt = cumulative weight of the models.

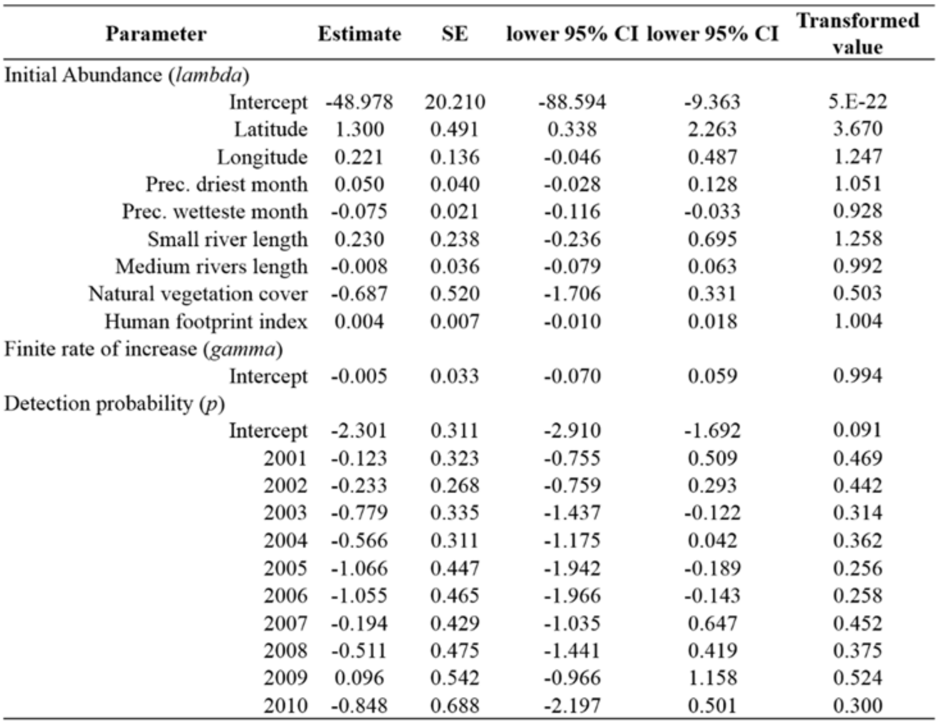
Models fit and selection

Seven models had most of the support, with a cumulative Akaike weight of 0.89 (Table 2). Moreover, the models fit well the data (best ranked model's GOF test: $\chi^2 = 599.85$, p-value = 0.977).

The model with the higher AIC score considered the effect of the latitude, longitude, precipitation of the driest and wettest month on the abundance and the effect of time (years) on the probability of detection.

The other supported models included (in order of AIC value) the influence on site abundance of the mean length of small and medium rivers, the proportion of natural vegetation and the Human Footprint Index and again the effect of time on detection probability. In all the best ranked models the finite rate of increase, gamma, was constant.

Parameters estimates derived from the average of these seven models, and their values, errors and transformed values are shown in Table 3.



Parameter	Estimate	SE	lower 95% CI	lower 95% CI	Transformed value
Initial Abundance (*lambda*)					
Intercept	-48.978	20.210	-88.594	-9.363	5.E-22
Latitude	1.300	0.491	0.338	2.263	3.670
Longitude	0.221	0.136	-0.046	0.487	1.247
Prec. driest month	0.050	0.040	-0.028	0.128	1.051
Prec. wetteste month	-0.075	0.021	-0.116	-0.033	0.928
Small river length	0.230	0.238	-0.236	0.695	1.258
Medium rivers length	-0.008	0.036	-0.079	0.063	0.992
Natural vegetation cover	-0.687	0.520	-1.706	0.331	0.503
Human footprint index	0.004	0.007	-0.010	0.018	1.004
Finite rate of increase (*gamma*)					
Intercept	-0.005	0.033	-0.070	0.059	0.994
Detection probability (*p*)					
Intercept	-2.301	0.311	-2.910	-1.692	0.091
2001	-0.123	0.323	-0.755	0.509	0.469
2002	-0.233	0.268	-0.759	0.293	0.442
2003	-0.779	0.335	-1.437	-0.122	0.314
2004	-0.566	0.311	-1.175	0.042	0.362
2005	-1.066	0.447	-1.942	-0.189	0.256
2006	-1.055	0.465	-1.966	-0.143	0.258
2007	-0.194	0.429	-1.035	0.647	0.452
2008	-0.511	0.475	-1.441	0.419	0.375
2009	0.096	0.542	-0.966	1.158	0.524
2010	-0.848	0.688	-2.197	0.501	0.300

Table 3. Model-averaged parameter estimates for the European mink initial abundance (lambda), the finite rate of increase (gamma) and detection probability (p)

European mink abundance

The finite rate of increase averaged from the seven best models resulted to be 0.994 ± 0.045 (Table 3) which indicated a population in slow decrease.

Based on this gamma value, estimated population size was of 599.75 individuals in 2000 and it decreased to 566.52 in 2010.

Mean estimate of number of individuals per site was 6.9 ± 3.6, and estimate in 2010 was 6.6 ± 3.6 individuals (Fig. 2). The lowest mean site abundance was 0.43 ± 0.008, and the site with the highest estimated abundance had 16.89 ± 0.31 individuals.

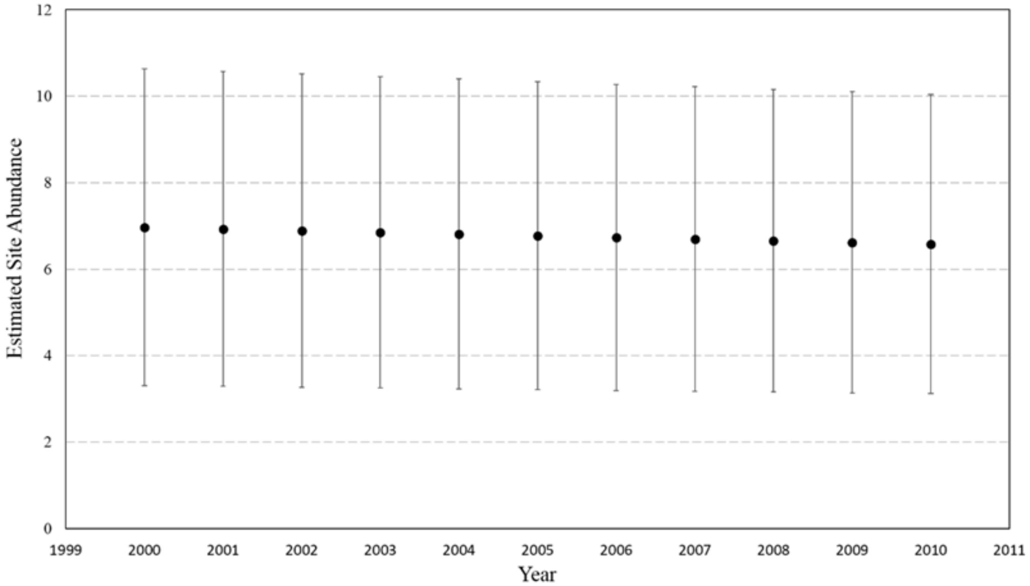


Figure 2. Estimated site abundance of the European mink in its Spanish range of distribution over the 10 years of the study using a dynamic N-mixture model.

Covariates effect

Spatial influence of the significant covariates on site abundance are shown in Figure 3. Highest abundance estimates were found between 42.4ºN - 42.6ºN and 3ºW - 1.5ºW (Fig.4a). These geographic coordinates include approximately Alava and Northern half of La Rioja, Southwest Navarre and Eastern Burgos.

Abundance progressively decreased with increasing precipitation of both the wettest and the driest month (Fig. 4b), and highest predicted values of abundance were found above 60-70 mm (range: 50 - 150 mm) and 25-30 mm (range: 15 – 60 mm) of rain respectively.

Mink was more abundant in sites where the availability of small and medium rivers was higher. A positive correlation between estimated abundance and the mean length of small rivers has been observed, and a less strong correlation between the same parameter and mean length of medium-size rivers resulted from our analysis (Fig.4c), whilst none of the models including big rivers had an AIC value ≤ 4.

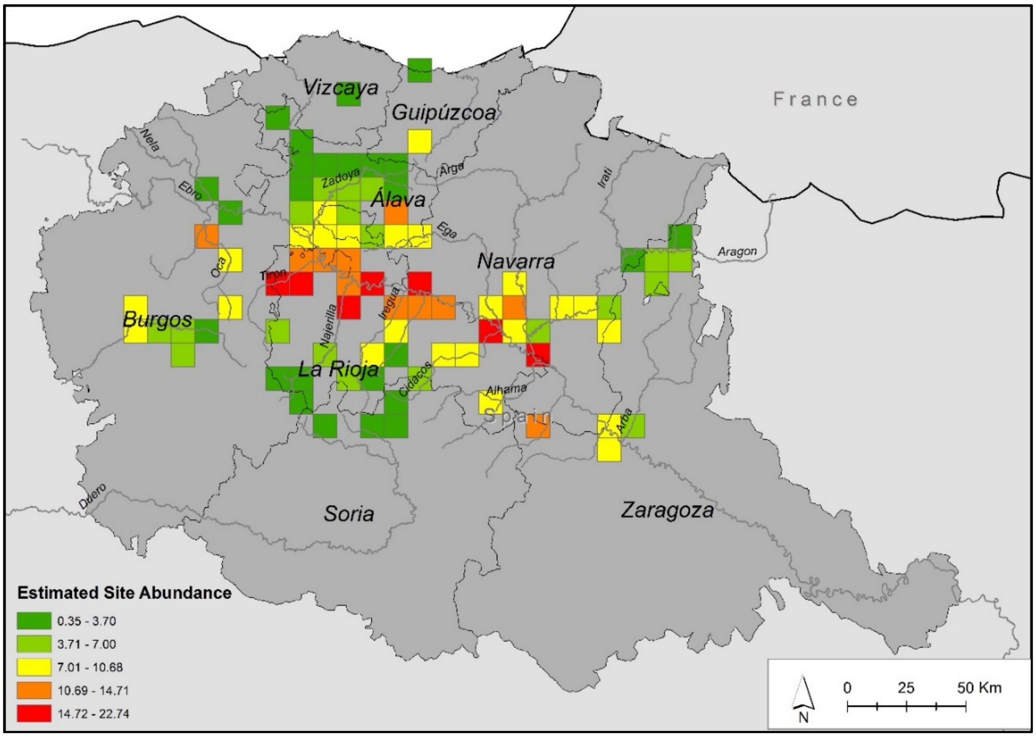


Figure 3 Spatial distribution of the estimated site abundance of the European mink in the 86 sampled sites (10x10km UTM) over the eight Provinces surveyed in Northern Spain

Finally, the mink estimated abundance was higher where the Human Footprint Index had higher values (which indicated a stronger anthropic pressure), whilst a negative correlation has been observed between the same parameter and the proportion of natural vegetation cover (Fig. 4d).

The only covariate that had an influence on detection probability was time (years): minimum detectability value was 0.256 in 2005 and maximum was 0.524 in 2009 (Table 3). American mink presence on the contrary did not show a significant influence on species detection.

DISCUSSION

The dynamic N-mixture model recently proposed by Dail and Madsen (2011) was applied to the critically endangered European mink count data collected between 2000 and 2010 in order to estimate population spatial and temporal trends in its entire Spanish range of distribution. Methodologically, the high number of counts repetitions and of sampled sites likely compensated missing values, since models showed a good fit and parameters estimations had a reasonable precision.

Slow decline and abundance heterogeneity of the European mink

A slow decrease of the population of the European mink has been detected, as the average finite rate of increase was slightly inferior to one (0.994). This value indicated that averagely each year between 2000 and 2010, the number of recruited individuals (by birth or immigration) was to some extent inferior to the previous year, though the observed spatial variability in the abundance showed that this process did not have an equal intensity at all the sampled sites.

Our results revealed that in the year 2000 estimated the population size was approximately of 600 individuals, whilst in 2010 this number decreased to 567 individuals. Interestingly this result is very close to the estimates proposed so far by Palazón *et al.* (2012) and Palazón *et al.*, (2006a).

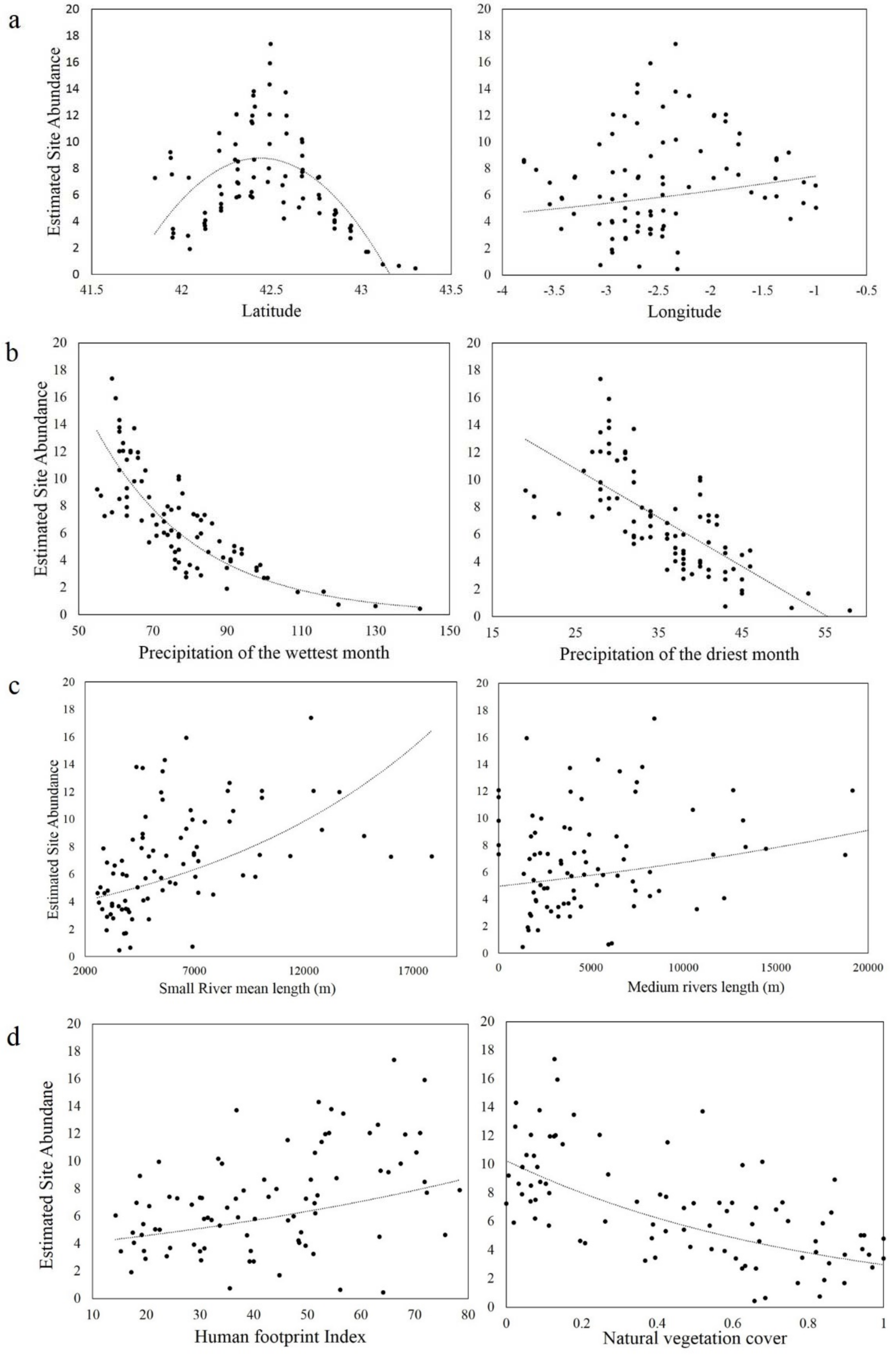


Figure 4. Estimated site abundance (vertical axis) plotted against: a) latitude and longitude, b) precipitation of the wettest and driest month, c) small and medium Rivers length, d) the human footprint index and the proportion of natural vegetation.

The heterogeneity in the European mink detection probability (values oscillated between 0.25 and 0.52), was likely related to a varying sampling effort over time. Although we tried to control this latter effect by weighting count data using the number of trap-nights in a secondary period, it is possible that to some extent lower mink detectability corresponded to years of lower trapping effort.

As no models relating gamma to some of the spatial covariates showed an acceptable fit, it has been impossible to make inferences on the spatial variability of the finite growth rate.

Highest values of estimated abundance, though, were concentrated in the central part of the species range of distribution, an area included in the regions of Alava, North La Rioja, Eastern Burgos and South Navarra, which correspond to the upper Ebro basin.

This central area showed lowest values of mean precipitation of both the driest and wettest months compared to the Atlantic river basins in the North and the Iberian System Mountain Range in the South. This indicated that precipitation is not a limiting factor to population abundance in this area and at the spatial scale of the analysis.

This is not a surprising result, since in the Mediterranean basin the European mink has been observed to inhabit drier habitats than in the rest of Europe (Youngman, 1982). The only work that explored the effect of precipitation on the European mink in Spain found that the species presence was positively correlated to annual mean values of rainfall higher than 1200 mm, but the study was restricted to the Atlantic basins (Palazón *et al.*, 2006c).

The area with highest European mink abundance presented higher human activity and less proportion of vegetation than sites with lower estimated densities. The low-lying areas along the Ebro River and its major tributaries are indeed characterized by agricultural activities, infrastructures as roads and railways and extended human-inhabited areas, larger than in the northern and southern part of the area of distribution of the European mink.

An important caveat must be associated to this result: although at the resolution of the analysis we did not observed a strong effect of land-use of the areas surrounding rivers inhabited by the species, it does not mean that human disturbance or scarce vegetation cover does not have an impact on the European mink abundance at a finer spatial scale.

The effect of these features has been indeed explored in several studies, focused on local- and micro-scale patterns, and results indicated that they could have a great importance in the conservation of the European mink. For example, in Navarra, the northeastern part of the study area, the species habitat selection has been observed to be positively linked to riverbanks vegetation with a width higher than 5 m and a proportion of vegetation cover between 25% and 75% (Palazón *et al.*, 2006c). Meanwhile in Biscay the species was absent from polluted catchments with altered riverbanks (Zabala *et al.*, 2006).

On the other hand at the scale of the analysis emerged clearly the positive correlation between the availability of small and, to a lesser extent, medium-size rivers and the mink abundance. In the study area, small rivers are mainly secondary tributaries of medium rivers, which are the major tributaries of rivers as big as the Ebro or Duero Rivers. (i.e. Najerilla, Tirón and Zadoya rivers).

Previous studies showed that the European mink selected these secondary tributaries, especially if they presented good coverage of riparian vegetation and water quality, in the medium and low sections of the medium rivers (MAGRAMA, 2009; Palazón and Ruiz-Olmo, 1998). Some evidence has been reported that these areas are occupied mainly by reproductive females and juveniles, while largest rivers with less suitable habitat conditions are tough to act mainly as corridors for young males dispersal (Palazón *et al.,* 2012; Zabala *et al.*, 2003). Similar results have been obtained in Belarus, where Sidorovich and Macdonald (2001) found highest number of individuals in moderately flowing small rivers of length from 10 to 100km.

The observed pattern of abundance of the European mink in Spain is the result of processes acting at different spatial scales: although direct determinants of species density did not emerged clearly from this study, some hypothesis may be formulated based on our results and on previous studies' findings in the same area. The Northern and Southern part of the European mink range have clearly less suitable environmental conditions than the upper Ebro basin.

In the North, the rivers of the Basque Country and North Navarre may show species' lower densities for three main causes: low quality of river's water (Palazón *et al.*, 2003); the introgression of the American mink in the area (Zabala *et al.*, 2006); and possibly the inherent characteristics of the rivers which are generally short, steep and fast-flowing, and hence poorly suitable for the mink.

In the South, the Northwestern end of the Iberian System Mountain Range (named Sierra de la Demanda), which reaches 2230 m a.s.l, can act as a geographical barrier for the European mink expansion and site abundance likely decrease with the increasing altitude. In the Mediterranean river basins indeed the species can be found between 300 and 1400 meters above sea level, whilst in the Atlantic basins it has been observed between 0 and 200 m of altitude (MAGRAMA, 2009).

Implications of the European mink conservation

Our study represent the first large-scale estimate of the spatial and temporal trend in abundance of the Spanish population of the European mink.

Although the causes of the species decline did not emerged clearly through the selected covariates, the negative trend of the population indicated that the ongoing conservation strategy is failing in halt the European mink decline.

The fact that at the spatial resolution of our analysis (10x10 km), land-use had little effect on species abundance suggested that conservation actions should focus on the area most closely related to rivers, water bodies and riverbanks, according to the knowledge on the effect of habitat features on species density gained in several local-scale studies. For example, the conservation of good riparian habitat, with a buffer of at least 10m of vegetation cover and a good water quality is essential for maintaining viable populations of the European mink (Palazón and Melero, in press).

The species abundance is unevenly distributed, with the most abundant population concentrated in the central part of the range along the tributaries of the upper Ebro River basin. This sub-population should receive a special attention, as it may act as a source for the sub-populations located to the north and the south of the Ebro basin, and for the potential expansion of the species southeast and westward.

In this analysis, the impact of the American mink on the native species abundance was not detected. One reason may be that in the model settings the only parameter that could be modeled in function of the invader presence was the detection probability. However, in a previous study (Santulli *et al.*, 2014) we observed that the European mink detectability is not affected by the competitor's presence: generally, if both species are present at a site, both are detected, probably thanks to the effectiveness of the live-trapping method used.

Another reason could be that the 86 sites selected in this study represent the core of the European mink distribution in Spain, where major efforts for the American mink culling are carried out, and where the local densities and the spread of the invader are to some extent controlled.

Although our model did not reflected the effect of the American mink on population abundance, this invader represent an actual threat, as demonstrated by several studies carried out in Spain (Palazón *et al.,* 2013; Zuberogoitia *et al.*, 2010; Zabala *et al.*, 2004; Palazón *et al.*, 2003). Controlling the invader inside and around the area of distribution of the European mink is hence essential to avoid the intensification of its ongoing decline.

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CHAPTER 3

REFINING SPECIES INVASIONS PREDICTIONS THROUGH THE HIERARCHICAL COMBINATION OF CLIMATIC ENVELOPES AND LAND-USE MODELS: THE CASE OF THE AMERICAN MINK IN THE IBERIAN PENINSULA

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ABSTRACT

Using Species Distribution Models (SDMs) to forecast potential geographic ranges of invasive non-native species (INNS) is particularly challenging because the core assumptions of species-environment equilibrium and niche conservatism can be easily violated. Recent studies showed that calibrating models with occurrences from INNS native and invaded range improves predictions of the extent of the invasion. Typically, large-scale screenings based on coarse resolution climatic factors are produced, but examples of their application in regional management planning are limited.

In this study we aim to produce fine-scale prediction of the invasive American mink potential spread in the Iberian Peninsula by applying an analytical framework which helps to mitigate the underestimation of predicted range and to incorporate the largest amount of available information on species global distribution.

We first calibrated three bioclimatic models at coarse scale with data from (a) the native, (b) the invaded and (c) both ranges of distribution, and we combined them with a fine scale regional land-use model using a multi-scale hierarchical approach.

Our results suggested that the American mink has not filled its potential niche in the invaded range so far, so that the combination of a regional land-use models with a climatic envelope calibrated with data from both ranges showed the highest accuracy in predicting the mink distribution in the Iberian Peninsula.

The proposed framework can be useful to obtain fine-scale maps of risk of invasion of INNS at non-equilibrium with their environment and to provide reliable predictions to support INNS management and prevention actions.

RESUMEN

El uso de los Modelos de Distribución de Especies (SDMs) para predecir las áreas potencialmente idóneas para especies exóticas invasoras (EEI) puede ser muy complejo porque las condiciones del equilibrio entre una especie y su entorno y de la conservación del nicho pueden ser transgredidas fácilmente.

Estudios recientes han demostrado que la calibración de los modelos con datos de presencias en el área invadida y original puede mejorar la predicción de invasión de una EEI. Sin embargo, generalmente se producen predicciones a amplia escala basadas exclusivamente en variables climáticas y existen pocos ejemplos de la aplicación de SDMs a la planificación de gestión de EEI a escala regional.

El objetivo del presente estudio es de realizar una predicción a escala fina de la expansión potencial del visón americano en la Península Ibérica, aplicando un enfoque analítico que amortigüe el riego de subestimar el área de distribución y que incorpore la mayor cantidad posible de información sobre la distribución global de la especie.

Se han calibrado tres modelos bioclimáticos a escala gruesa con datos procedentes del (a) área de origen, (b) área invadida y (c) ambas áreas de distribución, y se han combinado con un modelo regional a escala fina basado en variables de uso de suelo a través de un enfoque jerárquico multi-escala.

Los resultados indican que el visón americano no ha invadido todavía toda el área potencialmente idónea en Europa, así que la combinación de un modelo regional con un modelo bioclimático calibrado en ambas áreas de distribución, la original y la invadida, proporciona la mejor precisión a la hora de predecir la distribución del visón en la Península Ibérica.

El enfoque analítico propuesto puede ser útil para obtener mapas del riesgo de invasión de EEI a una resolución espacial fina, cuando estas especies no se encuentran en equilibrio con el propio ambiente y para proporcionar predicciones útiles para planificar la gestión y la prevención de las EEI.

INTRODUCTION

Successful management of biological invasions depends on the ability to predict potential geographic ranges of invasive non-native species (INNS) and to identify factors that promote their spread (Guisan *et al.,* 2013; Peterson & Vieglais, 2001). Species Distribution Models (SDMs) are being increasingly used to forecast the spatial extent of invasion and identify areas at risk of being invaded (Roura-Pascual *et al.*, 2008; Ficetola *et al.*, 2007; Ward, 2006). They aim to predict areas suitable for a target species by correlating environmental variables influencing species' ecology with current distribution (Guisan and Zimmermann, 2000) assuming that the observed occurrences represent the realized niche of the species (*sensu* Hutchinson, 1957).

Nonetheless, modelling INNS potential spread is particularly challenging because the core assumption of species-environment equilibrium in SDMs (i.e., a species occupies all suitable areas while being absent from the unsuitable ones) is rarely met in the case of an invasive species (Gallien *et al*, 2012; Václavík and Meentemeyer, 2009).

INNS, especially in early stages of expansion, may occur only in a subset of the potentially suitable habitats, simply due to lack of dispersal, invasion history or biotic interactions (Václavík and Meentemeyer, 2012; Araújo and Guisan, 2006). SDM calibration with non-equilibrium presence data and considering only the invaded range of the species, likely lead to the exclusion of sets of conditions potentially suitable for the species, and hence to underestimate the species potential distribution range (Guisan & Thuiller, 2005).

Peterson and Vieglais (2001) proposed to calibrate models considering the environmental conditions currently occupied in the native range, where the species is assumed to be in equilibrium with its environment, and then project the results in the invaded range under the hypothesis that the niche occupied by a species do not change over time and space (niche conservatism postulate). However, evidences that an INNS can occupy distinct niche spaces in the area of introduction has been recently reported (Petitpierre *et al.,* 2012; Fitzpatrick and Weltzin, 2007; Broennimann *et al.,* 2007). As a consequence, if the niche occupied in the new range is very different from the native one, the model calibrated with data from the species native area will likely predict erroneous potential ranges (Gallien *et al.,* 2010).

A possible solution to predict INNS potential spread in a new area is to consider all available information from the widest range of conditions currently occupied by the species of interest (Broennimann and Guisan, 2008). The studies that applied this scheme demonstrated that models calibrated in both native and invaded range lead to more accurate predictions than models calibrated in only one part of the range (e.g., Di Febbraro *et al.,* 2013; Beaumont *et al.,* 2009; Broennimann and Guisan, 2008).

However, the majority of these studies are based uniquely on climatic variables and usually they result in broad-scale predictions of the global conditions under which the species can persist. While representing remarkable improvement in forecasting INNS invasions, they are likely to over-predict potential distribution in the invaded range by providing coarse-resolution predictive maps (Gallien *et al.*, 2010), which limits their applications in practical INNS management plans.

Variables other than climate influence the likelihood of the establishment and invasion of an INNS, and their effect can be scale dependent (Mackey and Lindenmayer, 2001). When fine-scale occurrence data are available, the area at risk of being invaded by an INNS can be forecasted with a multi-scale approach, integrating models calibrated with predictors acting at different spatial scales. This approach is based on the assumption that climate defines species distribution at macro-scale, whilst land-use regulates species occupancy patterns at finer spatial resolution (Pearson and Dawson, 2003; Mackey and Lindenmayer, 2001). A multi-scale hierarchical approach can mitigate the risk of underestimating INNS potential spread by taking into account species adaptation to local conditions while considering its climatic limitations on a global scale (Gallien *et al.,* 2010; Pearson *et al.,* 2004).

However, surprisingly few of the SDM studies focused on predicting INNS invasion applied a multi-scale hierarchical approach (Jones *et al.,* 2010; Ficetola *et al.,* 2007).

In this study, we aimed to test the use of such multi-scale hierarchical framework to: a) produce reliable maps for regional management planning compared to large-scale screening approaches based on coarse-scale climatic predictors and b) mitigate the risk of underestimating invasive species potential spread, due to non-equilibrium calibration data.

We do this by providing an approach to INNS potential invasion modeling that include the largest amount of available information on species distribution while considering the spatial scale of influence of the environmental factors on species occurrence.

To do so, we used the American mink (*Neovison vison,* AM hereafter) in the Iberian Peninsula as a study system. The AM is a suitable species for our objectives, because it is a well-known species of economic and conservation interest worldwide, whose information on distribution and ecology is extensive. In the study area the species is found between N 25º50' and N 69º50'and it occupies a wide range of climatic conditions, but locally its presence is strictly related to riparian habitats (Dunstone, 1993).

Native of North America, the AM has been introduced in Europe at the beginning of the 20th century for fur farming, and it is currently present in at least 23 European countries (Bonesi and Palazon, 2007). In the Iberian Peninsula since the end of the 1950s massive escapes and intentional liberations from farms resulted in the establishment of six different populations distributed in the northern half of the country (Ruiz-Olmo *et al.*, 1997), and new areas are being colonized every year (Tragsatec-Magrama, 2012). The species can be detrimental for many native species and economic activities and in Spain it represent one of the mayor threat to the viability of the critically endangered European mink (*Mustela lutreola*)

(Maran *et al.*, 2011). Intensive control campaigns carried out since the late 1990s have slowed but not halted the spreading of the invader. Assessing AM potential spread in the Iberian Peninsula is hence critical to identify areas of conflict where management activities can potentially be important and effective.

MATERIALS AND METHODS

Analytical framework

The analytical framework presented in this study was composed by the following steps: a) testing for differences in the climatic niche occupied by the species in the native and in the invaded range; b) comparing three bioclimatic models calibrated in (i) the AM native range (North America), (ii) the invaded range (Europe) and (iii) in both ranges; c) building a hierarchical multi-scale model by combining the three bioclimatic envelopes produced with a fine scale land-use model calibrated at the extent of the Iberian Peninsula; d) evaluating the performance of the three combined models, in order to produce the most accurate fine-resolution final map suitable for regional management planning.

American mink records

AM occurrences at European and North America extent were extracted from the Global Biodiversity Information Facility 2012 database (GBIF; http://data.gbif.org). Because many of the records available in the GBIF were at a resolution of 30 arc-minutes (≈ 50km, as denoted hereafter), occurrences dataset was set at this cell size, in order not to lose useful information on environmental conditions occupied by the species. We obtained 1346 points of presence in the European continent and 1004 in North America (United States and Canada), the native range (Fig 1 a-b).

AM occurrence data at the extent of the Iberian Peninsula were gathered from live-trapping surveys conducted between 1999 and 2012 as part of the AM control plan implemented by technicians and forest rangers of regional governments coordinated by the Spanish Ministry of Agriculture, Food and Environment. All individuals trapped were euthanized following the Spanish Animal Welfare Law (Royal Act n. 32/2007). A set of 1311 occurrences was collected (Fig. 1 c).

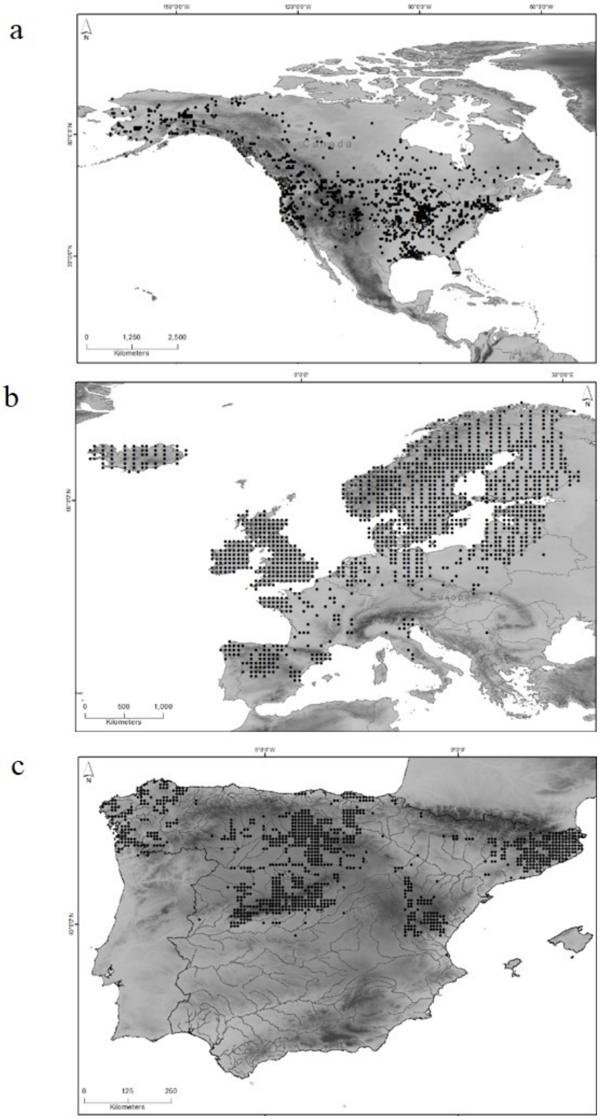

Figure 1. American mink occurrences (black points) in a) North America, the native range; b) Europe, the invaded range and c) Iberian Peninsula. Climatic models were calibrated in the range a and b and a + b, and projected in range c. A land-use model at fine resolution was trained at the Iberian Peninsula extent and combined with the three climatic models produced.

Climatic variables

Among the 19 current climate variables available from the Worldclim 1.4 database (Hijmans *et al.*, 2005), we first selected the ones which had the lowest par-wise correlations (Pearson $r \leq 0,7$) in both native and invaded ranges (Dormann *et al.*, 2013). Secondly, we chose the predictors that we considered more significantly related to the species ecological requirements. The AM presence is strictly related to water, and whereas it stands low temperatures, it avoids arid environments (Larivière, 1999). We selected two climatic variables representing the annual range of temperature (temperature seasonality, TS) and precipitation (precipitation seasonality, PS), as we expected the AM to be sensitive to a highly variable precipitation and temperature across the year, being a species inhabiting rivers and wetlands. The other two variables selected characterize extreme or limiting environmental factors related again to temperature and precipitation (mean temperature of the coldest quarter, MTCQ, and precipitation of the driest quarter, PDQ).

Land use variables

The presence of AM in the Iberian Peninsula is associated with large and medium size rivers at low and medium altitude (Ruiz-Olmo *et al.*, 1997). Three variables representing rivers dimension (Strahler order) were produced: distance from rivers of order 1 (SMALL), from rivers of orders 2-3 (MEDIUM) and from rivers of orders 4-5-6 (BIG). In the invaded range the presence of the AM has been reported to be associated with areas covered by trees and scrub and negatively with open areas (Melero *et al.*, 2008; Zabala *et al.,* 2007; Yamaguchi *et al.,* 2003). To represent different degrees of human intervention in the study area, we reclassified the Corine Land Cover 2000 database to create the following variables: proportion of agricultural (AGRIC), heterogeneous (HETERO) and forested areas (FOREST). The resolution of the land-use variables was set to 2.5 arc-minutes (≈ 5 km, as denoted hereafter).

The chosen resolution contains the average linear home range of the AM in Spain: between 6.8 and 0.89 km for males and 2.9 and 0.21 km for females (Melero *et al.*, 2008), which we considered appropriate to detect the effect of land cover on the species distribution.

Comparison of climatic niches in the native and the invaded range

To compare the niches occupied in the native and in the invaded range, we performed a niche equivalency and similarity test, initially described in Warren *et al.* (2008) and later improved by Broennimann *et al.* (2011). The latter version of these tests is based on the quantification of niche overlap between native and invasive populations with a Principal Component Analysis (PCA), through the calculation of density of occurrences weighted by environmental availability along the PCA axes (Guisan *et al.,* 2014).

Differences in the position along the principal component discriminated differences between the environmental space occupied by the species in the native and the invaded range.

The niche equivalency test determines whether niches of the two populations of the AM in North America and in Europe are identical and whether a same niche overlap value could be simply obtained by chance. The niche similarity test addresses whether the environmental niche occupied in the native range is more similar to the one of the invaded range than would be expected by chance, and vice versa. The niche overlap metric (D) varies between 0 (no overlap) and 1 (complete overlap).

Among the methods proposed by Broennimann *et al.* (2011), we chose the PCA-env ordination technique, which was reported to be the most accurate in terms of niche overlap detection. The data used to calibrate the PCA are the climatic variable from the entire environmental space of the two study areas, including species occurrences.

Species distribution modelling

At both continental and regional scale, species distribution models were performed using five statistical techniques available in the biomod2 R package (Thuiller *et al.*, 2013), consisting in three regression methods: Generalised Linear Models (GLM), Generalised Boosted Regression Model (GBM) and Generalised Additive Models (GAM); and two machine learning methods: Random Forest (RF) and Maximum Entropy (MAXENT).

All models were set to 10 repetitions (10 runs and one full model) and 10 different sets of pseudo-absences so that for each model 550 outputs were produced.

Models outputs were combined to obtain an ensemble prediction, using the ensemble forecasting function of biomod2.

Models were assembled combining the outputs from all the five algorithms, all the pseudo-absence datasets, and all the models repetitions. Consensus areas among predictions from different algorithms incorporate modelling uncertainties to produce a more reliable estimates of species potential distribution than a single modelling technique (Araújo and New, 2007).

The result was a map representing the percentage of agreement on species presence between various algorithms, rather than a probability of species occurrence. The ‘weighted mean of probabilities’ approach was used to combine the models: it returns an ensemble output in which the higher the evaluation score of the individual model, the more importance it has in the ensemble.

The evaluation metrics used to weight the models are described further down the section.

Continental-scale climatic models were trained using three occurrence datasets: i) from the native range, North America (modNA), ii) from the invaded range, Europe (modEU) and iii) from both ranges (modNAEU).

The ensemble output of each model was projected at the extent of the Iberian Peninsula and at a resolution of 10 km, in order to obtain finer-scale climatic envelopes more suitable for the hierarchical combination with the regional-scale model. SDMs predictions downscaling to resolution 100 times finer has been successfully applied to the Iberian desman (*Galemys pyrenaicus*) and the Eurasian otter (*Lutra lutra*) in the Iberian Peninsula (Barbosa *et al.*, 2010), and in this study we evaluated indirectly downscaled models performance after the combination with the regional-scale model. This latter model was calibrated at the extent of the Iberian Peninsula (modIP) using the land-use variables at a resolution of 5 km.

For the internal validation of the predictions, biomod2 uses a repeated split-sample procedure fitting models on a random sample of 80% of the initial data, and keeping 20% of them out as independent data for evaluation. The procedure was repeated 10 times.

To evaluate the ensemble models forecasting ability we used the following metrics: Area under the curve of the receiver-operating characteristic (ROC), Sensitivity and Bias.

The first metric is one of the most widely used threshold-independent accuracy measure (Liu *et al.*, 2009) and its scores vary from 0 (systematically wrong predictions) to 1 (perfect agreement with the observed data, not achievable when pseudo-absence data are used instead of true absence data (Phillips *et al.*, 2006)). The second two metrics are threshold-dependent, but they are independent from the false positive rate (the number of sites of the study area where the species is predicted to be present, but is not observed), and hence they are the most suited for the case of INNS, which may be not detected at a site simply because they has not yet filled the potential range. Sensitivity represents the rate of observed presences correctly predicted by the model, and Bias is the frequency of predicted presences compared to the observed presences.

Models hierarchical combination and external evaluation

To produce the final combined models, climatic ensemble models outputs were converted from continuous into binary maps, and used as nested areas to fit the regional land-use model. Eight threshold values between 0.1 and 0.8 were selected to produce 24 hierarchical combinations (8 binary maps for each climatic model).

Their predictive power was evaluated with an independent dataset of 392 occurrences (30% of the initial AM occurrence dataset) at the Iberian Peninsula extent, which did not enter in models calibration. Sensitivity was calculated for each threshold to perform models comparison and evaluation.

Models external evaluation was performed using PresenceAbsence R package (Freeman and Moisen, 2008). All environmental variables and models outputs were elaborated in ArcMap 10.1 (ESRI, 2012).

RESULTS

Niches similarity and equivalency

A partial overlap (D = 0.413) between the niche occupied in the invaded and in the native range resulted from the niche equivalency and similarity test performed. Equivalency between niches was not supported (P value = 0.0198), revealing a significant difference between the climatic niche occupied in North America and in Europe.

On the other hand, similarity test in both direction (Europe vs North America and vice versa) indicated that the species occupies environments more similar to each other than expected by chance (P value = 0.00198).

Indeed, the center of the species climatic niche in the two ranges had a similar position (Fig.2), indicating that the species occupied analogous climatic conditions in the native and in the invaded range. In North America, however, the available environment is larger than in the European continent, and the species is found in a wider variety of conditions.

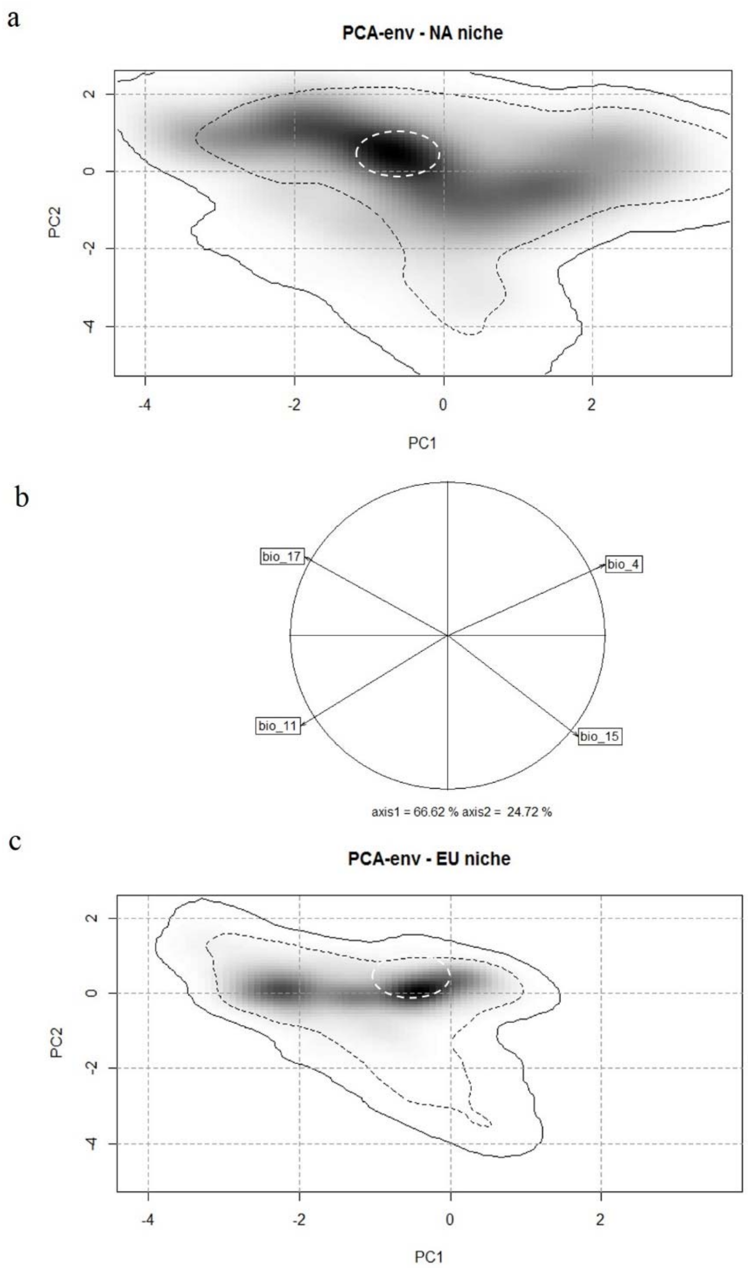

Figure 2. Representation of the American mink climatic niche along the first two axes of the PCA in the **a)** native range (North America) and **c)** invaded range (Europe). Grey shading shows the density of the occurrences of the species by cell. 100% and 50% of the available environment are illustrated by the solid and dashed contour lines respectively. Dashed white circles indicate the niche center in North America. In **b)** the contribution of the four climatic variables on the two axes of the PCA and percentage of inertia explained by the two axes. The variables are **bio 4** = Temperature seasonality, **bio 11** = Mean temperature of the coldest quarter, **bio 15** = Precipitation seasonality, **bio 17** = Precipitation of the driest quarter

Models performance

Ensemble predictions of the three climatic envelope models showed a good performance with ROC, Sensitivity and Bias lowest values of 0.89, 0.82 and 0.82 and maximum values of 0.92, 0.95 and 0.99 respectively.

Non-significant differences in the performance of the climatic models calibrated in both ranges (modNAEU) compared to the models calibrated in the invaded (modEU) and in the native range (modNA) (Fig.3 a-d) was detected, and they resulted to be highly correlated (Pearson r = 0.84 between the modNAEU and modEU, and 0.97 between modNAEU and modNA).

The differences between the three climatic models clearly emerged when projected at the Iberian Peninsula extent (Fig. 3 e-g). In this case the highest correlation was between modNA and modEU (0.81), while modNAEU and modNA correlation value was 0.74 and 0.61 for modNAEU and modEU.

Based on the ensemble forecasting map resulting from the modNAEU projection (Fig. 3e), almost all the Iberian territory is climatically suitable for the AM (99.1%, reference threshold: 0.5). On the other hand, modNA (Fig.3f) and modEU (Fig.3g) predicted as suitable respectively the 56.3% and the 37.6% of the Peninsula.

The four climatic variables used in the models calibration had indeed a different standardized importance in shaping each model spatial predictions: in the European range the temperature variables had a stronger effect than precipitation variables (TS= 0.74 ± 0.006 SD, MTCQ = 0.55 ± 0.05; PS= 0.45 ± 0.04; PDQ = 0.22 ± 0.1), and in the native range the mean temperature of the coldest quarter is by far the determining factor of the AM potential distribution (TS= 0. 18 ± 0.16, MTCQ = 0.97 ± 0.04; PS= 0.12 ± 0.14; PDQ = 0.22 ± 0.17); when considering both ranges of distribution though, the importance of the precipitation of the driest quarter emerged clearly (TS= 0. 35 ± 0.12, MTCQ = 0.47 ± 0.07; PS= 0.21 ± 0.26; PDQ = 0.42 ± 0.12).

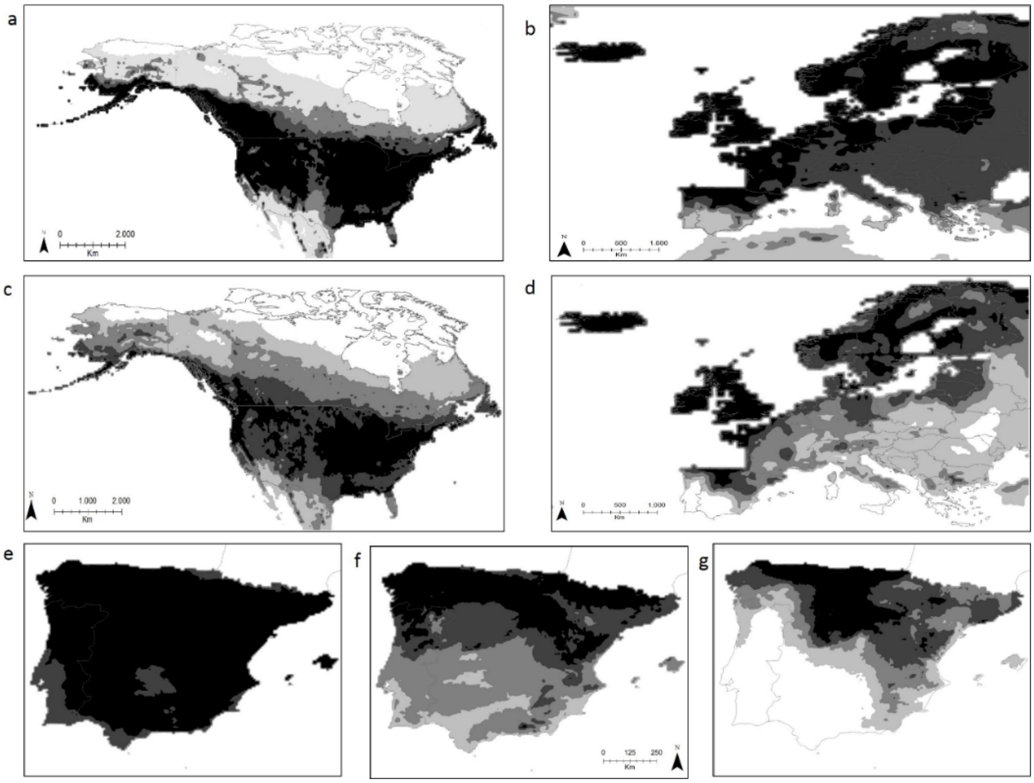

Figure 3. Maps representing the ensemble forecasting of the climatic envelopes calibrated in **a)** and **b)** both ranges of distribution, **c)** only in North America, the native range and **d)** only in Europe, the invaded range. Lower line maps illustrate the projection at the Iberian Peninsula extent of the climatic models calibrated in **e)** both ranges, **f)** the native range and **g)** the invaded range. In all maps darker colors indicate higher agreement among the five algorithms used in models calibration.

The land-use ensemble model calibrated at the extent of the Iberian Peninsula (modIP) showed high accuracy in predicting the area where the environmental conditions are suitable for the invader (lowest values for ROC = 0.90; Sensitivity =0.95; Bias = 0.95). The most influential variables were the distance from medium and big rivers whilst other land cover variables had almost no relevance (BIG= 0.27 ± 0.04 SD; MEDIUM = 0.39 ± 0.1; SMALL = 0.03 ± 0.02; AGRIC = 0.03 ± 0.02; HETERO= 0.02 ± 0.01; FOREST = 0.02 ± 0.02).

Combined models external evaluation and comparison

The maps resulting from the combination between the three climatic envelopes and the regional scale land use model are shown in Fig.4. Inside the area climatically suitable for the AM, those combinations defined the area which land-use conditions fit the species ecological requirements.

The combination of the regional land-use model with the three climatic envelopes produced in this study led to strongly refine the prediction of the area's at risk of being invaded by the AM in the Iberian Peninsula: while modEU identifies as suitable 9,2% of the study area, in modNA and modNAEU this percentage was 12.4% and 18,6% respectively (reference threshold: 0.5).

This means that approximately between 81% and 91% of the area predicted as suitable by the large-scale climatic models resulted as unsuitable when considering fine-scale land-use predictors.

The comparison between the performances of the three combinations (Fig. 5) showed that for all the possible thresholds between 0.1 and 0.8, the model calibrated in both ranges of distribution (modNAEU) predicted the highest proportion of AM presences correctly.

DISCUSSION

The analytical framework presented in this study resulted in a fine-scale prediction of the risk of spread of the AM in the Iberian Peninsula, and it helped mitigating the underestimation of the species potential range in the invaded area. Incorporating information on climatic conditions occupied in both native and invaded range and on local environmental conditions suitable for the species proved to be effective in refining predictive maps and lead to high-resolution models useful for regional management planning.

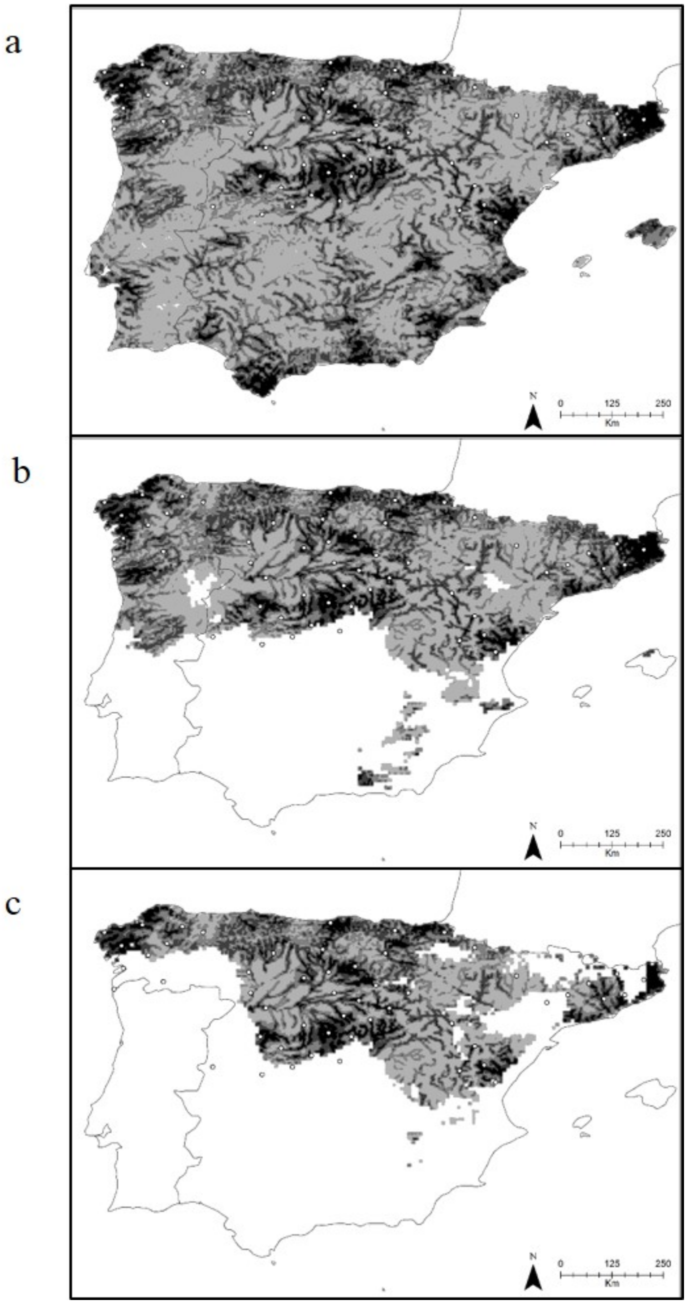

Figure 4. Maps resulting from the multi-scale hierarchical combination of a land use model calibrated at the Iberian Peninsula extent (modIP) with the climatic models calibrated **a)** in the native and the invaded range (modNAEU), **b)** only in the native range (modNA) and **c)** only the invaded range (modEU) (binary threshold 0,5). White points are a sample of 10% of the independent dataset used in models external evaluation

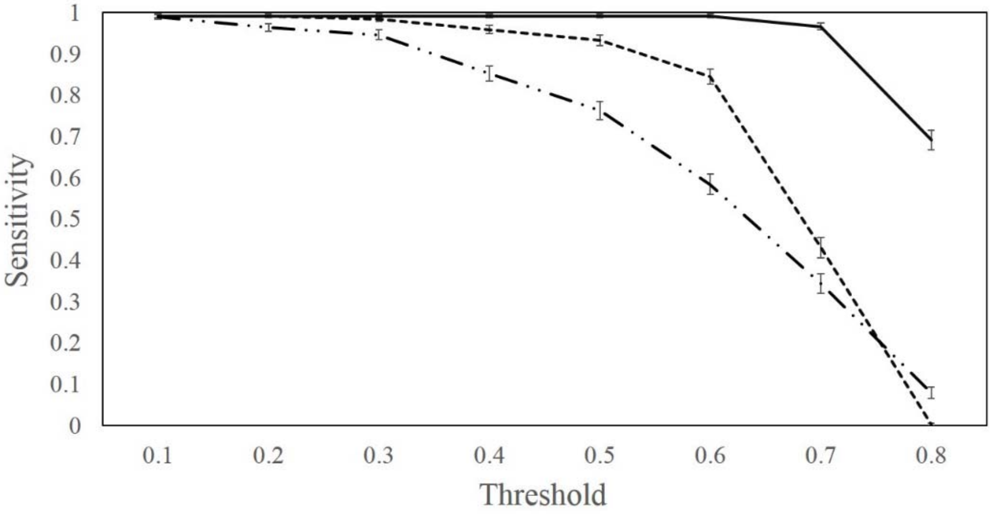

Figure 5. Sensitivity (True positive rate) resulting from the external evaluation of the models calibrated in both ranges of distribution (modNAEU - solid line), in the native range (modNA- dashed line) and in the invaded range (modEU - dash-dotted line)

Niche overlap and climatic envelopes comparison

The niche overlap analysis at continental scale indicated that in the invaded range the species occupied climatic conditions similar to the native range, even though in North America it is found in a wider set of climates, due to the larger extent of the available environments, which explains the non-equivalency of the niche spaces. Our result supported the hypothesis that the AM has not gone toward a climatic niche shift in Europe so far, although it is likely that it has not yet filled the potential niche (the intersection of the realized niche with the available environment) in the invaded range.

AM invasion history in Europe is indeed complex, due to the diversity of the time of introduction and of data availability between different countries. Moreover AM control and eradication programs carried out in at least seven European countries in the past decades may have slowed its invasion and avert its spreading in suitable areas (Bonesi and Palazón, 2007). The highest agreement of climate suitability predictions between the models produced in this study was in the northern

European countries (Scandinavian countries, United Kingdom, Estonia, Iceland), where the species has been introduced earlier in the past century (Macdonald and Harrington, 2003), and where distributional data are most abundant. In other countries (i.e. Poland, Germany, France and Spain) the first records of the AM proceed from the 1950s-1960s, and it is likely that in those areas the established populations are far from invading all the potential range.

Theoretically, following Gallien *et al.* (2012) and Peterson and Vieglais (2001), if niche spaces in the native and invaded ranges are similar and the AM has not filled the potential range in the invaded range, models calibrated only in the native range and in both ranges of distribution should have an analogous performance. While this was true for models predictions at continental scale, as revealed by the high correlation values, the projection at the Iberian Peninsula extent and at a finer resolution emphasized the differences between models outputs.

We suppose that the small differences observed at coarse resolution were magnified when models were projected at a finer grain size and smaller extent, a behavior reported in model projections to future climate (Beaumont *et al.*, 2009; Thuiller, 2003).

Models' downscaling is known to add uncertainty to predictions due the increase of false positives (Araújo *et al.*, 2005). Nevertheless, we addressed this problem providing an external evaluation of the models, which showed, unambiguously, that the calibration with data from the native and the invaded range decreases the risk of underestimating species potential range of distribution.

Combined predictions at the Iberian Peninsula extent

The hierarchical combination between modNAEU and the regional land-use model modIP gave the highest proportion of observed presence correctly predicted for all possible thresholds, which makes it the most accurate model in forecasting species potential invasion in the Iberian Peninsula, and the most reliable for management planning purposes. The combination with the model calibrated in only the invaded range (modEU) had the worst performance, showing the effect of training SDMs with non-equilibrium data, and hence the consequences of relying in an incomplete information on conditions potentially suited for the species.

The modNAEU predicted as climatically suitable almost all the Iberian territory, whilst both the modNA and the modEU indicated that the species can persist only in part of the Northern half of the Peninsula, where the Atlantic climate prevails (Köppen-Geiger climate classification, Peel *et al.* 2007). From our best model emerged that the AM can invade temperate and arid areas with dry and hot summer, which is the principal climate classification of Southern half of the Peninsula.

In fact, in its native range, the species has been reported to inhabit xeric habitats as long as permanent water and preys are present (Larivière 1999). Recent records from the AM control campaign in Spain also indicated that the species can be found in dry areas in the central part of the Peninsula, where water bodies are available (Palazón, pers. comm.).

The best hierarchical model identify as suitable rivers from almost all the principal basins of the Iberian Peninsula (Fig.4a). Species probability of presence resulted to be related to rivers of medium and big dimensions (Strahler order respectively 2-3 and 4-6), whilst others land cover variables had apparently little influence. This result is consistent with several studies carried on in the Iberian Peninsula in which the species was found to be associated to slow-flowing rivers (Ruiz-Olmo *et al.*, 1997), and to select habitat mainly in relation to prey and shelter availability, even in areas with presence of human activity (Melero *et al.* 2008; Zabala *et al.* 2007).

The prediction from the modNA - modIP combination (Fig. 4b) represented most closely the current situation of AM invasion, whilst the modNAEU- modIP combination (Fig. 4a) can be interpreted as a longer-term prediction, in which the species likely colonizes river basins of the southern half of the Peninsula. The implications in management and prevention planning of the predictions generated by the two models can be very different, and so their projection to future climate scenarios.

A constant increase in the probability of occupancy of the AM has been recently revealed in Northern Spain, showing that the ongoing species management is failing to halt its spread in the Iberian Peninsula and the strong necessity for a substantial improvement in the intensity and spatial extent of the culling effort (Santulli *et al.*, 2014).

The AM is currently found in rivers of 12 of the 24 principal basins of the Peninsula, and the prediction presented in this study can be used to identify where to focus the monitoring of the areas at risk of being invaded and the early detection of new populations, especially inside and at the periphery of the actual distribution, along the routes that host threatened native species, such as the critically endangered European mink, which occupies a similar niche.

Conclusions

In this study, we stressed the importance of including the largest amount of available information on species distribution in SDMs while hierarchically considering the spatial scale of influence of the environmental factors on species occurrence, in order to obtain fine scale regional prediction suitable for local management planning.

Climate envelope calibration at continental-scale with data from both native and adventive ranges, produced a high performance prediction when projected at regional extent, and the regional model calibrated with land use predictors shaped a suitability surface based on the interaction of the AM with local environmental features. The hierarchical combination of those models increased the resolution of the prediction of invasion, without losing information on continental- and regional-scale environmental influence on species distribution.

Results obtained with our framework proved to be potentially more informative and reliable than the usual large extent screening approaches, which consider mainly the coarse-scale climatic influence on species distribution and hence tend to over-predict their potential ranges.

Despite the challenges in meeting the assumption underlying SDMs when modelling INNS potential distribution, they are being increasingly used to predict spatial patterns of biological invasion and prioritize locations for their early detection and control. The analytical framework presented in this study can be used to reduce the negative effects of non-equilibrium data and to improve the effectiveness of SDMs in properly inform INNS management and prevention actions, by providing fine-scale mid-long term predictions based on the largest available amount of information on target species-environment relationship.

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CHAPTER 4

IDENTIFYING PRIORITY CONSERVATION AREAS FOR A CRITICALLY ENDANGERED SPECIES ON THE BASIS OF THE POTENTIAL SPREAD OF AN INVASIVE COMPETITOR USING SPECIES DISTRIBUTION MODELS: THE EUROPEAN AND THE AMERICAN MINK IN THE IBERIAN PENINSULA

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ABSTRACT

Non-native invasive species (INNS) may have a destructive impact on critically endangered species that are already facing dramatic reductions in population size and geographic range. An effective method to assess the INNS pressure on an endangered species and identify areas where to focus their management is to detect areas of conflict by overlapping predicted distribution of the target species, using Species Distribution Models (SDMs). This strategy have rarely been applied, likely for the challenge posed by modeling the distribution of species that likely fill only part of their potential range and building models at a spatial scale suitable to detect species interaction.

In this study, we developed a spatial analysis of the distributions' overlap of the critically endangered European mink and the invasive American mink in the Iberian Peninsula to provide sound basis in order to guide local conservation efforts.

To deal with the non-equilibrium state of both species and to obtain fine-scale predictions we applied a multi-scale hierarchical approach to SDMs including information from the widest range of environmental conditions currently and historically occupied by the two mink species.

The risk maps produced can help managers make informed decisions on the allocation of resources in the areas where the control of the American mink is most urgent, but also to identify where to focus monitoring in order to detect early signals of impacts, prevent the conflict, and facilitate the European mink expansion. Moreover, our study showed that SDMs can be a powerful tool to identify conflict areas between endangered species and invasive competitors, if reliable predictions are produced by applying the existing techniques to mitigate the risk of underestimate potential ranges of non-equilibrium distributions.

RESUMEN

Las especies exóticas invasoras alóctonas (EEI) pueden tener un impacto destructor sobre las especies en peligro crítico de extinción que se enfrentan a reducciones drásticas en la dimensión de la población y en su área geográfica de distribución.

Un método eficaz para evaluar la presión de una EEI sobre una especie amenazadas e individualizar donde orientar la gestión, es el de analizar las áreas de conflicto sobreponiendo las predicciones de distribución potencial de las especies de interés, usando Modelos de Distribución de Especies (SDMs).

Esta estrategia ha sido raramente aplicada, posiblemente a causa de la dificultad de predecir la distribución de especies que no ocupan la totalidad de sus áreas potenciales de distribución (como se observa comúnmente para las EEI y las especies en peligro de extinción) y de construir modelos predictivos a una escala espacial idónea para detectar la interacción entre las especies de interés.

En el presente estudio se propone un análisis espacial del solapamiento entre las distribuciones potenciales del visón europeo, una especie en peligro de extinción, y el visón americano, una especie exótica invasora, para mejorar la planificación de gestión y conservación en la Península Ibérica.

Para reducir los efectos negativos del estado de no-equilibrio de ambas especies y para producir predicciones a resolución espacial fina, se ha aplicado un enfoque jerárquico multi-escala a los SDMs incluyendo información sobre las condiciones ambientales ocupadas por ambas especies en el históricamente y en la actualidad.

Los mapas de riesgo producidos pueden ayudar a las administraciones a tomar decisiones sobre cómo distribuir los recursos en las áreas donde el control del visón americano es más urgente y sobre donde centrar el monitoreo para detectar rápidamente señales de conflicto para favorecer la expansión del visón europeo.

Además el presente estudio se demuestra que los SDMs pueden ser una herramienta poderosa para individualizar las áreas de conflicto entre especies

amenazadas y competidores invasores, mientras se produzcan predicciones fiables basadas en técnicas que mitiguen el riesgo de subestimar las áreas potenciales de especies en no-equilibrio con su ambiente.

INTRODUCTION

Non-native invasive species (INNS) are widely accepted as one of the major threat to the viability of many native species, but their impact can be particularly destructive in the case of critically endangered species, which are already facing an extremely high risk of extinction due to a dramatic reduction in population size and geographic range (Hoffmann *et al.*, 2010; Gurevitch and Padilla, 2004; Mack *et al.*, 2000; Parker *et al.*, 1999).

Due to the frequently limited funding and the high cost of conservation actions, an important applied question is how to maximize critically endangered species viability while minimizing economic costs.

Commonly, we have partial knowledge of the distribution of a species of interest as only small proportions of landscapes are surveyed to detect its presence (Wilson *et al.*, 2005). Predicting the potential distribution of an endangered species is hence essential for land-use planners to prioritize areas where to focus management and monitoring efforts, identifying and protecting important habitat resources and mitigating threatening factors, such as INNS spread (Rodríguez *et al.,* 2007; Johnson and Gillingham, 2005).

For example, forecasting the potential distribution of invasive and native species and determining their geographic overlap can be an effective approach to assess the INNS pressure on an endangered species, and to identify areas where to focus invaders management (Gallien *et al.,* 2012; Guisan and Thuiller, 2005).

However, while studies on potential distribution of rare or endangered species and potential spread of INNS abound (Roura-Pascual *et al.*, 2008; Steiner *et al.*, 2008; Ward, 2006; Maggini *et al.*, 2002), the conflict between a native rare and invasive species through predicted overlapping distributions has rarely been explored (but see Gallardo and Aldridge, 2013; Vicente *et al.*, 2011).

Predicting INNS and endangered species potential distribution can be indeed very challenging, because they are commonly at non-equilibrium with their environment (they do not occupy all suitable habitats), the former due i.e. to lack of dispersal and invasion history (Václavík and Meentemeyer, 2012; Araújo and Guisan, 2006), and the latter mainly as a consequence of range contraction. Models calibration with non-equilibrium data likely lead to the exclusion of sets of conditions potentially suitable for the species, and hence to underestimate potential distribution range (Guisan and Thuiller, 2005).

Moreover, in order to be useful predictive maps should be produced at a spatial scale suitable for detecting species interaction, which usually means a fine resolution over a significant geographic extent: a target that requires high quality data for all the species in conflict.

In the previous Chapter, we tested and provided a modelling framework to produce fine-scale predictions of potential distribution of species at non-equilibrium with their environment. In this study, we applied this framework to develop a spatial analysis of the potential conflict between a native endangered and an invasive species through the overlapping of their predicted distributions. We aimed to exemplify the applicability of this type of spatial analysis in identifying areas with different level of risk of conflict and in evaluating the effectiveness of the protected areas system.

The purpose was to provide sound basis in order to guide local conservation efforts, by defining high quality areas for the native species conservation and areas where prioritize the control of INNS.

The study system was composed by the critically endangered European mink (*Mustela lutreola*, EM hereafter) and the INNS American mink (*Neovison vison*, AM hereafter), and the study area was the entire Iberian Peninsula.

The EM and the AM are semi-aquatic mustelid which have fairly identical habitat requirements and potentially compete for the same resources, although the larger body size, larger litters and ecological plasticity of the AM provides a strong advantage for the invasive over the native species (Põdra *et al.*, 2013; Sidorovich *et al.*, 2009; Maran *et al.*, 1998).

In the European continent, over the last century, the EM disappeared from 85% of its original range. This was mainly due to habitat loss, road casualties, river water pollution and over-hunting (Palazón *et al.*, 2012; Maran, 2007; Lodé *et al.*, 2001; Maran and Henttonen, 1995), but currently the impact of the AM is considered the main threat to EM's viability where the species co-occur (Palazón *et al.*, 2003; Sidorovich, 2001).

Both mink species are likely far from the equilibrium state in the study area. In fact both the EM and the AM colonized the Iberian Peninsula only in the last few decades (Bonesi and Palazon, 2007; Zabala and Zuberogoitia, 2003; Palazón and Ruiz-Olmo, 1998; Ruiz-Olmo *et al.*, 1997). Evidences indicated that the EM entered in Spain in the 1950s and since then has been slowly expanding its range in the northern half of the country (Gómez *et al.,* 2011; Zabala *et al,.* 2004; Palazón *et al.,* 2003). The AM was introduced in the 1950s, and currently six different expanding populations occur in the northern half of the Peninsula (Melero and Palazón, 2011; Bonesi and Palazon, 2007; Ruiz-Olmo *et al.*, 1997) as a consequence of massive escapes and intentional liberations from farms. Moreover, while a rapid increase of the area occupied by the invasive mink is very likely and has already been detected in the last years both in Spain (Bonesi and Palazon, 2007) and in Portugal (Rodrigues *et al.*, 2014), a contracting distribution of the EM resulting from the expansion of the AM has been recently reported (Santulli *et al.,* 2014).

An informed planning of the areas where to monitor the expansion and prioritize the control of the American mink is hence essential to mitigate the impact of this INNS on the endangered European mink.

MATERIALS AND METHODS

The EM conservation spatial prioritization analysis was based on the (a) prediction of suitable area for the EM and the AM in the Iberian Peninsula, the (b) identification of areas at low, medium and high-risk for the EM conservation, based on the degree of overlap of suitable areas for both species and (c) the quantification of the areas suitable for the EM included in the Iberian system of protected areas, and of the proportion of this area potentially threatened by the spread of the invasive mink.

Species records

Historical and current records for both species were collected at two different extents (continental and regional) and spatial resolutions.

Geographic coordinates of the historical distribution of the European mink at European scale (Fig. 1a) were geo-referenced from Maran (2007), Maizeret *et al.* (2002), Lodé *et al.* (2001) and Youngman (1982); moreover, part of the used occurrences were extracted from the Global Biodiversity Information Facility 2012 database (GBIF; http://data.gbif.org). We obtained 523 points of EM presence between 1939 and 2012.

Current AM presence data in the native (North America) and invaded range (Europe) were partly extracted from the GBIF 2012 database and partly digitalized from the studies of Kay and Wilson (2009), Bluett *et al.* (2006), Viljugrein *et al.* (2001) and Ensor (1991). We obtained 1346 points of presence in the European continent and 1004 in United States and Canada (Fig. 1 a-b), all data been collected between the 1980s and 2012.

Original resolution of the digitalized data did not allow getting to a grain-size finer than 10 arc-minutes (≈ 50km, as denoted hereafter); moreover, many of the records available in the GBIF were at this spatial resolution. Consequently, for both species presence data was set to this resolution in order to preserve useful information on environmental conditions occupied by the species.

At the Iberian Peninsula extent, mink records were gathered from live-trapping surveys conducted between 1999 and 2012 as part of the EM conservation plan and AM control plan implemented by technicians of regional governments, coordinated by the Spanish Ministry of Agriculture, Food and Environment. The native species was marked with a subcutaneous passive transponder and released, whilst invasive mink individuals were euthanized, following the Spanish Animal Welfare Law (Royal Act n. 32/2007). A set of 357 EM occurrences and 1311 AM occurrences was collected (Fig. 1 c).

At this extent, data resolution was set to 2.5 arc-minutes (≈ 5 km, as denoted hereafter). The chosen resolution contains the average linear home range of the two mink species in the Iberian Peninsula (EM: 13.1 ± 2.8 SD km for males and 3.4 ± 2.8 km for females , Palazón and Ruiz-Olmo, 1998; AM: 7.05 ± 7.78 km for males and 4.92 ± 3.79 km for females, Zabala *et al.*, 2007). We assumed that it is relevant to detect the effect of land-use variable on the species distribution.

Environmental data

As both mink species have near identical habitat requirements (Maran, 2007; Sidorovich *et al.*, 1999), predictive models were calibrated using the same set of environmental data.

Climatic envelopes were calibrated at coarse resolution (50 km) and continental extent: Europe for the EM and North American and Europe for the AM.

Between the 19 current climate variables available from the Worldclim 1.4 database (Hijmans *et al.*, 2005), we selected the uncorrelated ones (Pearson r ≤ 0,7) which we considered more significantly related to species ecological requirements.

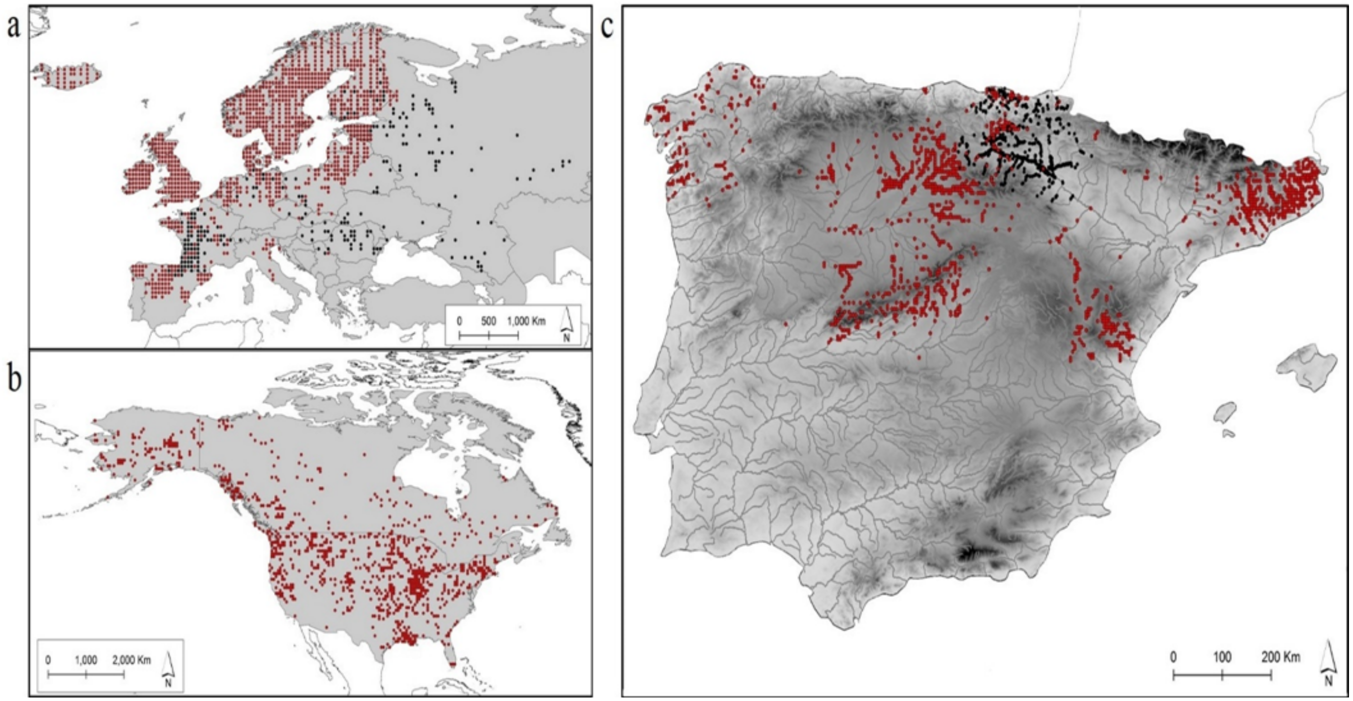


Figure 5. European mink and American mink occurrence data used in models calibration at continental (a and b) and regional (c) scale. **(a)** Occurrences of the European mink (black points) and the American mink (red points) in the European continent. **(b)** Occurrences of the American mink (red points) in its native range, North America. **(c)** Occurrences of the European mink (black points) and the American mink (red points) in the Iberian Peninsula.

Both AM's and EM's presence is strictly related to water, and whereas they stand low temperatures, they avoid arid environments (Larivière, 1999; Youngman, 1990).

Accordingly, we selected two climatic variables representing the annual range of temperature (temperature seasonality; TS) and precipitation (precipitation seasonality; PS), and two variables characterizing extreme or limiting temperature and precipitation conditions (mean temperature of the coldest quarter, MTCQ, and precipitation of the driest quarter, PDQ).

At the Iberian Peninsula extent, models were trained using land-use variables with a 5 km resolution. Slow-flowing medium size rivers at low and medium altitude represent the highest quality habitat for both species (Melero *et al.*, 2008; Zabala *et al.*, 2003; Ruiz-Olmo *et al.*, 1997), although EM has narrower habitat requirements than AM, selecting territories with non-polluted watercourses (Lodé, 2002), dense riparian vegetation and low human disturbance (Zabala *et al.*, 2006).

In ArcMap 10.1 (ESRI, 2012), we elaborated the following variables: three variables representing rivers' dimension (Strahler order) (i) distance from rivers of order 1 (SMALL), (ii) from rivers of orders 2-3 (MEDIUM) and (iii) from rivers of orders 4-5-6 (BIG) (data gathered from CCM River and Catchment Database, version 2.1, http://ccm.jrc.ec.europa.eu) and three variables representing different degrees of human intervention (i) proportion of agricultural (AGRIC), (ii) heterogeneous (HETERO) and (iii) forested areas (FOREST) (reclassified from the Corine Land Cover 2000 database, http://www.eea.europa.eu).

Species distribution modelling

At both continental and regional scales, species distribution models were performed using five statistical techniques available in the biomod2 R package (Thuiller *et al.*, 2013), consisting in three regression methods: Generalized Linear

Models (GLM), Generalized Boosted Regression Model (GBM) and Generalized Additive Models (GAM); and two machine learning methods: Random Forest (RF) and Maximum Entropy (MAXENT).

All models were set to 10 repetitions (10 runs and one full model) and 10 different sets of pseudo-absences and for each model 550 outputs were produced. Models outputs were combined to obtain an ensemble prediction, using the ensemble forecasting function of biomod2 in order to incorporate modelling uncertainties to produce more reliable estimates (Araújo and New, 2007). The result was a map representing the percentage of agreement on species presence between various algorithms.

The ensemble outputs of the climatic envelopes calibrated at continental scale were projected at the extent of the Iberian Peninsula at a resolution of 10km, in order to obtain finer-scale predictions more suitable for the hierarchical combination with the regional-scale models. This latter model was calibrated at the extent of the Iberian Peninsula using the land-use variables at a resolution of 5 km.

For the internal validation of the predictions, biomod2 uses a repeated split-sample procedure to keep 20% of the initial data out of the calibration. To evaluate the ensemble models forecasting ability we used the following metrics: Area under the curve of the receiver-operating characteristic (ROC), Accuracy (proportion of correctly predicted presence) and BIAS (frequency of predicted presence compared to the observed presence).

These metrics were calculated taking as reference the ‘weighted mean of probabilities’ algorithm, which returns an ensemble output in which the higher the evaluation score of the individual model, the more importance it has in the ensemble.

In order to produce the final combined models, for each species climatic ensemble outputs were converted from continuous maps (ranging from 0 to 1) into binary maps. This transformation translated the climatic envelopes in presence-absence classification maps that were used as nested areas to fit the regional land-use models.

As cut-offs, we chose three thresholds which defined three scenarios with different implications in terms of management effort: 1) a conservative one (all values ≥ 0.3 were considered as a presence) which included the greatest proportion of potentially suitable area for both species; 2) a moderate threshold (0.5) and 3) a strict threshold which translate into 'presence' only the cells with the highest ensemble agreement (0.7) (EM ensemble climatic prediction range was 0 - 884.11, and AM range was 0 – 897.9).

Moreover, we quantify the degree of similarity between the predictions for the two species with a Pearson's product-moment correlation test.

Identification of the European mink conservation priorities

For each one of the three thresholds used to obtain the final combined models, we quantified the proportion of area predicted as suitable for the EM that fell inside the Iberian Protected Areas and the proportion that was free of risk of the AM's invasion.

The geographic distribution of the Iberian Protected Areas was extracted from the World Database on Protected Areas 2014 (WDPA, http://www.wdpa.org). It included Regional, National and International designated protected areas and the IUCN Protected Areas categories (Ia: Strict Nature Reserve; Ib: Wilderness Area; II: National Park; III: Natural monument or feature; IV Habitat/Species Management Areas; V: Protected Landscape; VI: Managed Resource Protected Area).

In the Iberian Peninsula "International" Protected Areas referred to Ramsar sites, wetlands of international importance; the "Regional" category included Sites of Community Importance (Habitats Directive) and Special Protection Areas (Birds Directive) whilst "National" category was composed by different type of managed areas: Biosphere Reserve, Integral Nature Reserve, National Parks, Natural Monuments, Natural Parks, (Partial) Nature Reserves, Protected Landscapes, Regional Parks, Special Areas of Conservations (SAC) and Wildlife Nature Reserves.

To identify the critical areas for the EM's conservation in the Iberian Peninsula based on AM risk of invasion we first transformed the predictive maps obtained for both species into *hotspot* maps using the Getis-Ord Gi statistic (Getis and Ord, 1992). This method identifies statistically significant spatial clusters of high values (hotspots) and of low values (coldspots) which in our analysis corresponded to areas of high and low suitability respectively (assuming that areas with the highest percentage of agreement on species presence between various algorithms are the most suitable).

For each one of the proposed scenarios, hotspots maps of the EM and the AM were multiplied and standardized into a 0 to 1 scale, in order to provide a map representing the areas where the highest values of suitability for the two species coincided.

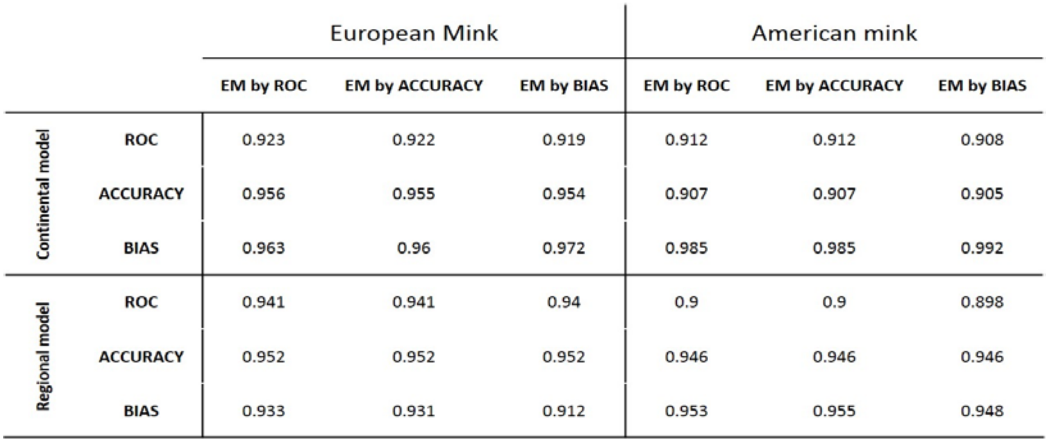
Finally, hotspots maps have been reclassified in areas at low, medium and high risk for the EM's conservation using the Jenks natural breaks classification algorithm, which chooses the class breaks that best group similar values and that maximizes the differences between classes (Jenks, 1967).

Once obtained the risk map, we calculated the proportion of each class in all the Iberian territory and for each category of the Iberian Protected Areas. Only the Protected Areas that intersected the areas predicted as suitable for the EM were included in the spatial analysis.

RESULTS

Spatial predictions and models performance

Models calibrated at continental and regional scales showed a good performance for both species.



		European Mink			American mink		
		EM by ROC	EM by ACCURACY	EM by BIAS	EM by ROC	EM by ACCURACY	EM by BIAS
Continental model	ROC	0.923	0.922	0.919	0.912	0.912	0.908
	ACCURACY	0.956	0.955	0.954	0.907	0.907	0.905
	BIAS	0.963	0.96	0.972	0.985	0.985	0.992
Regional model	ROC	0.941	0.941	0.94	0.9	0.9	0.898
	ACCURACY	0.952	0.952	0.952	0.946	0.946	0.946
	BIAS	0.933	0.931	0.912	0.953	0.955	0.948

Table 1. Results of the metrics (ROC, ACCURACY and BIAS) used in the evaluation of the ensemble models (EM) calibrated at continental and regional scale for the two mink species. The ensemble output was calculated using an algorithm in which the higher the evaluation score of the individual model, the more importance it has in the ensemble (see text). EM by ROC, EM by ACCURACY and EM by BIAS indicated the Ensemble Model in which the individual evaluation score was ROC, ACCURACY and BIAS respectively.

The lowest value of the three evaluation metrics used (ROC, ACCURACY and BIAS) was 0.898 which indicated that good predictions of species potential distribution were produced (Table 1).

The extent of the potential range for the two species was substantially different for all the thresholds (conservative, moderate and strict; Fig. 2).

In fact correlation between the final combined models predictions of the EM and the AM resulted low for all thresholds (conservative: Pearson r = 0.29, p-value= 2.2^{-16} ; moderate: Pearson r = 0.25, p-value= 2.2^{-16} ; strict: Pearson r = 0.12, p-value= 2.2^{-16}).

The extent of the suitable area (agreement between the five algorithms > 0.5) for the EM was 7.3%, 5.6% and 2.4% of the Iberian territory considering the conservative, moderate and strict threshold respectively.

In the case of the AM the proportions were 18.7% (conservative threshold), 18.6% (moderate) and 15.9% (strict). Only river basins of the Northern part of the Peninsula resulted to be suitable for the EM, whilst the AM can potentially occupy basins of almost the entire study area.

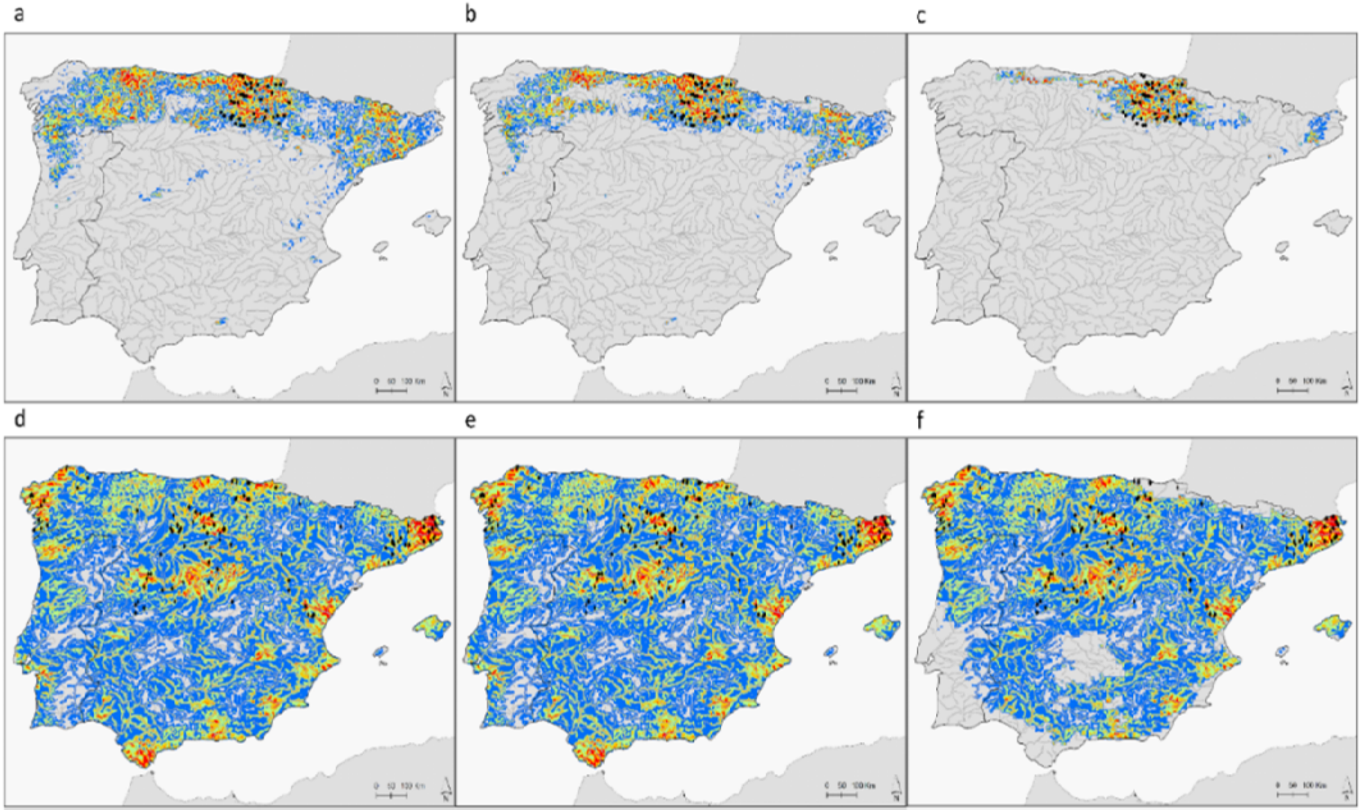


Figure 2. Maps representing European mink (upper line) and American mink (lower line) potential distribution in the Iberian Peninsula modelled using a multi-scale hierarchical approach. For both species to combine climatic envelope with the regional scales models three different threshold were used: 0.3 (a, d), 0.5 (b, e) and 0.7 (c, f). Black points in the upper line and black diamonds in the lower line represent a sample of 10% of the original data set of model calibration of the European mink and the American mink respectively. Red and blue colors indicate highest and lowest suitability respectively.

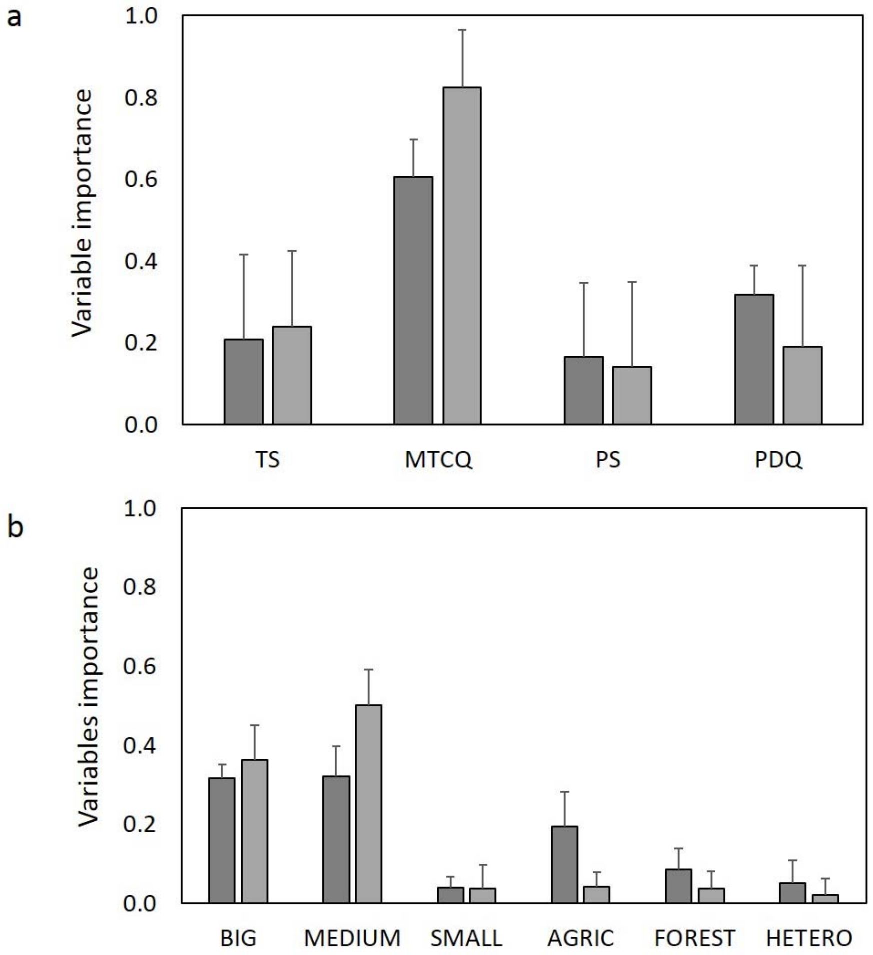


Figure 3. Standardize permutation importance of the climatic **(a)** and land-use variables **(b)** used in the calibration of the models built to predict the potential range of the European mink (dark gray) and the American mink (light gray) in the study area. Variables name in (a): **TS** = Temperature Seasonality; **MTCQ** = Mean temperature of the Coldest Quarter; **PS** = Precipitation Seasonality; **PDQ** = Precipitation of the Driest Quarter; in (b) **BIG** = Distance from rivers of Strahler order 4-6; **MEDIUM** = Distance from rivers of Strahler order 2-3; **SMALL** = Distance from rivers of Strahler order 1; **AGRIC** = proportion of agricultural land; **FOREST** = proportion of forest cover; **HETERO** = proportion of heterogeneous land-use

Interestingly, the comparison of the environmental variables importance at both continental and regional scale showed a similar influence on model predictions (Fig. 3). For both mink species the mean temperature of the coldest quarter (MTCQ) was the strongest driver of climatic envelope forecasting, being the second most important variable the precipitation in the driest quarter (PDQ) in the case of the EM and the temperature seasonality (TS) for the AM.

At regional extent the EM probability of presence was related to rivers of big and medium dimensions (Strahler order respectively 4-5-6 and 2-3), and to a lesser degree to the proportion of agricultural areas along rivers.

In the case of the AM, the most influential land-use variables were once again the distance from medium and big rivers, whilst others land cover variables had almost no relevance.

Identification of priority conservation areas

Of the area suitable for the EM (suitability ≥ 0.1) the 90.8 %, 93.4 % and the 84.2 % overlapped with the area of potential invasion of the AM, and the 24.8 %, 21.8 % and 18 % fell inside the protected areas in the conservative, moderate and strict scenarios respectively.

A total of 494, 443 and 184 Protected Areas contained conflict areas between the EM and the AM, following a conservative, moderate and strict threshold respectively. On average 93.6 ± 2.9 % of the Iberian territory was classified as at low risk for the EM conservation, whilst medium and high risk areas occupied respectively 2.5 ± 1.3 % and 3.8 ± 1.6 % of the study area. Of these percentages 15.6 ± 0.4 %, 30.2 ± 3.1 % and 22.5 ± 0.9 % respectively fell inside the Protected Areas system (Fig. 4).

On average, “Regional” category occupy 86.9 ± 3.3 % of the total Protected Areas. National and International designated areas represented respectively the 9.1 ± 3.4 % and the 0.01 ± 0.001% and all the IUCN categories the 0.7 ± 0.9 % of the Iberian Protected Areas.

The IUCN protected areas categories where the mean predicted suitability of the EM was highest were the VI, II and III, while the highest values for the AM were found inside the categories Ib, III and IV (Fig. 5 a).

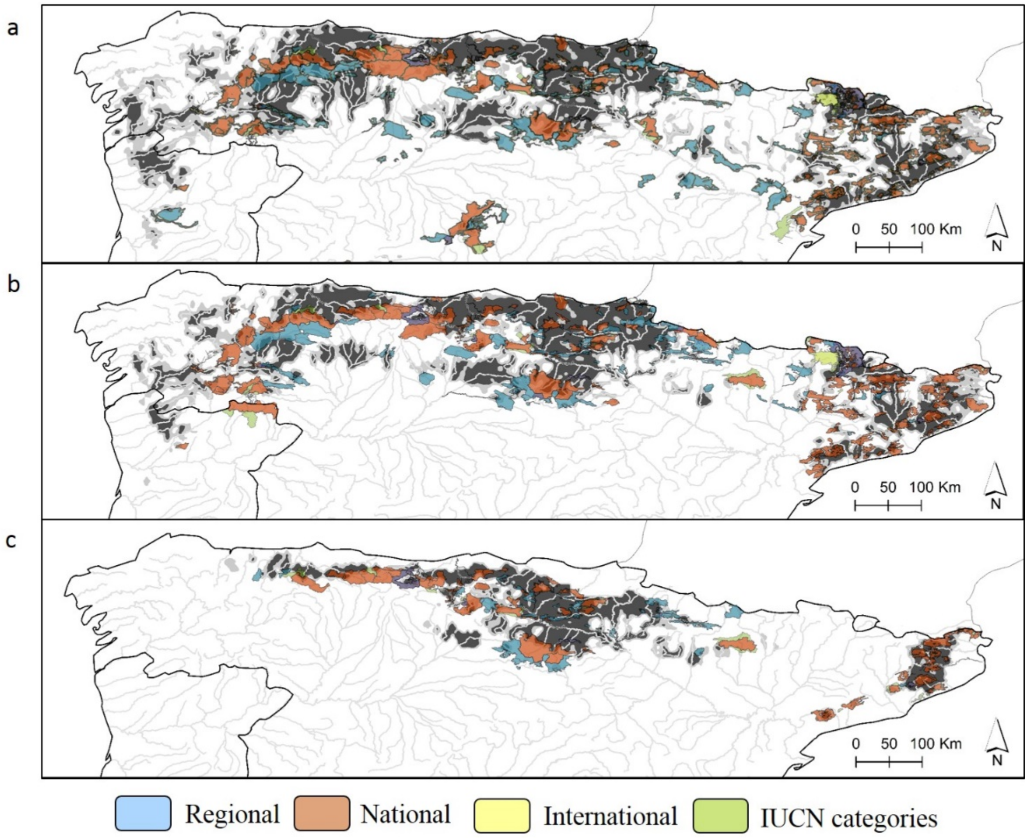


Figure 4. Maps representing the areas at high (dark gray) and medium risk (light gray) for the European mink conservation, resulting from the overlapping of the predicted distribution of the European mink and the invasive American mink in the Iberian Peninsula. The protected areas (Regional, National, International and IUCN categories I – VI) that intersect medium and high risk areas are shown in the figure. The conflict areas were selected using three different thresholds to transform continuous probability output into binary predictions (see text): **(a)** conservative, **(b)** moderate and **(c)** strict threshold.

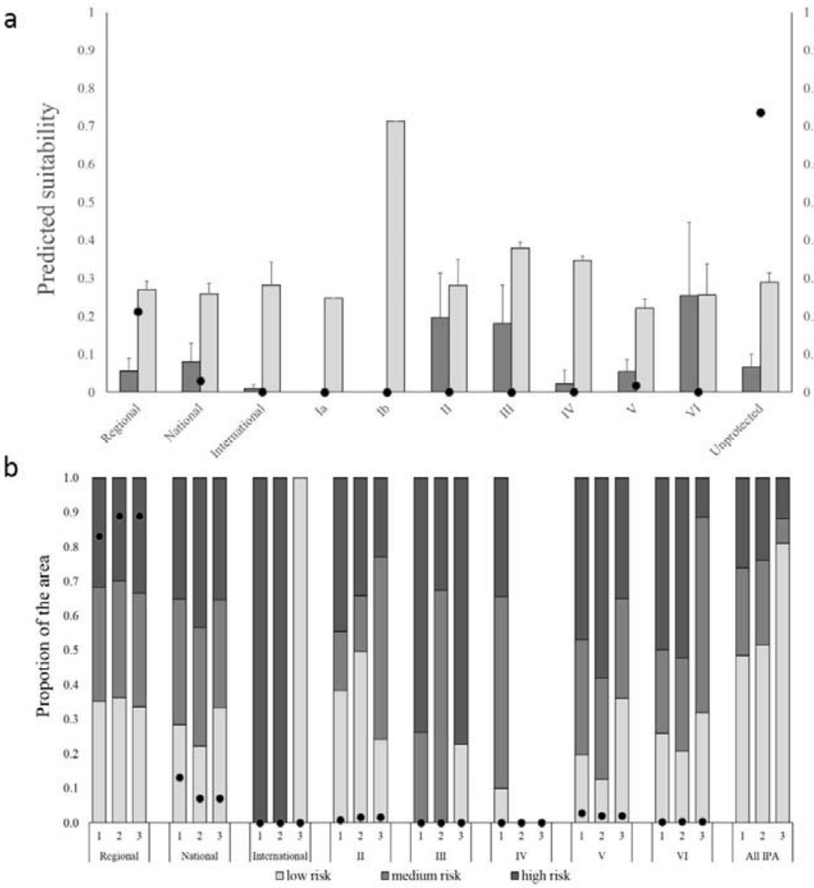


Figure 5. Summary of the spatial analysis for the identification of priority conservation areas for the critically endangered European mink. **(a)** Mean probability of presence of the European mink (dark gray) and the American mink (light gray) inside the Regional, National, International and IUCN designated protected areas (from II to VI), and in the unprotected territory of the Iberian Peninsula. The proportion of the area of each category on the total area occupied by protected areas in the Iberian Peninsula (black points) is reported on the vertical axis on the right of the chart. **(b)** Proportions of the areas at low (light gray), medium (medium gray) and high risk (dark gray) inside of each protected area category and of the total of the Iberian Protected Areas for the conservative (1), moderate (2) and strict thresholds (3) used to transform continuous probabilities of presence to binary maps.

The proportion of the three categories of risk inside each Iberian Protected Areas category was variable and depended upon the scenario considered (Fig. 5b). The largest absolute proportion of high-risk areas was found inside the International designated protected areas in the conservative and moderate scenarios, even though they represent a marginal proportion of the Iberian Protected Areas system. In the Regional Protected Areas, the proportion of the high-risk category was 32.6 ± 1.4 % (average of the three proposed scenarios). Nevertheless, the categories where the proportion of high-risk areas was higher compared to the other two risk categories were the III, IV, V and VI, the latter category being present only in the conservative scenario.

By averaging all the categories, the high-risk category occupied the 26.1%, 23.9% and 11.9% of the selected Protected Areas in the conservative, moderate and strict scenarios respectively.

DISCUSSION

In this study, we used Species Distribution Models to identify the crucial areas for the European mink's conservation through the spatial analysis of the overlap of its potential distribution with the prediction of the risk of invasion of the American mink, which represent one of the greatest threat to its viability.

We provided accurate regional predictions of both species potential distribution by applying a multi-scale hierarchical approach based on the largest amount on information on the environmental conditions occupied by the species at continental scale, currently and historically, and on the local features suitable for both species.

Models predictions

Although the two mink species have very similar habitat requirements, as reflected in the pattern of influence of environmental variables on models outputs (Fig. 3), very different predictions of their potential ranges emerged from our models.

Only some of the river basins of the northern part of the Iberian Peninsula were suitable for the critically endangered mink, whilst the invasive AM could inhabit river catchments from almost the entire Iberian territory, in all of the three scenarios proposed. Still, our results indicated that the EM can potentially expand over the limits of its current distribution in the Iberian Peninsula, and so the AM. The main reason of the difference in the predictions of the potential range of the two mink species is because the AM inhabits a wider range of climatic conditions than the ones currently and historically occupied by the EM.

Indeed, the AM can be found in a territory almost three times bigger than the EM, considering both the native and the invaded range, and its range encompass higher and lower latitudes than the one of the European mink.

This can be related to differences in the biogeography and biological traits of the two mink species. In fact, genetic evidences indicated that the EM expanded westward in Europe from an eastern refuge only recently after the last glaciation (Michaux *et al.*, 2005), which, in conjunction with the following historical decline and fragmentation of the population, may explain its absence in several countries of Southern and Northern Europe and the extremely recent colonization of Spain (Palazón *et al.*, 2003).

On the contrary, AM colonized and settled in less than a century in 20 European countries (Bonesi and Palazon, 2007). This process was enormously facilitated by deliberate or accidental introductions, a higher dispersal capacity, a higher adaptability to bad habitat quality, a higher population density and reproductive capacity than the endemic mink (Maran *et al.*, 1998; Melero and Palazón, 2011; Sidorovich *et al.*, 1997; Sidorovich, 2001).

All these factors certainly contribute to the rapid spread of the invader and its competitive advantage on the European counterpart.

Methodologically, the use a multi-scale hierarchical framework incorporated a large proportion of the two mink realized niches (*sensu* Hutchinson, 1957) in models calibrations and allowed to mitigate the negative effects of non-equilibrium data.

A model based only on the EM's current distribution in Europe, for example, would have likely underestimated the species potential range by missing conditions occupied by the species before disappearing from most of its original range. Moreover, the approach used, allowed us to identify the processes acting at a significant spatial scale and potentially provided more informative insights on species-environment relationship, as revealed in previous studies (Vicente *et al.*, 2011; Lomba *et al.*, 2010; Pearson *et al.*, 2004).

As the two mink species likely did not fill their potential range in the study area, the predictions provided are useful to identify the dynamic of the two populations in the short term, by defining the areas with suitable environment that may be most likely colonized.

In the long term, possible changes in climate conditions and in the land-use will certainly produce a change in the distribution of the suitable area for both species, which can be explored in further analysis.

European mink's conservation priorities

Our results showed that the areas where the AM could represent a threat for the EM are found in the northern part of the Iberian Peninsula. Particularly, the most threatened areas are found in the following principal river basins: the Internal Catalonian basins, the upper part of the Ebro river basin, the northern part of the Duero river basin, the Western Cantabria basin, the Miño – Sil basin and the Galician Coast basin, ordered from the east to the west.

Our analysis showed that approximately among 84% and 93% of the predicted range of the EM in the Iberian Peninsula was prone to the risk of the AM's invasion. A worrying result if we consider that other threats such as habitat loss and fragmentation and river pollution can undermine the EM viability in the study area (Zuberogoitia *et al.*, 2013; Palazón *et al.*, 2002) and that less than a quarter of the area potentially suitable for the EM fell inside protected areas.

Moreover, most of the conflict areas (high and medium risk classes) were found in unprotected territory.

Considering the current distribution of the EM in the Iberian Peninsula, the strict scenario identified the areas where management actions are most pressing. This scenario indeed included the areas where the environmental conditions for the EM had the highest values of suitability and closely reproduced the current range of the species in the Iberian Peninsula. In particular, the upper river Ebro basin and the northeastern part of the Duero river basin, the Western Cantabria basin and some of the Internal Basins of Catalonia (although the EM is not present there) resulted to be the areas more threatened by the AM expansion.

In this strict scenario, the protected areas that included the largest absolute extent of conflict areas between the two mink species were the Regional and National designated. In the Iberian Peninsula, those categories include mainly Special Protection Areas, Special Areas of Conservation, Regional and National Parks and Nature Reserves managed mainly by the Regional Governments supervised by Ministry of Environment. The remaining protected areas categories covered only a small proportion of the area at risk for the EM's conservation, and they were IUCN category III ('Natural monuments or feature') and V ('Protected Landscape'), which resulted the ones with the highest relative proportion of high risk areas.

The conservative and moderate scenarios incorporated the areas that should be managed and monitored to facilitate the expansion of the critically endangered mink. They indeed included areas suitable for the EM that are already or can be eventually invaded by the AM, but which the critically endangered species has not yet colonized (i.e. the Western Cantabria, the Galician Coast and the Internal Catalonian basins). In these scenarios Regional and National designated protected areas were again the ones including the largest proportion of conflict area.

Ideally, for an effective conservation of the EM, the prioritization of the areas in need for action should be centered in the zones of high and medium risk of conflict, particularly in protected areas where human activities are expected to accommodate to the conservation of threatened species (Araújo *et al.*, 2002).

The largest (in area and number) protected areas category including areas of medium and high risk of conflict, was the “Regional”, which included mainly Sites of Community Importance (Habitats Directive) and Special Protection Areas (Birds Directive) managed by the Regional Governments supervised by Ministry of Environment.

On the other hand, focusing conservation efforts only in protected areas would inevitably fail in enhancing the viability of the endangered mink and in halt the spread of the invader. Indeed, most of the conflict areas and the EM’s suitable habitat is found outside of the areas managed for conservation and the great majority of the territory suitable for the EM is at risk being invaded by the AM.

The risk maps, especially the strict scenario, which focused on the area where the European mink is currently distributed, can help managers to make informed decisions on the allocation of resources.

For example, it can be used to select the areas where the control of the AM is most urgent to mitigate its impact on the native mink, but also to identify the areas that should be monitored to detect early signals of impacts, prevent the conflict, and help the EM expansion by preserving the connectivity between suitable areas.

To conclude, our study showed that SDMs can be a powerful tool to identify conflict areas between endangered species and invasive competitors, if reliable predictions are produced by applying the existing techniques to mitigate the risk of underestimate potential ranges of non-equilibrium distributions.

Although the last IUCN red list assessment found the EM’s population in the Iberian Peninsula quite stable due to the intensive AM control measures during the last decade (Maran *et al.*, 2011), in the last years the population trend seems to have become negative (Santulli *et al.*, 2014). This indicates that without an intensive effort over the totality of the conflict areas where the two mink species are currently present, it would be difficult to succeed in the conservation of the critically endangered European mink.

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Results and Discussion

RESULTS AND DISCUSSION

In this section, the main results of the four Chapters of the thesis are reported and discussed, and practical guidelines for the management of the European mink and the American mink in the Iberian Peninsula are suggested.

The first two chapters focused on the dynamic of co-occurrence of the two mink species and on exploring changes in the critically endangered mink abundance in Northern Spain.

In the second part of the thesis we used Species Distribution Models to predict the expansion of the American mink in the Iberian Peninsula, and to analyze the spatial conflict between the two mink species.

Competitive exclusion by the American mink and decreasing abundance of the European mink

In the first Chapter we used detection data of the European and the American mink collected over 204 sites of 10x10 km between 2000 and 2011 to apply a multi-season two species occupancy model (MacKenzie *et al.*, 2006).

This model estimated four types of parameters (occupancy, detection, colonization and extinction) as a function of presence and absence of each one of the two species, and an interaction factor which measured how likely the co-occurrence of the target species was.

In the second Chapter, we used count data from 86 site of 10x10km collected between 2000 and 2010, as input of a dynamic N-mixture model (Dail and Madsen, 2011) to estimate the European mink abundance, detection probability and the finite rate of increase of the population.

Although these data were not collected with an analytical framework in mind and there was a great spatial and temporal variability in sampling effort (high numbers of missing values), in both cases models showed a good fit and parameters were estimated with an acceptable precision. It is likely that the high number of surveys repetitions and of sampled sites compensated for the heterogeneity of the data. Indeed dynamics and patterns of occupancy and abundance emerged clearly from these studies.

In Chapter 1, evidences of competitive exclusion of the critically endangered European mink by the invasive mink were found.

The best ranked model indicated that the probability of occupancy of the European mink decreased substantially since year 2000 (from 0.407 ± 0.062 in 2000 to 0.195± 0.062 in 2011) while the American mink occupancy simultaneously increased (from 0.351 ± 0.054 in 2000 to 0.480 ± 0.054 in 2011). The two mink species co-occurred less often than expected as revealed by a value of the Interaction Factor inferior to 1 (0.717 ± 0.063) (Fig. 1). Moreover, parameters estimates (Fig. 2) showed that the invasive mink preferentially colonized sites already occupied by the European mink (probability of colonization: 0.129 ± 0.033 *versus* 0.090 ± 0.026), whilst the native mink had a small probability of colonizing areas already occupied by the alien mink (0.014 ± 0.007).

The highest value of probability of extinction was for the American mink in sympatry with European mink (0.254 ± 0.081), consistent with the local impact of the control of the invader not being compensated by re-colonization, at least in the next year, but at the same time the native mink was more likely to become extinct from sites occupied by the invasive species (probability of extinction: 0.130 ± 0.045 *versus* 0.072 ± 0.024).

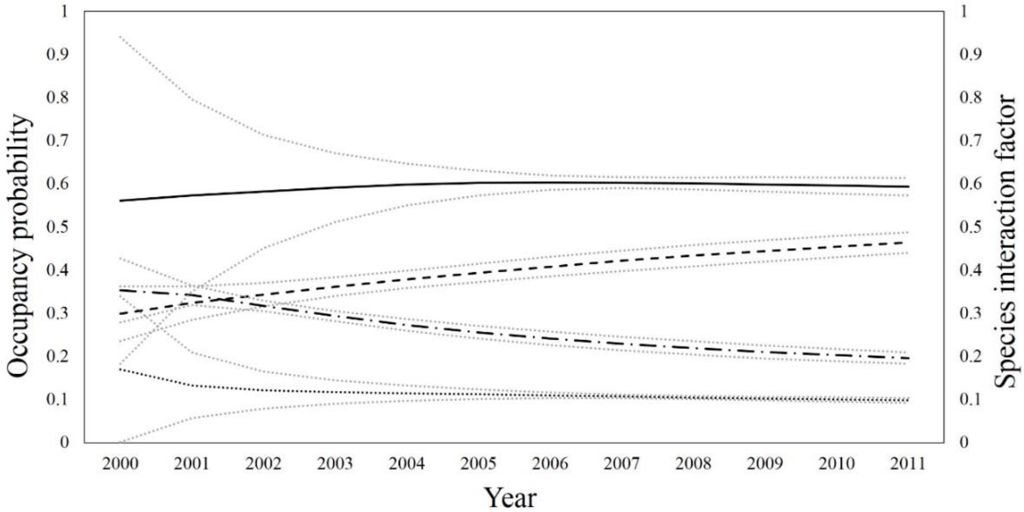

Figure 6 Seasonal probability of occupancy (left vertical axis) obtained from the best AIC ranked model of three possible states: only American mink present (dashed line), only the European mink present (dash-dotted line) and both species present (dotted line). On the right vertical axis: seasonal Species Interaction Factor (SIF) represented by the solid line. Standard errors in light grey dotted line.

Overall, these results revealed that in Northern Spain the spread of the American mink is leading to the displacement of the native mink. This is a realistic scenario considering that this process has been already observed in other European countries (Sidorovich, 2001; Maran *et al.*, 1998b), and even inside the study area at local-scale (Carreras *et al.,* 2006; Ceña *et al.*, 2003).

Interestingly, it seems that locally the control of the invader suppresses its density and slows down the process of replacement of the European mink, although the overall increase in the occupancy of the American mink indicates that ongoing management actions should be improved to halt its spread.

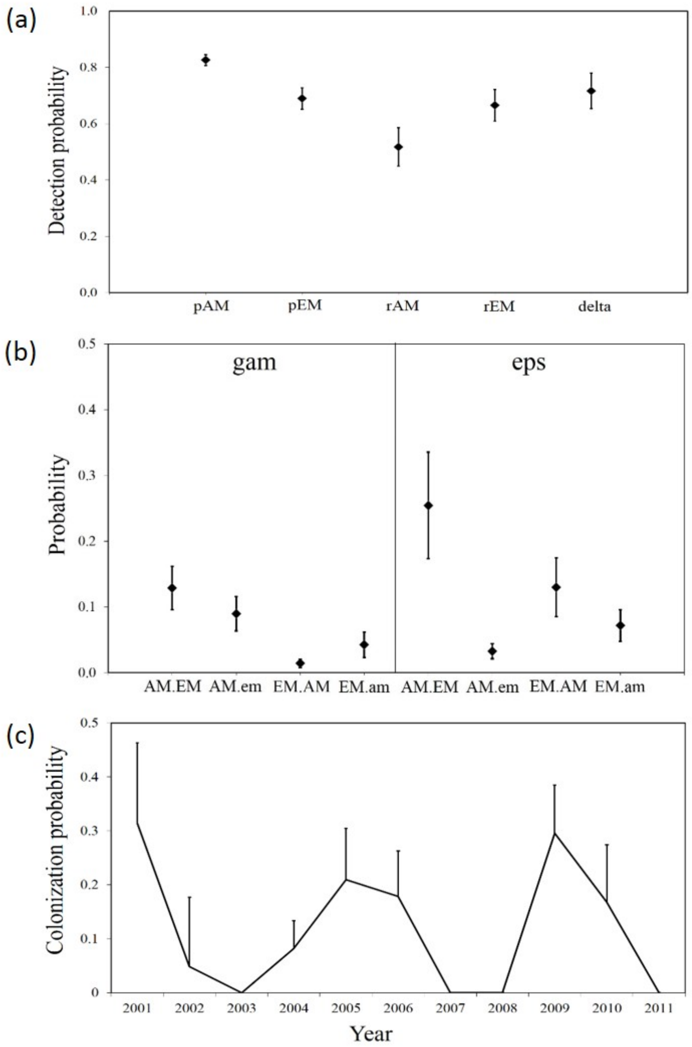

Figure 2 Results of detection (a), colonization (b and c) and extinction (b) probabilities estimations obtained in the study. **a)** Detection probabilities estimated by the best ranked model. AM = American mink and EM = European mink. pAM= probability of detecting AM, given only AM present, pEM = probability of detecting EM, given only EM present, rAM = probability of detecting AM, given both species are present and EM not detected, rEM = probability of detecting EM, given both are present and AM not detected, delta = detection species interaction factor. **b)** Colonization (gam) and extinction (eps) probabilities from the best ranked model. AM.EM = probability of AM colonizing / becoming extinct at one site, given EM present. AM.em = probability of AM colonizing / becoming extinct at one site, given EM absent. EM.AM = probability of EM colonizing / becoming extinct at one site, given AM present. EM.am = probability of EM colonizing / becoming extinct at one site, given AM absent. **c)** Time varying American mink colonization probability derived from the second best ranked model.

The high re-colonization capacity of the American mink, revealed in this study and in other areas invaded by the species (Bryce *et al.*, 2011; Zalewski *et al.*, 2009; Nordström *et al.*, 2002), indicated that contrasting the flow of the dispersers that could readily recolonize areas where the invader is culled is a priority. This implies a constant effort of removal as well as a continuous verification of the absence of the alien mink from previously controlled areas.

As abundance enables finer questions on population dynamics to be addressed than occupancy (MacKenzie and Nichols, 2004), in Chapter 2 we focused on the European mink changes in abundance over time and space, modeled over its entire Spanish range of distribution.

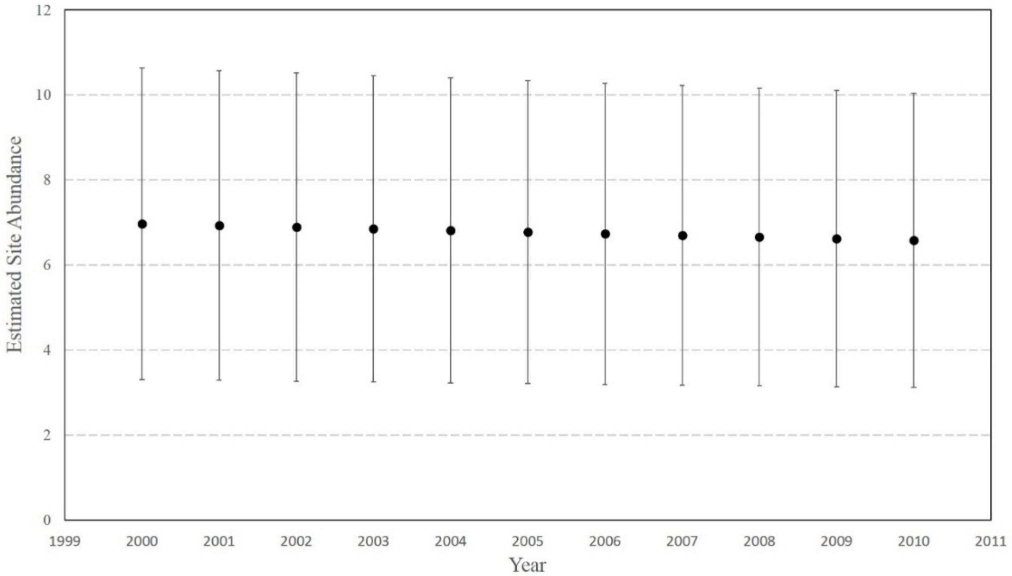

Figure 3. Estimated site abundance of the European mink in its Spanish range of distribution over the 10 years of the study using a dynamic N-mixture model.

A slow decline in the population abundance since year 2000 has been detected, as the average finite rate of increase was slightly inferior to 1 (0.994 ± 0.045).

According to this parameter, the mean number of individual per site changed from 6.9 ± 3.6 in 2000 to 6.6 ± 3.6 in 2010 (Fig.3). Although this may not seem a striking decline, our results indicated that on average the number of recruited individuals (by birth or immigration) is to some extent inferior to the previous year.

Spatially, the European mink's abundance showed a great variability, being highest values concentrated in the central part of its range, an area included in the regions of Alava, North La Rioja, Eastern Burgos and South Navarre, which correspond to the upper Ebro basin (Fig. 4).

Precipitation, proportion of natural vegetation and human disturbance were not limiting factors to species' abundance at the resolution (10 km) and extent (eight Spanish Provinces) of the analysis. Indeed sites where abundance was highest, the low-lying areas along the Ebro River and tributaries, were also the most affected by human presence and the one with lowest mean precipitation values.

An important caveat must be associated to this result: while the cited environmental factors seemed not to have a negative influence on species abundance at the spatial scale of the analysis, they may have a strong impact at finer scale.

In fact, previous studies indicated that factors as width of riverbank vegetation, water quality and degree of alteration of riverine habitat have a substantial effect in determining species presence at micro-scale (Zabala *et al.*, 2006; Palazón *et al.*, 2006c).

On the other hand, at the scale of the analysis emerged clearly the positive correlation between the availability of small and, to a lesser extent, medium-size rivers and the mink abundance. In the study area, small rivers are mainly secondary tributaries of medium rivers, which are the major tributaries of rivers as big as the Ebro or Duero rivers.

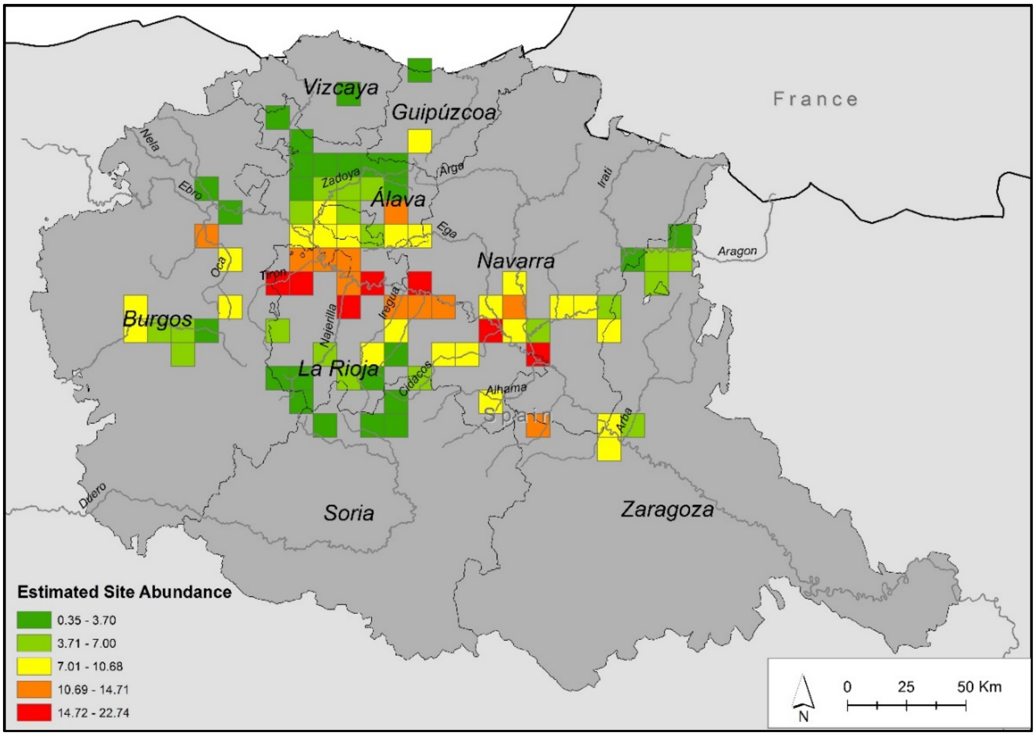

Figure 4. Spatial distribution of the estimated site abundance of the European mink using a dynamic N-mixture model in the 86 sampled sites (10x10km UTM) over the eight Provinces surveyed in Northern Spain

Although not much published information exists on the dimension of rivers selected by the European mink, it seems that small tributaries with good vegetation coverage and water quality are occupied mainly by reproductive females and juveniles, while big rivers act as corridors for young dispersal male, which may explain lower densities in bigger rivers (MAGRAMA, 2009; Palazón and Ruiz-Olmo, 1998a).

We hypothesized that Atlantic basins and the Southern part of the species' range have lower abundance values for different causes. Rivers of the Basque Country are short, fast-flowing and steep, with poor water quality (Palazón *et al.*, 2003), and suffers the introgression of the American mink since at least two decades (Zabala *et al.*, 2006). In the Southern part of the range lower densities may be linked to the presence of the "Sierra de la Demanda", the Northwestern end of the

Iberian System Mountain range, which reaches 2230 m.a.s.l. and which can act as a geographical barrier for the species.

In this Chapter, the impact of the American mink on the native species' abundance was not detected. One reason may be that in model setting the only parameter that could be modeled in function of the invader presence was the detection probability.

But in a previous study (Chapter 1), we observed that the European mink detectability is not affected by the competitor's presence: generally if both species are present at a site, both are detected, probably thanks to the effectiveness of the live-trapping method used.

Another reason could be that the 86 sites selected in this study represent the core of the European mink distribution in Spain, where major efforts for the American mink culling are carried out, and where local densities and spread of the invader are to some extent controlled, as revealed in Chapter 1.

Finally, we stressed that, although in this study the causes of the observed decline of the European mink did not clearly emerged, the slow decreasing of the number of individuals indicates that ongoing management effort are failing in maintaining a viable population.

Conservation actions should focus on the area more closely related to rivers and riverbanks, on the central and most abundant sub-population that may act as a source of individuals for other less abundant groups, and on counteracting the spread and settlement of the American mink in the area.

Prediction of the American mink expansion and identification of areas of potential conflict of the two mink species

In the third Chapter we aimed to produce a fine-scale prediction of the potential expansion of the American mink in the Iberian Peninsula by correlating environmental factors influencing its ecology with its current distribution in the study area.

Forecasting distribution of species not in equilibrium with their environment, such and invasive species spreading in new areas, may lead to underestimate species range, because a set of environmental conditions potentially suitable for the species are not included in models' calibration. For this reason, we developed an analytic framework that incorporated the largest amount of available information on species global distribution in the prediction at regional scale.

We calibrated a coarse scale model at the extent of North America, species' native range, and Europe, the invaded range, using climatic predictors, and we combined it with a fine resolution model calibrated in the Iberian Peninsula using land-use variables.

We tested difference on models prediction using different amount of information: 1) only from the invaded range, 2) only from the native range or 3) from both ranges of distribution.

Once projected at the extent of the Iberian Peninsula these three climate envelopes gave fairly different predictions (Fig.5 e, f, g), difference that was obviously reflected in the hierarchical combination with the land-use fine scale model (Fig. 6).

The model that included the largest amount of information on environmental conditions potentially suitable for the American mink (from both the native and the invaded range of distribution) was the one with the highest performance (measured with Sensitivity: proportion of presence correctly predicted). The model calibrated only in the invaded range, the European continent, had the lowest predictive power, probably because in Europe the American mink is far from the equilibrium state (far from filling the potentially suitable niche).

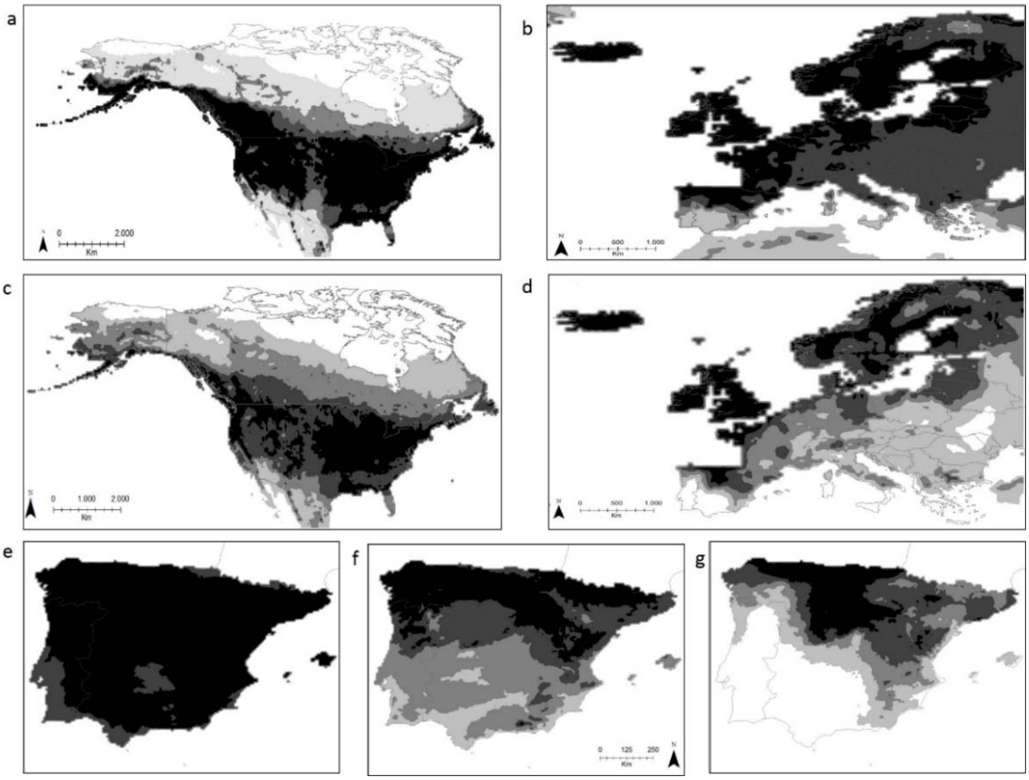

Figure 5. Maps representing the ensemble forecasting of the climatic envelopes calibrated in a) and b) both ranges of distribution, c) only in North America, the native range and d) only in Europe, the invaded range. Lower line maps illustrate the projection at the Iberian Peninsula extent of the climatic models calibrated in e) both ranges, f) the native range and g) the invaded range. In all maps darker colors indicate higher agreement among the five algorithms used in models calibration.

The model with the best performance predicted as climatically suitable almost all the Iberian territory (Fig. 5 e), revealing that the species can inhabit arid areas with dry and hot summer, which is the prevalent climate in the Southern half of the Peninsula. The combined model (Fig. 6 a) identified as suitable rivers from almost all the principal Iberian river basins, especially the ones of medium and big size.

This is the first analysis of the potential expansion of the American mink at the extent of the whole Iberian Peninsula, and although currently the species is spreading in the Northern half of the Peninsula, our results suggested that the dry and hot conditions of the Southern half of the study area would not halt the species' invasion.

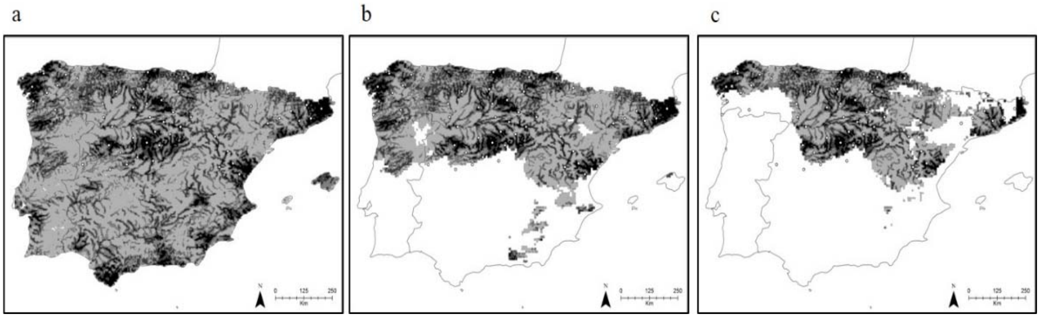

Figure 6 .Maps resulting from the multi-scale hierarchical combination of a land use model calibrated at the Iberian Peninsula extent (modIP) with the climatic models calibrated **a**) in the native and the invaded range (modNAEU), **b**) only in the native range (modNA) and **c**) only the invaded range (modEU) (binary threshold 0,5). White points are a sample of 10% of the independent dataset used in models external evaluation

Through this analysis, we showed the effect of training Species Distribution Models with non-equilibrium data, and hence the consequences of relying in an incomplete information on the conditions potentially suited for the species.

The analytical framework presented in this Chapter can be used to reduce the negative effects of non-equilibrium data and to improve the effectiveness of Species Distribution Modeling in properly inform INNS management and prevention actions, by providing fine-scale mid- and long-term predictions based on the largest available amount of information on the target species-environment relationship.

The same modelling framework has been applied in Chapter 4 to predict the areas potentially suitable for the persistence of the European mink in the Iberian Peninsula.

Critically endangered species are commonly far from the equilibrium state due to the extreme reduction of their geographic range, whereby modeling their distribution presents the same challenges of invasive species.

In this case, the prediction was the result of the combination of a climatic envelope calibrated with historical data of distribution of the endemic mink in Europe (before going extinct in the 85% of its original range) and a land-use model trained at the extent of the Iberian Peninsula.

The spatial prediction of environmental suitability obtained (Fig. 7, upper line) was combined with the model of potential invasion of the American mink produced in Chapter 3 (Fig. 7, lower line). This was done in order to: 1) identify potential areas of conflict between the endemic and the invasive mink and 2) analyze the effectiveness of the Iberian protected areas system in including areas potentially suitable for the critically endangered species.

Although the two mink species have very similar habitat requirements, very different predictions of their potential ranges emerged from our models (Fig. 7). Only some of the river basins of the northern part of the Iberian Peninsula were suitable for the critically endangered mink, whilst the invasive American mink could inhabit river catchments from almost the entire Iberian territory, as reported in Chapter 3.

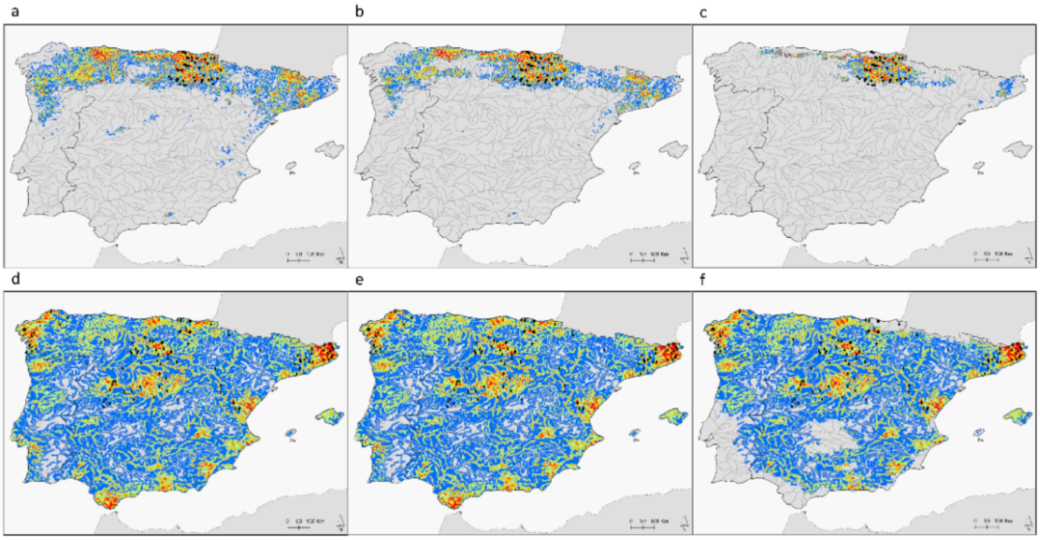

Figure 7. Maps representing European mink (upper line) and American mink (lower line) potential distribution in the Iberian Peninsula modelled using a multi-scale hierarchical approach. For both species to combine climatic envelope with the regional scales models three different threshold were used: 0.3 (a, d), 0.5 (b, e) and 0.7 (c, f). Black points in the upper line and black diamonds in the lower line represent a sample of 10% of the original data set of model calibration of the European mink and the American mink respectively.

We put this difference in relation to dissimilarities in the biogeography and biology between the two mink species. The American mink has a higher ecological plasticity compared to the European counterpart, which is expressed by a higher dispersal capacity, a higher adaptability to bad habitat quality in the range of introduction, a wider trophic niche and a higher reproductive capacity (Melero and Palazón, 2011; Sidorovich and Macdonald, 2001; Maran *et al.*, 1998b; Sidorovich *et al.*, 1997).

This invader colonized and settled in less than a century in 20 European countries (Bonesi and Palazón, 2007), although this process was enormously facilitated by deliberate or accidental introductions. The European mink is less adaptable, and never reached the most Southern and Northern countries of Europe and entered in Spain extremely recently (Palazón *et al.*, 2003; Youngman, 1982; Rodríguez de Ondarra, 1955).

Our analysis showed that approximately among 84% and 93% of the predicted range of the European mink in the Iberian Peninsula was prone to the risk of the American mink invasion (Fig. 8). This is a worrying result if we consider that other threats such as habitat loss and fragmentation and river pollution (Zuberogoitia *et al,* 2013; Palazón *et al.,* 2002), diseases (Mañas *et al*., 2003) and human-induced mortality (Palazón *et al*., 2012a) can undermine the endangered mink viability in the study area,

Moreover, less than a quarter of the area potentially suitable for the European mink fell inside Protected Areas and most of the conflict areas (high and medium risk classes) is found in unprotected territory.

Ideally, for an effective conservation of the European mink, the prioritization of the areas in need for action should be centered in the zones of high and medium risk of conflict, particularly in Protected Areas where human activities are expected to accommodate to the conservation of threatened species (Araújo *et al.,* 2002).

The largest (in area and number) Protected Areas category including areas of medium and high risk of conflict was the “Regional” one which included mainly Sites of Community Importance (Directive 92/43/CEE, “Habitats”) and Special

Protection Areas (Directive 79/409/CEE, "Birds") managed by the Regional Governments supervised by the Spanish Ministry of Environment.

On the other hand, focusing conservation efforts only in Protected Areas would inevitably fail in enhancing the viability of the endangered mink and in halt the spread of the invader because most of the conflict areas and the European mink's suitable habitat is found outside of the areas managed for conservation.

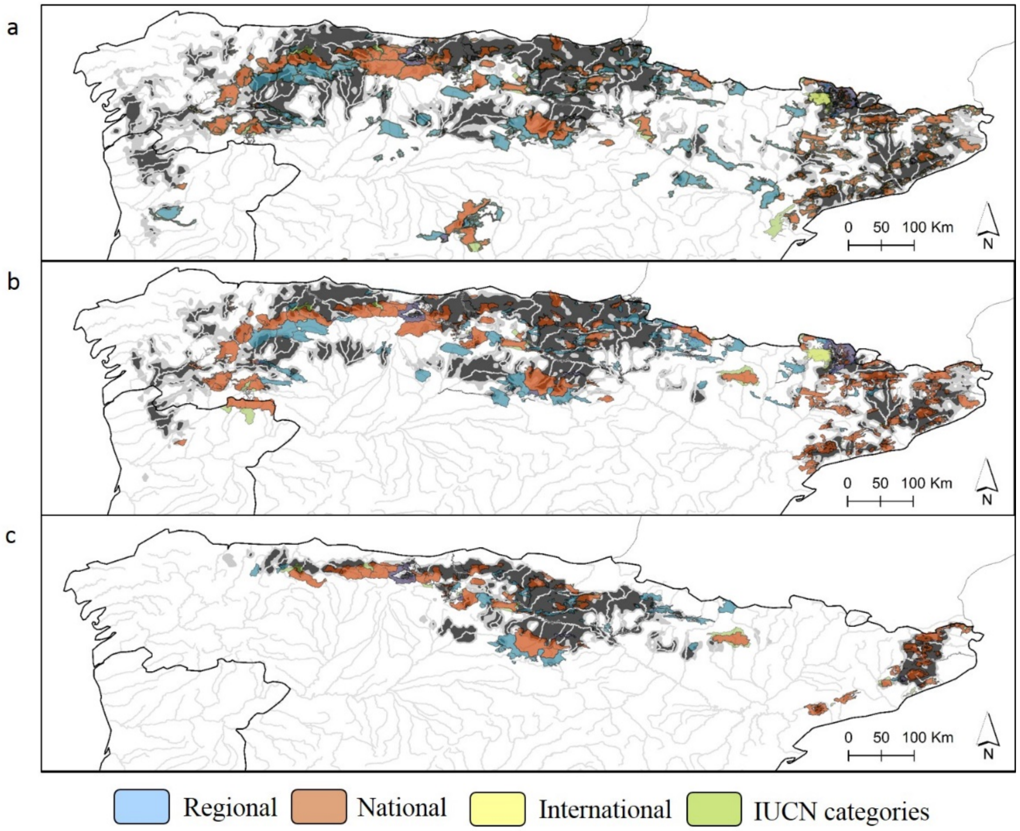

Figure 8. Maps representing the areas at high (dark gray) and medium risk (light gray) for the European mink conservation, resulting from the overlapping of the predicted distribution of the European mink and the invasive American mink in the Iberian Peninsula. The protected areas (Regional, National, International and IUCN categories I – VI) that intersect medium and high risk areas are shown in the figure. The conflict areas were selected using three different thresholds to transform continuous probability output into binary predictions (see text): (a) conservative, (b) moderate and (c) strict threshold.

In this last Chapter, we provided risk maps, especially the strict scenario that focused on the area where the European mink is currently distributed, which can help managers make informed decisions on the allocation of resources for the species' conservation and management. For example, they can be used to select the areas where the control of the invader is most urgent, but also to identify the areas that should be monitored to detect early signals of impacts, prevent the conflict and help the European mink expansion by preserving the connectivity between suitable areas.

Without an intensive effort over the totality of the conflict areas where the two mink species are currently present, it would be difficult to succeed in the conservation of the critically endangered European mink.

Implications for the management and conservation of the two mink species

Despite the resources and efforts that have been spent in the last decades in the conservation of the European mink and the control of the invasive American mink, from the analysis developed in this thesis emerged that overall the ongoing actions (2000 - 2014)are not having the expected outcome.

A possible reason can be the spatial and temporal variation in American mink culling effort, due to variable funding and lack of coordinated regional policies, which allows the establishment of compensatory mechanisms in reproduction and immigration of the invasive population.

Given the high recolonization ability of the American mink, much more intensive efforts are required to provide a comprehensive spatial coverage to remove mink from the whole of the European mink range and a suitably large buffer area around it.

River basins of the entire Iberian territory are potentially suitable for the American mink, which implies that monitoring the southward expansion of the American mink is necessary, as it is essential to verify the continuing absence of the invader from previously controlled areas, in order to obtain evidence that management efforts are successful (or not).

Actions aimed to protect the European mink should focus on the area most closely related to rivers, water bodies and riverbanks, for example by preserving or by restoring the riparian vegetation and by reaching an acceptable water quality, i.e. through a good system of Water Treatment Plants.

Only a small part of the area suitable for the European mink falls inside protected areas, and although areas managed by Regional Governments may be an important spot of the European mink conservation, all the areas at risk of conflict inside and around its current range of distribution should be constantly monitored, in order to prevent or mitigate the invader impact on the native species.

The sub-population of the European mink inhabiting the central part of the range, along the tributaries of the upper Ebro River basin, has the highest densities and should receive a special attention when planning species' conservation, as it may act as a source of individuals for the sub-populations located on the north and the south of the range, and for the potential expansion of the species southeastward and westward.

Stronger efforts (economic, equipment and human resources) should be allocated to halt the spread of the American mink right in the core of this sub-population range. Is essential to maintain low densities of the invasive population especially in Alava, in the Atlantic basins (Biscay and Guipúzcoa), and in the southeastern part of the European mink range (Burgos and La Rioja), currently the area most threatened by its expansion.

Overall, a better coordination between local policies as well as a greater constancy in monitoring and controlling the American mink is imperative to improve the conservation strategy of the European mink in Spain.

Conclusions

CONCLUSIONS

1. The spread of the invasive American mink is leading to the displacement of the critically endangered European mink from its range in Northern Spain.

2. The American mink preferentially colonizes sites occupied by the native mink that is more likely to become extinct from sites occupied by the invasive species than from sites where the invader is absent.

3. Locally, especially inside the area of distribution of the European mink, the control of the invader suppresses its density and slows down the replacement of the native mink but overall the ongoing management actions are not adequate to halt this process.

4. The abundance of the European mink is gradually decreasing, which indicates that the number of recruited individuals by birth or immigration every year is lower than the previous year.

5. The estimate of the European mink population size in the study area in year 2000 was of 599.75 individuals, and in 2010 it showed 566.52 individuals.

6. The abundance of the European mink is spatially variable and the highest densities are located in the central area of its range, in the upper river Ebro and tributaries, in the regions of Alava, North La Rioja, Eastern Burgos and South Navarre.

7. The European mink population is more abundant in small and medium rivers than in big ones, and the fine-scale characteristics of the area most closely related to rivers (i.e. water quality, riparian vegetation) have more influence in its density than coarse-scale features such as human disturbance or proportion of natural vegetation.

8. Almost all of the Iberian territory is climatically suitable for the American mink, and the species can potentially colonize river basins of the entire Peninsula whilst only some of the river basins of the northern part of the Iberian Peninsula are suitable for the European mink.

9. Less than a quarter of the area suitable for the European mink is found inside Protected Areas, the great majority (about 90%) of this potentially suitable territory is prone to the risk of the American mink's invasion and most of the conflict areas is found in unprotected areas.

10. Conservation and management action should focus inside and outside Protected Areas, in order to preserve the suitable habitat for the European mink and to mitigate or prevent the conflict between the two mink species.

11. A better coordination between local policies as well as a greater constancy in monitoring and controlling the American mink population is imperative to improve the conservation strategy of the European mink in Spain.

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Spanish summary

SPANISH SUMMARY

INTRODUCCIÓN

El último análisis sobre las causas globales de extinción propuesta por la lista roja (Baillie *et al*., 2004) de la Unión Internacional para la Conservación de la Naturaleza (IUCN) indica que las amenazas que tienen más impacto para los mamíferos son la destrucción y la fragmentación del hábitat, la sobre-explotación, las enfermedades, la contaminación, las muertes accidentales y las invasiones biológicas.

Se piensa que la mayoría de estas amenazas actúan a escala de paisaje (Boyd *et al*., 2008) (concebida como un área cuyas dimensiones van de pocos kilómetros a pocos centenares de kilómetros, Forman and Godron, 1986) que es la escala a la que la mayor parte de las investigaciones están desarrolladas. Los componentes más importantes de la escala especial son el “grano”, la resolución espacial mínima de los datos o la dimensión de la unidad de observación, y la “extensión”, el ámbito o el dominio de los datos, que corresponde típicamente al área de estudio.

Analizar el estatus y la distribución de las especies de interés a una escala amplia (por ejemplo a nivel regional o de país) es crítico para definir las prioridades de conservación: a nivel de país se establecen las normas, se definen las áreas protegidas y se pueden realizar otras estrategias de conservación, y posteriormente pueden ser adaptadas y aplicadas a escala local (Turner, 2005).

Además la escala espacial puede afectar la capacidad para interpretar correctamente las interacciones biológicas: por ejemplo para detectar la influencia de una especie sobre otra es importante que la unidad de observación sea lo suficientemente grande para englobar los dominios vitales de diferentes individuos y el área de estudio debería comprender una área donde la dinámica de la interacción sea significativa.

Esto puede ser particularmente importante para entender el efecto de una especie exótica invasora (EEI) sobre la biodiversidad autóctona. Una EEI se define como "una especie ajena que se establece en un ecosistema o en un hábitat natural o semi-natural, que no podría ocupar sin la introducción directa o indirecta o la ayuda de parte de la especie humana y que se convierte en un agente de cambio y amenaza para la diversidad biológica autóctona" (DAISIE, 2009; IUCN, 2000).

Las EEI están consideradas como la segunda causa de pérdida de biodiversidad, después de la pérdida, alteración y fragmentación del hábitat, y su impacto económico y ecológico ha sido ampliamente estudiado (Hoffmann *et al.*, 2010; Gurevitch and Padilla, 2004; Mack *et al.*, 2000; Parker *et al.*, 1999).

Las EEI pueden tener un impacto destructivo especialmente sobre las especies en peligro de extinción, que sufren reducciones extremas de las dimensiones poblacionales y del área geográfica de distribución (IUCN, 2013).

Esta tesis está focalizada sobre el visón europeo (*Mustela lutreola*) y el visón americano (*Neovison vison*) que son respectivamente uno de los carnívoros más amenazados (Maran *et al*., 2011) y una de las peores especies invasoras en Europa (DAISIE, European Invasive Alien Species Gateway (http://www.europe-aliens.org), y sobre su interacción, ocupación, abundancia y distribución potencial, que ha sido analizada en sus áreas de distribución en la Península Ibérica.

El visón europeo es una especie endémica del continente europeo y su área de distribución histórica se extiende desde los Urales a la costa atlántica francesa y desde Finlandia hasta el Cáucaso (Maran, 2007; Youngman, 1982). El área original del visón americano ocupa casi todo el norte de América, excluyendo el norte del Círculo Polar Ártico y la parte más meridional de los Estados Unidos (Larivière, 1999), la especie se ha establecido en veintiún países europeos y ha sido introducida también en Argentina, Chile, Rusia, China, Japón, Kazajistán y

Nueva Zelanda (Ibarra *et al.*, 2009; Reid and Helgen, 2008; Bonesi and Palazón, 2007; Previtali and Cassini, 1993).

El visón europeo y el visón americano: caracteres biológicos i ecológicos

Ambos visones son mustélidos semi-acuáticos que viven en sistemas de agua dulce y costero y que tienen morfologías y requerimientos de hábitats prácticamente idénticos (Sidorovich *et al.,* 2009; Maran *et al.*, 1998a).

El visón europeo se encuentra principalmente en pequeños ríos, donde selecciona la parte alta de pequeños afluentes y raramente se observa en grandes ríos (Youngman, 1990), mientras que el visón americano se observa en un espectro de hábitats más amplio y a veces inusuales para una depredador semi-acuático (como prados pantanosos y también bosques no pantanosos lejos de los ríos) (Sidorovich and Macdonald, 2001). Los dos visones utilizan lugares de descanso a lo largo de las orillas de los ríos, normalmente debajo de raíces, rocas o arbustos (Yamaguchi *et al.*, 2003; Zabala *et al.*, 2003).

Las dos especies de visones son solitarias y territoriales, no hay solapamiento entre los dominios vitales de machos residentes, aunque sí en algún caso se han observado individuos transeúntes en los territorios de estos machos (Melero, 2008; Yamaguchi *et al.*, 2003), y las hembras tienen territorios más pequeños que se solapan a los territorios de los machos (Dunstone, 1993).

Los dominios vitales del visón europeo son en promedio más grandes que los del visón americano; estudios realizados en la Península Ibérica aportan valores de 13,1 ± 2,8 km para los machos y de 3,4 ± 2,8 km para las hembras en el caso del visón europeo (Palazón and Ruiz-Olmo, 1998a), mientras que los dominios vitales del visón americano están comprendido entre 0,89 – 6,8 km para los machos y entre 0.21 – 2.9 km en el caso de las hembras (Melero *et al.*, 2008a).

El visón americano es sustancialmente más grande del europeo; el peso promedio de los machos de la especie invasora es de 1500 g, mientras los machos de la autóctona pesan 700 - 900 g, y las hembras de visón americano pesan de promedio

900 g mientras que la de europeo 450 – 600 g (Melero *et al.,* 2012b; Palazón *et al.,* 2006b; Sidorovich, 1997; Palazón and Ruiz-Olmo, 1995; Birks and Dunstone, 1985).

En la Península Ibérica la reproducción del visón americano se produce entre Febrero y Abril (Melero and Palazón, 2011), mientras que el estro del visón europeo ocurre entre finales de Marzo y Junio (Youngman, 1990). Estudios realizados en cautividad indican que el visón americano tiene una mayor fecundidad comparado con la especie autóctona, siendo 5,4 y 4,3 el número promedio de crías por camada, respectivamente (Amstislavsky *et al.,* 2008).

Las analogías en la ecología y la apariencia de las dos especies de visones son tan fuertes que durante mucho tiempo se pensó que eran subespecies (Maran *et al.,* 1998, Novikov, 1939), mientras que recientes estudios filogenéticos han asignados el visón americano a un diferente linaje del Nuevo mundo, el género Neovison, creado ad-hoc (Harding and Smith, 2009; Kurose *et al*., 2008).

El visón europeo: declive histórico y amenazas presentes

En las listas rojas de la IUCN, el estatus de conservación en Europa del visón europeo ha cambiado de “en peligro” a “en peligro crítico de extinción” en el 2011 (Maran *et al*., 2011). Además, está incluido en el Catalogo de la Directiva Hábitat (Directiva 92/43/CEE, modificada por la Directiva 97/62/CE).

El declive y la extinción local de la especie fueron observados inicialmente en Europa central en el siglo diecinueve. Antes de los años cincuenta del siglo pasado se extinguió en la mayoría de los países del Europa del Este y a partir de entonces el visón ha desaparecido de casi el 85% de su área de distribución original (Maran *et al*., 2011). Actualmente se encuentran solo tres poblaciones en enclaves aislados y fragmentados: una en el Oeste de Europa (el norte de España y el suroeste de Francia), una en el Delta del Danubio en Rumania y una en Ucrania y Rusia (dividida en diferente sub-poblaciones) (Maran, 2007; Michaux, 2004;

Palazón *et al.*, 2002, 2003; Sidorovich, 2001). Las tres poblaciones están en regresión y presentan bajas densidades (Maran *et al.*, 2011).

Hay muchas causas implicadas en las extinciones locales y en la desaparición del visón europeo de casi toda su área de distribución original. La alteración del hábitat producida por el hombre a gran escala tiene un impacto considerable en la mayoría de los países, y ha actuado en conjunto con otros factores para incrementar y acelerar el declive de la especies (Maran, 2007). Aunque en general se piensa que diferentes combinaciones de amenazas están presentes en diferentes regiones, se considera que los factores clave principales pueden ser: el exceso de caza, la degradación y la pérdida de hábitat, la contaminación de los ríos y la invasión del visón americano (Lodé *et al.*, 2001; Maran *et al.*, 1998a; Maran and Henttonen, 1995).

La población de visón europeo del Oeste Europa (en Francia y España) ha recibido una atención particular en las últimas décadas por su valor en la conservación de la especie en la Unión Europea y por su historia única.

El primer registro de la especie en Francia es sorprendentemente reciente (del año 1839, Youngman, 1982) y aún más reciente en España, en 1951 (Palazón and Ruiz-Olmo, 1992; Rodríguez de Ondarra, 1955). No está claro si en estos países la especie fue introducida por el hombre o si se trató de una colonización natural, pero esta población tiene una variabilidad genética muy reducida, probablemente a causa de un “cuello de botella” durante su establecimiento (Michaux *et al.*, 2005; Michaux, 2004). Esto ha llevado a algunos autores a sugerir que la población occidental de visón europeo tiene que ser considerada una unidad de gestión distinta respecto a las poblaciones orientales, principalmente como medida preventiva para evitar la depresión por exogamia en potenciales programas de reintroducción (Michaux, 2004).

La situación de la población occidental es de hecho preocupante. En Francia el visón europeo ha sufrido una rápida reducción: en pocas décadas al final del siglo veinte desapareció en la mitad norte del país, y actualmente se encuentra solo en el suroeste (Maizeret *et al.*, 2002). Su declive ha sido atribuido principalmente a la sinergia entre un trampeo intensivo, la alteración de la calidad del agua de los ríos y la modificación del hábitat, mientras que la competición con el visón americano no puede haber sido una causa decisiva, porqué en esta área el europeo desapareció varios años antes de la introducción de este (Lodé *et al.*, 2001).

La población española del visón europeo deriva verosímilmente de la expansión de la francesa, que colonizó a principios de la década de los '50 del siglo pasado las cuencas atlánticas, donde ahora se encuentra en pequeñas poblaciones fragmentadas, y se expandió sucesivamente a lo largo de los ríos de La Rioja y Navarra, el País Vasco, Castilla y León (en la provincias de Burgos y Soria) y Aragón (en la provincia de Zaragoza) (Gómez *et al.*, 2011; Palazón *et al.*, 2003).

A pesar de las evidencias de una reciente expansión de la población hacia el sureste a lo largo del rio Aragón y Ebro (Gómez *et al.*, 2011), en España el visón europeo está amenazado por diferentes factores que está poniendo en riesgo su supervivencia a corto y medio plazo.

La expansión del visón americano en el centro y alrededor de su área de distribución está considerada como una de las peores amenazas para el visón europeo (Põdra *et al.*, 2013; Bonesi and Palazon, 2007; Maran, 2007; Zabala, 2006; Palazón *et al.*, 2003), aspecto que se profundizará en la siguientes secciones.

La pérdida, la fragmentación y el deterioro del hábitat también amenazan el visón europeo, especialmente a causa de la alteración del hábitat de ribera a través de la destrucción de la vegetación esencial para mantener la diversidad de presas (Palazón *et al.*, 2006c). Además, un estudio realizado en el País Vasco (Zuberogoitia *et al.*, 2013) indica que la fragmentación del hábitat reduce la persistencia del visón europeo y su impacto sobre flujo genético entre sub-poblaciones aisladas, ya afectadas por una baja diversidad genética, puede ser catastrófico.

También la contaminación de los ríos puede afectar severamente la población: los compuestos organoclorados (PCBs) pueden perjudicar la reproducción y el crecimiento de los individuos (Lopez-Martin *et al.*, 1994), tal y como ocurre en el visón americano, la nutria euroasiática y otros mamíferos semi-acuáticos (Zwiernik *et al.*, 2009; Harding *et al.*, 1999; Aulerich *et al.*, 1990).

En las últimas dos décadas los atropellos han sido la causa principal de muerte causada directamente por la especie humana, y afectan sobre todo a los machos durante el periodo reproductor (Palazón *et al.*, 2012a). El parvovirus de la enfermedad aleutiana del visón (ADV), probablemente introducida por el visón americano, tiene una incidencia muy alta en la población española del visón europeo (Mañas *et al.*, 2001).

Cada vez hay más pruebas de que el visón europeo ha estado disminuyendo desde la década de los '90 del siglo pasado (Palazón and Melero, *in press*; Palazón *et al.*, 2003). Diferentes estudios realizados desde el 1992 han conducido a estimar una dimensión de la población de aproximadamente 500 individuos distribuidos a lo largo de 2300 km de ríos (Palazón *et al.*, 2013; Palazón *et al.*, 2012b).

Desde el 2005 el Ministerio de Medio Natural, Rural y Marino está llevando al cabo una estrategia nacional de conservación del visón europeo, y precedentemente o contemporáneamente se han realizado una serie de proyectos europeos LIFE para la conservación del visón dirigidos por las comunidades autónomas de La Rioja (LIFE 00/NAT/ E/7331: 2001-2004), Álava (LIFE 00/NAT/E/7335: 2001-2004), Castilla y León (LIFE 00/NAT/7299: 2001-2004), Catalunya (LIFE 02/NAT/E/8604: 2002-2005) y Navarra (2005-2008 y 2010-2014). Actualmente se está desarrollando un nuevo proyecto LIFE Plus (2014 – 2018) en La Rioja, Aragón, País Vasco y Valencia (LIFE13 NAT/ES/001171).

Todos estos proyectos está focalizado principalmente en la monitorización de la población del visón europeo, en la regeneración de su hábitat, en desarrollar un programa de cría en cautividad y en el control de la población invasora de visón americano.

La invasión del visón americano

El visón americano fue introducido en Europa a principios del siglo veinte para la producción de pieles en granjas peleteras, y, como consecuencia de escapes y liberaciones intencionadas en todos los sitios donde fueron instaladas las granjas, está actualmente presente en 21 países europeos, aunque su abundancia y distribución varía mucho según el país (Bonesi and Palazon, 2007).

Diferentes estudios en Europa han demostrado que esta especie invasora puede tener un impacto considerable sobre aves acuáticas, roedores y anfibios, así como sobre el visón europeo y el turón europeo (*Mustela putorius*) (Põdra *et al.*, 2013; Melero *et al.*, 2012a; Brzezinski *et al.*, 2010; Banks *et al.*, 2008; Bonesi *et al.*, 2007; Bartoszewicz and Zalewski, 2003; Macdonald and Harrington, 2003; Nordström *et al.*, 2002; Aars *et al.*, 2001; Sidorovich *et al.*, 1999).

En España las granjas fueron instaladas a partir de finales de los años ’50, y desde el principio de los ’90 se contaban por lo menos 220 granjas en territorio ibérico (Bonesi and Palazon, 2007; Ruiz-Olmo *et al.*, 1997). Escapes masivos y liberaciones intencionales culminaron en el establecimiento de seis poblaciones diferentes: una en España central (desde el centro de Burgos hasta Portugal, en toda Castilla y León, Madrid, Castilla-La Mancha y el norte de Extremadura), una en Galicia, una en Catalunya, una en Teruel, Zaragoza y Castellón, una en Álava y una en el norte del País Vasco (Melero and Palazón, 2011; Ruiz-Olmo *et al.*, 1997), encontrándose estas últimas dos actualmente fusionadas (Palazón, comunicación personal).

En la actualidad existen 37 granjas en el territorio español, dos de las cuales se encuentran adentro o muy cerca del área de distribución del visón europeo (MAGARMA, 2013).

En Portugal la primera cita del visón americano data de 1985 en la frontera entre Portugal y Galicia (Vidal-Figueroa and Delibes 1987) y desde entonces se han aportado solo observaciones esporádicas en el noroeste del país (Santos-Reis and Petrucci-Fonseca 1999). Sin embargo recientemente se ha detectado la expansión de la especies hacia la cuenca del Duero, aunque se trata de un proceso relativamente lento (unos 55 km in 20 años) (Rodrigues *et al.*, 2014).

Muchos estudios han investigado el impacto del visón americano sobre especies autóctonas en territorio ibérico a través de mecanismos de competición y depredación.

La especie puede causar la diminución y la extinción local de especies amenazadas como el cangrejo de río (*Austropotamobius pallipes*), el desmán ibérico (*Galemys pyrenaicus*) o la rata de agua (*Arvicola sapidus*) (Palomo and Gisbert, 2002; Palazón and Ruiz-Olmo, 1998b). Además el visón americano puede afectar a la estructura poblacional de depredadores que habitan en ríos como el turón europeo, la nutria euroasiática (*Lutra lutra*) y el visón europeo a través de la competición y la transmisión de enfermedades (Melero *et al.*, 2012a; Mañas *et al.*, 2001; Ruiz-Olmo and Palazón, 1991).

Desde el 2001 se está llevando al cabo en España un programa de control intensivo de esta EEI principalmente como parte de la estrategia de conservación nacional del visón europeo. Inicialmente el programa ha sido implementado con trampeos en vivo en Álava, Burgos y Teruel y Castellón y sucesivamente se ha expandido a todas (seis) las poblaciones.

La eficacia de estas campañas de control ha sido evaluada solo localmente, y las evidencias demuestran que el principal efecto del control es la reducción de la densidad de la especie invasora a escala local y que la erradicación a un costo bajo-moderado es factible solo en pequeñas áreas (Melero *et al.*, 2010; Zabala *et al.*, 2010; Zuberogoitia *et al.*, 2010).

Las razones del conflicto

El conflicto entre el visón americano y el europeo deriva de la fuerte competición ecológica entre las dos especies. Se considera que los tres principales mecanismos a través de los cuales el visón americano puede causar el declive de la especie autóctona son la competición por los recursos, la agresión inter-específica y la transmisión de enfermedades (Macdonald and Harrington, 2003).

Existe un solapamiento considerable entre la dieta de las dos especies y aunque el visón europeo tiene una dieta más especializada, ambos se alimentan de un amplio espectro de especies de pequeños mamíferos, anfibios, peces y otras presas (Palazón *et al.*, 2004; Sidorovich, 2001; Maran *et al.*, 1998b).

Además el vison europeo tiene requerimientos de hábitat más especializados que el visón invasor, y selecciona territorios con ríos de caudal lento y no contaminados, elevada biomasa de peces, una densa vegetación de ribera y bajo impacto antrópico (Zuberogoitia *et al.*, 2013; Zabala, 2003; Lodé, 2002; Lodé *et al.*, 2001), características que son muy atractivas también para el americano (Maran *et al.*, 1998a).

La especie invasora tiene dimensiones un 40% mayores que la autóctona (Maran, 2007; Sidorovich *et al.*, 1999); presenta implantación diferida de embriones, que puede aumentar la probabilidad de supervivencia de los recién nacidos (Thom *et al.*, 2004; Maran *et al.*, 1998a) y tiene camadas más numerosas, lo cual facilita una rápida expansión (Bonesi *et al.*, 2006; Sidorovich *et al.*, 1997).

Además, el visón americano tiene dominios vitales más pequeños y puede alcanzar densidades más elevadas. En general la mayor plasticidad ecológica del invasor le permite tener una ventaja competitiva sobre el visón europeo.

En Estonia se ha observado al visón americano expulsar agresivamente al visón europeo de territorios de alta calidad (Maran *et al.*, 1998a); en Bielorrusia el visón europeo ha desaparecido rápidamente de los ríos donde vivía simultáneamente con el americano tras su expansión (Sidorovich, 2001); en el País Vasco se ha comprobado la sustitución del visón europeo por el americano después de un breve periodo de coexistencia (Carreras *et al.*, 2006; Ceña *et al.*, 2003).

La presencia de la especie invasora puede ser perjudicial también en bajas densidades, como demuestran Põdra *et al.*, (2013) que aportaron pruebas de la muerte de varios ejemplares de visón europeo por parte del americano en una área protegida de la provincia de Vitoria, en el País Vasco.

En España el visón americano está considerado como el vector principal de la transmisión del parvovirus de la enfermedad aleutiana del visón (ADV) a la población española del visón europeo (Mañas *et al.*, 2003). Este virus, que tiene una elevada prevalencia en las granjas peleteras en España, y además de mortalidad directa puede producir un decremento en la fertilidad y provocar abortos espontáneos, disfunciones fisiológicas y problemas inmunológicos (; Palazón and Melero, *in press*; Mañas *et al.*, 2001), factores que pueden ser letales en una población en declive.

El visón americano está invadiendo rápidamente, desde el suroeste y el norte, el área de distribución del europeo (MAGRAMA, 2013). Hay tres poblaciones de visón americano que se están expandiendo en el País Vasco (en Álava, en el centro del área de distribución del visón europeo, en el norte de Vizcaya y en el oeste de Guipúzcoa) y que pueden fundirse en un futuro próximo, si no lo están ya, desplazando al visón europeo (Palazón and Melero*, in press*; Carreras *et al.*, 2006; Zabala *et al.*, 2006; Ceña *et al.*, 2003; Zuberogoitia and Zabala, 2003).

¿Qué información se necesita en la Península Ibérica?

En la Península Ibérica en las últimas décadas se ha generado muchos conocimientos y se ha obtenido datos de alta calidad sobre las dos especies gracias a los esfuerzos de investigadores, gestores y técnicos que han trabajado o colaborado con academias e instituciones españolas y portuguesas, gobiernos regionales y ministerios del medio ambiente.

Se han producido muchos estudios de investigación e informes técnicos para conocer la ecología, la distribución, el hábitat, las causeas del declive y de la expansión, la interacción competitiva entre el visón europeo y el americano; la mayoría de las políticas de conservación y las estrategias de gestión llevadas a cabo hasta la fecha han sido basadas en este valioso trabajo.

Comprensiblemente, la mayoría de estos estudios se han focalizado en una parte del área de distribución de la especie, explorando características biológicas, procesos ecológicos y opciones de gestión a escala local.

Se han realizado varios estudios en Vizcaya (País Vasco) para explorar los factores ambientales y bióticos que afectan la ocupación del visón europeo, revelando que en esta zona la calidad del agua, alteración de las riberas y la fragmentación del hábitat pueden tener un impacto más importante sobre el visón europeo que la presencia de visón invasor (Zuberogoitia *et al.*, 2013; Zabala *et al.*, 2006, 2003).

En Vitoria-Gasteiz (País Vasco), la expansión del visón americano dentro del área de distribución del visón europeo se ha relacionado con la desaparición local de las especies nativas (Carreras *et al*, 2006; Ceña *et al*, 2003).

En Cataluña Melero *et al*. (2012a) han encontrado una relación negativa entre la abundancia del visón americano y la presencia de dos competidores, la gineta (*Genetta genetta*) y el turón europeo, y tres especies de peces locales.

En 2007 se aportaron los primeros registros del visón europeo en Aragón, lo que llevó a sugerir una expansión del área de la especie hacia el sureste (Gómez *et al*., 2011).

Mientras el conjunto de estos trabajos contribuye a delinear el panorama del estatus del visón autóctono y del invasor en la Península Ibérica, una visión global de la interacción, la distribución potencial y dinámica espacial de las dos especies en la totalidad de su área de distribución no ha sido propuesta hasta la fecha.

Este tipo de planteamiento es crucial para entender los procesos que se están llevando a cabo en las poblaciones de ambas especies y puede proporcionar información esencial para la conservación y el manejo de los dos visones en la Península Ibérica.

OBJETIVOS

Objetivo principal

El objetivo principal de esta tesis es contribuir al conocimiento del estatus del visón europeo, especie catalogada "en peligro crítico de extinción", y del visón americano, una especie exótica invasora, en la Península Ibérica mediante el análisis de la distribución potencial, la ocupación, la abundancia y la competencia espacial en la totalidad de sus áreas de distribución. Con esta contribución se propone proporcionar bases sólidas para orientar las acciones de conservación y gestión de las poblaciones de ambas especies en el territorio ibérico.

Objetivos Específicos

Para lograr este objetivo, la tesis se ha estructurado en cuatro capítulos y una discusión global, en los que se proponen los siguientes objetivos específicos:

1. Analizar los cambios en la ocupación de las dos especies de visones dentro del área de distribución del visón europeo en la Península Ibérica desde el año 2000, y buscar pruebas de una exclusión competitiva de la especie autóctona (Mustela lutreola) por parte del visón invasor (Neovison vison) a gran escala. (Capítulo 1)
2. Evaluar las tendencias espaciales y temporales en la abundancia del visón europeo desde el año 2000 e identificar los factores ambientales que tienen una mayor influencia en este parámetro. (Capítulo 2)
3. Predecir la expansión potencial del visón americano en la Península Ibérica, testando un enfoque jerárquico multi-escala para modelizar la distribución de las especies en estado de no-equilibrio con su ambiente. (Capítulo 3)
4. Identificar las áreas prioritarias de conservación para el visón europeo en base al análisis del solapamiento espacial de la distribución potencial de las dos especies de visones en la Península Ibérica. (Capítulo 4)

5. Proporcionar un análisis global de la situación de las dos especies de visones en la Península Ibérica y sugerir directrices prácticas para su conservación y gestión en base a los resultados obtenidos en la tesis. (Discusión)

MATERIALES Y MÉTODOS

Muestreo de las especies y procesamiento de los datos

Desde el 1992 la metodología de monitorización de las poblaciones de visón europeo y de control de las de visón americano en España sigue un protocolo desarrollado conjuntamente por Francia y España, y que ha sido perfeccionado a lo largo de los años. Este protocolo se ha puesto en práctica por los técnicos, la guardería y los profesionales que participan en los diferentes estudios, controles y en el desarrollo de la "Estrategia nacional de conservación del visón europeo en España".

El procedimiento está basado en trampeos en vivo, con al menos una estación de captura por cuadrícula de 10x10 km (sistema geográfico de referencia UTM - Universal Transversal Mercator) en Navarra, Aragón (Zaragoza y Huesca), La Rioja, País Vasco (Vizcaya, Guipúzcoa y Álava), Castilla y León (Burgos y Soria), Cantabria y Catalunya (Palazón y Melero, *in press*) llevadas a cabo por los gobiernos provinciales y regionales, coordinados por el Ministerio Español de Agricultura, Alimentación y Medio Ambiente.

Las estaciones de trampeo están compuestas por diez trampas metálicas (15 cm x 15 cm x 60 cm), con una única entrada, apropiadas para la captura en vivo de ambas especies de visones, situadas a lo largo de las orillas de los ríos en secciones de 1 a 5 km, a una distancia de 100 - 300 m entre trampas contiguas, y quedan activas por 10 noches consecutivas.

El visón europeo se anestesia, se pesa y se mide; por último se marca con un *transponder* subcutáneo y se libera una vez que el individuo se ha recuperado totalmente de la anestesia. En cambio el visón americano es sacrificado siguiendo las normas de la Ley Española de Bienestar Animal (Real Decreto n. 32/2007).

Las localizaciones de las trampas se registran con un receptor GPS, generalmente con una precisión de +/-10 m.

Los parámetros biométricos (sexo, edad, longitud del cuerpo, de la pata delantera, de la pata trasera y de la oreja) no han sido utilizados en esta tesis.

Este protocolo permite detectar la presencia o ausencia de las dos especies de visón con alta precisión, también de manejar los animales capturados de manera segura, de recoger parámetros biométricos y, por último es un método altamente selectivo (la gran mayoría de los animales capturados son visones europeos y/o americanos).

Dentro del área de distribución del visón europeo, los muestreos se han realizado dos veces al año en el periodo pre-reproductivo (de enero a mediados de marzo) y en el período post-reproductivo (de septiembre a diciembre), aunque el esfuerzo de captura ha variado dependiendo de la disponibilidad de financiación de los diferentes gobiernos con competencias en materia de conservación y gestión de fauna.

Fuera del área de distribución del visón europeo, donde el objetivo ha sido el control y el seguimiento de la población de visón americano, los muestreos se realizan durante todo el año y en general una vez que se detecta el invasor en una determinada localización, el número de estaciones de trampeo se incrementa en ese tramo de río y en los sitios cercano para maximizar el número de individuos eliminados (Palazón, com. pers.).

En esta tesis los registros de visón europeo y americano recogidos en la Península Ibérica entre los años 1999 y 2012 fueron utilizados como tres tipos de datos diferentes dependiendo del tipo de análisis realizado y del objetivo del estudio: (1) datos de detección / no-detección para el análisis de ocupación (Capítulo 1), (2) contabilización de los individuos para el análisis de abundancia (Capítulo 2) y (3) datos de geolocalizaciones de los individuos capturados para la modelización de la distribución (Capítulos 3 y 4).

Para ambas especies, las historias de detección y las contabilizaciones de individuos se han elaborado a una resolución espacial de 10km2 (cuadrículas UTM - un valor por celda), mientras que las geolocalizaciones se han re-muestreado a la resolución de 2,5 km y se han utilizado como datos de sola presencia para predecir la distribución potencial de las dos especies.

Además, mientras que para el análisis de ocupación y abundancia se han utilizado solo datos procedentes del rango español de distribución de las dos especies, para los modelos de distribución potencial en la Península Ibérica, además de las geolocalizaciones procedentes de la Península Ibérica, se recopilaron datos de presencia en el rango histórico de distribución del visón europeo, y datos del rango nativo (Norte de América) e invadido (Europa) del visón americano. Estos datos fueron en parte extraídos de la base de datos *Global Biodiversity Information Facility* (http://www.gbif.org) y en parte geo-referenciados a partir de diferentes estudios realizados sobre las dos especies en Europa y en América del Norte. Las coordenadas geográficas de la distribución histórica del visón europeo se recopilaron de Maran (2007), Maizeret *et al.* (2002), Lode *et al.*, (2001) y Youngman, (1982).

Los datos sobre la distribución del visón americano en América del Norte se elaboraron a partir de Kay and Wilson (2009), Bluett *et al.* (2006), Viljugrein *et al.* (2001) and Ensor (1991).

Área de estudio

El área de estudio fue la totalidad de la Península Ibérica, aunque dos de los estudios de esta tesis, el análisis de ocupación y abundancia (Capítulos 1 y 2), se centraron, respectivamente, en nueve y ocho provincias españolas.

La Península Ibérica se encuentra entre 36º00'N - 43º47'N y 9º29'W y 3º19'E, tiene un área de aproximadamente 582.000 km2 y está compuesta por tres países: Portugal, España y Andorra.

Las características ambientales más importantes que afectan a la presencia y a la propagación del visón europeo y del visón americano, son el sistema hidrológico (ambos visones son especies semi-acuáticas) y el clima, especialmente por su influencia en el balance hídrico de los ríos.

En la más reciente revisión de la clasificación climática de Köppen-Geiger (Peel *et al.*, 2007) se reportan tres categorías generales de clima que dominan en la

Península Ibérica: 1) Árido: en el sureste de la Península, principalmente en las provincias de Almería, Murcia y Alicante (semi-desierto y desierto), en el valle del Ebro y en Extremadura (estepas), 2) Templado: en la parte sur de la Península y en las zonas costeras del Mediterráneo; este tipo de clima presenta veranos secos y calurosos y es el tipo de clima más frecuente ya que cubre aproximadamente el 40% de la Península, mientras que en el Norte (Sistemas montañosos: Cantábrico, Sistema Ibérico y Pirineos) la estación seca está ausente, 3) Frío con invierno seco en la Cordillera Cantábrica, Sistema Ibérico, Sistema Central y Sierra Nevada.

Los regímenes de precipitación y caudal de los ríos están caracterizados por una gran variabilidad interanual, con grandes disparidades entre los años húmedos y secos, especialmente en el sur de la Península (Trigo *et al.*, 2004).

Los valores más altos de la media anual de precipitación (2200 mm) se registran en las zonas montañosas y boscosas en el noroeste de Portugal, en el noroeste de Navarra y en algunas zonas del sudoeste Galicia. Los valores más bajos se observan en el sudeste de España, en las provincias de Murcia y Almería, con una precipitación media anual de 200 – 300 mm. Por otra parte, la precipitación media mensual indica una fuerte estacionalidad, especialmente en el sur de la mitad de la Península, y una clara disminución de las precipitaciones durante el verano, mientras que el mes más lluvioso es, en general, diciembre (AEMET, 2011).

Alrededor de tres cuartos de la península están ocupados por la "Meseta Central", un vasto altiplano que tiene una altitud entre los 610 y los 760 m y está rodeado por las montañas de donde nacen la mayor parte de los ríos. Los principales ríos son el Ebro, el Duero, el Tajo, el Guadiana y el Guadalquivir. El Tajo es el río más largo de la Península y el Ebro es el río más caudaloso, y nace en Cantabria, fluyendo hacia el este hasta desembocar en el Mediterráneo. Aparte de las áreas atlánticas y de algunos grandes ríos, los ríos ibéricos están en general sujetos a fuertes variaciones estacionales de caudal y a sequías en periodos de estiaje, especialmente en el sureste de la Península.

Análisis estadísticos

Para analizar los datos se utilizaron tres técnicas estadísticas diferentes: Modelos de Ocupación, los Modelos N-mixture y los Modelos de Distribución de Especies (SDMs). En esta sección se presentan las principales características de cada técnica, mientras que en cada capítulo se proporciona una explicación más detallada de su aplicación.

Modelos de Ocupación

La estimación y la interpretación de los patrones de ocupación es central en muchas preguntas ecológicas y en las problemáticas de conservación de especies (Rota *et al.*, 2009; MacKenzie *et al.*, 2006).

Los modelos de ocupación tienen como objetivo la estima de la proporción de sitios ocupados por una especie que se detecte de manera imperfecta (MacKenzie, 2005) y pueden ser útiles, tanto en los programas de seguimientos a amplia escala, como en estudios sobre meta-poblaciones. Por ejemplo, la probabilidad de ocupación de un sitio por parte de una especie puede ser un buen indicador del estado de una población.

La literatura sobre los modelos de ocupación ha crecido mucho en los últimos años y existen muchas aplicaciones aparentemente exitosas. Esta metodología parece haber logrado el estatus de 'estándar de oro' para el análisis de datos ecológicos sujetos a errores en la detección de las especies de interés (Welsh *et al.*, 2013).

El clásico modelo de ocupación multi-estacional desarrollado por MacKenzie *et al.*, (2003) se basa en la estimación de cuatro parámetros fundamentales: ocupación (φ), detección (p), colonización (γ) y extinción (ε).

La probabilidad de ocupación puede ser interpretada como la proporción de sitios ocupados; la probabilidad de extinción como la proporción de sitios ocupados al tiempo t y no ocupados al tiempo $t+1$; y la probabilidad de colonización como la proporción de sitios no ocupados al tiempo t que están ocupados al tiempo $t+1$.

Comúnmente estos parámetros se estiman a través de las técnicas de máxima verosimilitud.

MacKenzie *et al.*, (2006) afirman que el estado de ocupación inicial antes del primer muestreo de la primera estación se puede representar como

$$\varphi_0 = [\varphi_1 \;\; 1 - \varphi_1]$$

Y la matriz que determina la probabilidad de que un sitio pase de un estado de ocupación al otro entre la estación *t* y la *t+1* es (para $t \geq 1$)

$$\varphi_t = \begin{bmatrix} 1 - \varepsilon_t & \varepsilon_t \\ \gamma_t & 1 - \gamma_t \end{bmatrix}$$

Así que la probabilidad de ocupación estacional se calcula usando la relación

$$\varphi_t = \varphi_t - 1(1 - \varepsilon_t - 1) + (1 - \varphi_t - 1)\gamma_t - 1$$

Estos modelos admiten la incorporación de variables específicas de un sitio o de un evento de muestreo usando un modelo logístico donde la probabilidad de interés es

$$\Theta = \exp(\mathrm{Y}\beta) / 1 + \exp(\mathrm{Y}\beta)$$

Donde Y es la matriz con los valores de la variable, y β es el vector de los coeficientes del modelo logístico estimados.

Las asunciones a la base de la estima de la ocupación son 1) que los sitios muestreados sean ocupados por la especie de interés a lo largo de todo el estudio, y los sitios no pueden ocuparse o desocuparse dentro de un periodo de muestreo (las poblaciones son cerradas), 2) que los parámetros son constantes entre sitios diferentes (por ejemplo no hay heterogeneidad en la probabilidad de detección en el área de estudio), 3) no hay error en la detección de una especie, pero puede no detectarse aunque esté presente, 4) la detección de una especie en un sitio es independiente de la detección en otros sitios.

Estos modelos se han perfeccionado recientemente para investigar los patrones de coocurrencia entre dos o más especies utilizando datos de detección (Richmond *et al.*, 2010; MacKenzie *et al.*, 2004,). Estos modelos, comúnmente denominados "modelos de ocupación de dos especies", estiman un factor de interacción de las especies (SIF) que es la razón entre la probabilidad que dos especies coocurran y los que se esperaría bajo la hipótesis de independencia de ocurrencia.

Además de los parámetros mencionados anteriormente, un modelo de ocupación de dos especies multi-estacional estima la ocupación, la detección, la colonización y la extinción en función de la presencia o la ausencia de las especies que coexisten y, por lo tanto, puede ser muy útil para detectar el impacto de una especie sobre la otra.

Por ejemplo, es posible detectar la exclusión competitiva entre dos especies demostrando que los aumentos o las disminuciones en la probabilidad de ocupación de las especies de interés están vinculados a través de la influencia de una especie en la extinción local y la colonización de la otra (MacKenzie *et al.*, 2006), tal y como se ha estudiado en el capítulo 1.

Mientras los estudios basados en una sola especie o en una sola estación de muestreo son abundantes, son pocos los estudios que han alcanzado el nivel para detectar una interacción asimétrica entre dos o más especies a través de un análisis multi-estacional (Lazenby and Dickman, 2013; Bailey *et al*, 2009).

Modelos N-mixture

Entre los modelos propuestos en las últimas décadas para estimar la abundancia total de organismos a partir de contabilizaciones repetidas, el modelo propuesto por Royle (2004) parece tener mejor rendimiento, especialmente cuando las contabilizaciones son irregulares (Dail and Madsen, 2011).

Este modelo está clasificado como N-mixture, que es un tipo de modelo jerárquico para estimar la abundancia y la probabilidad de detección en poblaciones animales a partir de contabilizaciones de individuos, el cual asume que la distribución de los organismos en el espacio sigue una distribución de Poisson y que la probabilidad de detección de “n” organismos corresponde a una Binomial (“mixture”, mezcla, que se refiere a la combinación de dos distribuciones estadísticas).

El modelo requiere una serie de contabilizaciones replicadas en el tiempo en un cierto número *i* de sitios muestreado al tiempo *t*, contabilizaciones que se consideran como realizaciones independientes de una variable aleatoria binomial con parámetro índice N_i (la abundancia local) y como resultado la probabilidad p de detección.

$$y_{it} \sim \text{Binomial}(N_i, p)$$

$$N_i \sim \text{Poisson}(\lambda_i)$$

Donde y_{it} es el número de individuos distintos contados en el sitio *i* al tiempo *t* y λ_i es la dimensión esperada de la población en el sitio *i*. Este esquema analítico es extremadamente flexible: es posible modelar ambos parámetros (abundancia y probabilidad de detección) en función de variables que varían en el tiempo y en el espacio (por ejemplo la características del hábitat o el esfuerzo de muestreo), y también modelar el efecto simultaneo de una única variable en ambos parámetros (Kéry *et al.*, 2009).

Sin embargo, el mayor límite de este modelo es la asunción de una población cerrada en cada sitio, una población donde no hay nacimientos, muertes o migraciones, y que entonces no cambia a lo largo de la duración del estudio. Este enunciado puede ser válido para una única estación reproductiva, pero puede ser fácilmente violado en estudios plurianuales. Además, con este modelo no es posible estimar la tendencia en la abundancia de una población, que es comúnmente un parámetro de gran interés en estudios de conservación de especies.

Dail and Madsen (2011) han propuesto recientemente una generalización del modelo de Royle, denominada modelo "N-mixture" dinámico. El modelo dinámico relaja la premisa de población cerrada y estima los cambios de una población entre periodos muestreados incluyendo expresamente los parámetros del estado inicial de la población (o sea la abundancia en el primer año de muestreo, k) y la tasa de reclutamiento (nacimientos e inmigraciones, γ) y la supervivencia aparente (1- muertes y emigraciones, ω). El modelo describe también el proceso de observación en la base de la colección de datos (la detección, p).

La dimensión de una población en cada periodo puede ser estimada a partir de estos parámetros usando recursivamente una ecuación del tipo

$$N_{it} = N_{i,t-1}\ \omega^{t-1} + \gamma(1 - \omega^{t-1})/(1-\omega)$$

El modelo asume que: 1) no hay cambios en la abundancia en un sitio entre la primera y la última visita en una misma estación; 2) las variables pueden ser puestas en relación con la heterogeneidad en la detección de individuos en el tiempo y en el espacio; 3) las detecciones en cada sitios son independientes; y 4) la abundancia puede modelarse con variables a través de un modelo con una distribución apropiada (por ej., Poisson, binomial negativa, Poisson zero – inflado).

En el capítulo 2, el objetivo es evaluar la tendencia en la abundancia de la población española de visón europeo, así que se ha aplicado la versión de “crecimiento exponencial” del modelo de Dail y Madsen, la cual permite estimar la tendencia de una población estableciendo la dependencia entre la tasa de reclutamiento γ y la abundancia en un sitio i durante el periodo de muestreo anterior:

$$N_{it} = N_{i,t-1}\ \gamma$$

En este caso γ se convierte en la “tasa finita de crecimiento” de la población (la que comúnmente se define “lambda”). La opción seleccionada en este capítulo se puede resumir de la siguiente forma:

$$N_{i1} \sim \text{Poisson}(\lambda)$$

$$N_{it} \sim \text{Poisson}(\gamma\ N_{it-1})$$

$$y_{ijt} \sim \text{Binomial}(N_{it}, p)$$

En los últimos años, desde que ha sido propuesto, el modelo se ha aplicado en algunos pocos estudios, por ejemplo en la evaluación de la disponibilidad de cavidades pen la dinámica poblacional de la ardilla voladora del Norte (*Glaucomys sabrinus*) en Canadá (Priol *et al.*, 2014), en testar la eficacia del modelo en estimar la abundancia de la perdiz roja (*Alectoris rufa*) en una zona mediterránea (Jakob *et al.*, 2014) o en examinar los efectos de senderos recreativos en comunidades de aves en New Hampshire, USA (Deluca and King, 2014).

Una de las grandes ventajas de este método, según los resultados de los estudios citados, es que es más efectivo económicamente para el monitoreo de especies que los métodos de captura-recaptura y son más fiables que los índices de abundancia relativa que se usan comúnmente para establecer y aplicar muchos planes de acción (gestión y/o conservación).

Modelos de distribución de especies

La predicción de la distribución de especies se ha convertido en una componente importante de la planificación de la conservación en los últimos años y para este propósito se han desarrollado un gran número de técnica de modelización (Guisan and Thuiller, 2005).

Los modelos de distribución de especies (SDMs) son técnicas correlativas que estiman las condiciones ambientales idóneas para una especies a través de la asociación de los puntos de presencia de la especies con un grupo de variables que puedan tener un efecto significativo sobre su ecología o su probabilidad de persistencia.

El uso de estos modelos en apoyo a decisiones sobre la conservación espacial de especies de interés ha crecido exponencialmente en la última década, por ejemplo para la selección y el diseño de reservas (Carvalho *et al.*, 2010; Loiselle *et al.*, 2003), para evaluar la idoneidad de las reservas (Marini *et al.*, 2009; Catullo *et al.*, 2008), para localizar "hotspots" de biodiversidad y priorizar áreas de conservación (Rodríguez-Soto *et al.*, 2011; Rondinini *et al.*, 2011; Peralvo *et al.*, 2006) e identificar áreas de conflicto entre especies autóctonas e invasoras (Gallardo and Aldridge, 2013; Vicente *et al.*, 2011).

Los registros de presencia de una especie y las variables ambientales se introducen en un algoritmo que tiene como objetivo el de encontrar la relación entre las presencias y las condiciones ambientales. El "output" es un mapa que muestra la predicción de la distribución de la especie.

La habilidad de un algoritmo de predecir los datos se evalúa con un test estadístico ad-hoc. Normalmente los modelos predicen una distribución continua de idoneidad ambiental (por ej., una predicción entre 0 y 1), mientras que a veces es necesario transformar las predicciones en un espacio idóneo (1) o non idóneo (0) para poder aplicar un test de evaluación estadística.

Una característica importante de los SDMs es el hecho de estar basados en el concepto de nicho (Guisan and Zimmermann, 2000). En este caso la definición más relevante es la de "nicho realizado" según Hutchinson (1957) en el cual una especie queda excluida de parte de su nicho fundamental (sensu Grinnell, 1917) por las interacciones bióticas y los límites a la dispersión, dando como resultado el nicho que se observa en la naturaleza (Guisan and Thuiller, 2005). Se considera que, dado que los SDMs se basan en la distribución observada de una especie, lo que cuantifican es de hecho el nicho realizado, aunque si para especies dominantes que pueden llegar a llenar todo su área, el nicho realizado puede ser muy parecido al nicho fundamental (Araújo and Pearson, 2005).

Existen dos premisas fundamentales en los SDMs: 1) el estado de equilibrio (o pseudo-equilibrio) entre una especie y su ambiente, que significa que una especie tiene que ocupar todas las áreas idóneas y ser ausente de las no-idóneas y 2) el conservadurismo del nicho, que indica que el nicho ocupado por una especies no cambia en el tiempo y en el espacio.

El primer postulado es fácilmente violado sea en el caso de especies en peligro crítico de extinción que han desaparecido de la mayor parte de sus área, sea en el caso de EEI que no han invadido todavía todo el rango potencial (Václavík and Meentemeyer, 2012; Araújo and Guisan, 2006). Además se ha probado en los últimos años que las EEI pueden ocupar nichos diferentes en el área de introducción (Petitpierre *et al.*, 2012; Broennimann *et al.*, 2007), cosa que potencialmente contradice la premisa de conservadurismo del nicho.

Las consecuencias principales de esta violación son: 1) que la calibración de los modelos con datos de presencia de especie en no-equilibrio con su entorno puede llevar a la exclusión de condiciones idóneas para la especie, y entonces a subestimar el área de distribución potencial (Guisan and Thuiller, 2005) y 2) que si el nicho ocupado por una invasora en el área de introducción es muy diferente del original, el modelo calibrado con datos del área original para predecir la distribución en el área invadida daría resultados erróneos (Gallien *et al.*, 2010).

Aunque si la aplicación de los SDMs en el caso de especies amenazadas e invasoras puede parecer poco conveniente, estos modelos han sido ampliamente utilizados en la planificación de la conservación de especies. Para mitigar los efectos de la violación de los postulados en base a estos modelos se han propuestos diferentes estrategias, de las cuales tres han sido utilizadas en esta tesis (en los capítulos 3 y 4):

1. La combinación de las predicciones obtenidas a través de diferentes técnicas de modelización, con el objetivo de ajustar la incertidumbre inherente a cada técnica (Araújo and New 2007)
2. Un enfoque jerárquico multi-escala (Pearson and Dawson, 2003; Mackey and Lindenmayer, 2001;), basado en la combinación de modelos calibrados a diferentes escalas espaciales, que permite tener en cuenta la adaptación de una especie a las condiciones locales y al mismo tiempo de incluir las limitaciones climáticas a escala global, cosa que ayuda a afinar las predicciones y hacerlas más informativas (Guisan *et al.*, 2006).
3. En el caso de las EEI, la calibración de los modelos con datos procedentes del área original y la de introducción y, para las especies críticamente amenazadas, con datos de la distribución histórica, antes de las extinciones locales; esto tendría que producir predicciones más fiables por el hecho de incluir la máxima cantidad de información disponible sobre las condiciones ambientales

ocupadas por la especies de interés (Broennimann and Guisan, 2008; Peterson and Vieglais, 2001).

RESULTADOS Y DISCUSIÓN

En esta sección se indica y se discute los principales resultados de los cuatro capítulos de la tesis, y se sugiere una serie de líneas de actuación prácticas para la conservación del visón europeo y la gestión y control del visón americano en la Península Ibérica.

Los primeros dos capítulos están focalizados en la dinámica de co-ocurrencia de las dos especies y en el análisis de los cambios en la abundancia poblacional de la especie autóctona en el norte de España.

En la segunda parte de la tesis se ha utilizado los Modelos de Distribución de Especies (SDMs) para predecir la expansión del visón americano en la Península Ibérica y para analizar el conflicto espacial entre las dos especies diana del estudio.

La exclusión competitiva por parte del visón americano y el decremento en la abundancia del visón europeo

En el primer capítulo se ha utilizado datos de detección de las dos especies de visones, recolectados en 204 puntos de cuadrículas UTM 10x10km entre los años 2000 y 2011. Sobre ellos se ha aplicado un modelo multi-estacional para las dos especies (MacKenzie *et al.*, 2006).

Este modelo utiliza cuatro tipos de parámetros (ocupación, detección, colonización y extinción) en función de la presencia y ausencia de cada una de las especie; además utiliza un factor de interacción que mide la probabilidad de co-ocurrencia de las dos especies.

En el segundo capítulo se ha utilizado los datos de captura de individuos procedentes de 86 cuadrículas UTM 10x10km recolectados entre los años 2000 y 2010 como input de un modelo dinámico N-mixture (Dail and Madsen, 2011), con el objetivo de estimar la abundancia del visón europeo, su probabilidad de detección y la tasa de crecimiento de su población.

Estos datos no fueron recogidos expresamente para aplicar estos esquemas analíticos y debido a ello existe una gran variabilidad espacial y temporal en el esfuerzo de captura (muchos huecos en los datos). A pesar de ello, en ambos capítulos los modelos han tenido un buen rendimiento y los parámetros han sido estimados con una precisión aceptable. Es posible que el elevado número de repetición de visitas y de cuadrículas muestreadas compense la heterogeneidad de los datos originales.

De hecho, a partir de estos dos estudios se ha extraído claramente las dinámicas y los patrones de ocupación y abundancia de las dos especies.

En el capítulo 1 se ha encontrado pruebas de la exclusión competitiva del visón europeo por parte de la especie invasora.

El modelo mejor clasificado por el AIC (Akaike Information Criterion) indica que la probabilidad de ocupación del visón europeo ha disminuido notablemente desde el año 2000 (desde 0,407 ± 0,062 en el 2000 hasta 0,195± 0,062 en el 2011), mientras que la ocupación del visón americano ha aumentado de forma importante (desde 0,351 ± 0,054 en el 2000 hasta 0,480 ± 0,054 en el 2011). Las dos especies co-ocurren más raramente de lo esperado, como revela el valor estimado del factor de interacción inferior a 1 (0,717 ± 0,063) (Fig. 1). Además, la estima de los parámetros (Fig. 2) muestra que la especie invasora coloniza preferentemente cuadrículas ocupadas por el visón europeo que cuadriculas donde la especie autóctona es ausente (probabilidad de colonización: 0,129 ± 0,033 *versus* 0,090 ± 0,026, respectivamente), mientras que la probabilidad que la especie autóctona colonice áreas ya ocupadas por el visón americano es muy pequeña (0,014 ± 0,007).

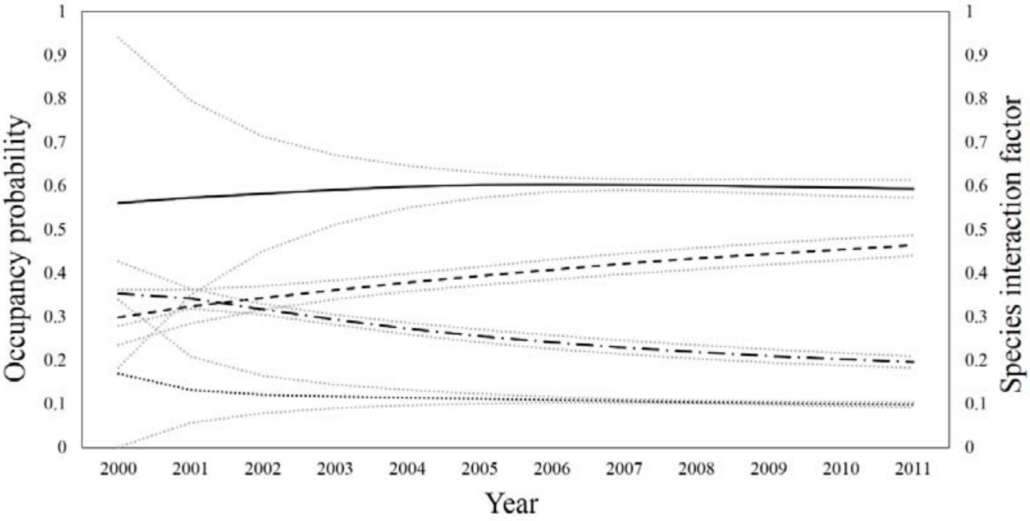


Figura 1. Probabilidad estacional de ocupación (eje vertical izquierdo) resultante del mejor modelo (clasificados con AIC) de tres posibles estados: 1. Exclusivamente el visón americano presente (línea de trazos), 2. Exclusivamente el visón europeo presente (línea de trazos y puntos), 3. Ambas especies presentes (línea de puntos). En el eje vertical de la derecha, el Factor Estacional de Interacción de Especies (SIF) está representado por la línea continua. El error estándar está representado por las diferentes líneas grises punteadas.

Como resultado, el valor más alto de la probabilidad de extinción corresponde al visón americano en simpatria con el visón europeo (0,254 ± 0,081), observación consistente con el impacto local del control que se realiza actualmente y en los últimos años de la especie invasora, que no viene compensado por la recolonización por lo menos en el mismo año. Al mismo tiempo se ha observado que el visón europeo se extingue más fácilmente en aquellas cuadrículas ocupadas por la especie invasora (probabilidad de extinción: 0,130 ± 0,045 versus 0,072 ± 0,024).

En general, estos resultados indican que en el norte de España la expansión del visón americano provoca el desplazamiento del visón europeo, un proceso que ya ha sido observado en otros países europeos (Sidorovich, 2001; Maran *et al*., 1998), y también dentro del área de estudio a escala local (Carreras *et al*., 2006; Ceña *et al*., 2003).

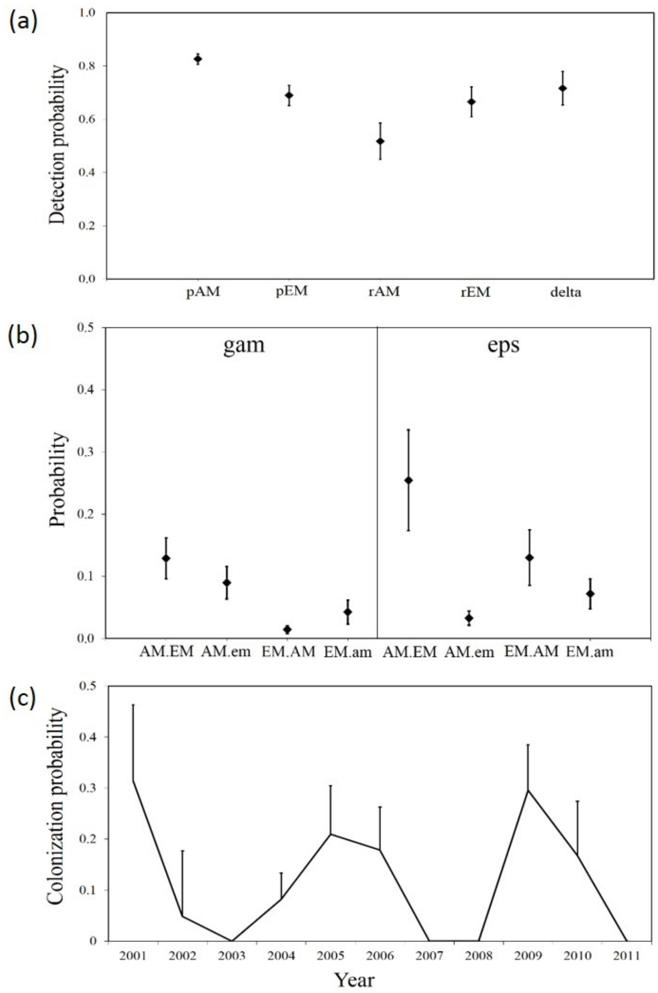


Figura 2. Resultados de las estimas de las probabilidades de detección (a), la colonización (B y C) y la extinción (b) de las dos especies de vison obtenidas en el estudio. a) las probabilidades de detección estimadas por el modelo mejor clasificado: AM = visón americano; EM = visón europeo; pAM = probabilidad de detectar AM, dado que solo AM está presente; pEM = probabilidad de detectar EM, dado que solo EM está presente; rAM = probabilidad de detectar AM, con ambas especies presentes y EM no detectado; rEM = probabilidad de detectar EM, con ambas especies presentes y AM no detectado; delta = factor de interacción de detección de las especies. b) Probabilidades de colonización (gam) y extinción (eps) obtenidas con el modelo mejor clasificado: AM.EM = probabilidad de que AM colonice / se extinga en un sitio, dado EM presente; AM.em = probabilidad de que AM colonice / se extinga en un sitio, dado EM ausente; EM.AM = probabilidad de que EM colonice / se extinga en un sitio, dado AM presente; EM.am = probabilidad de que EM colonice / se extinga en un sitio, dado AM ausente. c) Variación en el tiempo de la probabilidad de colonización de AM derivada del segundo modelo mejor clasificado.

El modelo revela que localmente el control de la especie invasora mantiene baja su densidad y ralentiza el proceso de sustitución de la especie autóctona. Aunque en general el hecho de que la probabilidad de ocupación del visón americano haya aumentado indica que las acciones de control/gestión que se realizan actualmente no consiguen controlar su expansión.

La elevada capacidad de recolonización de esta invasora, revelada por este estudio y otros trabajos en áreas invadidas (Bryce *et al*., 2011; Zalewski *et al*., 2009; Nordström *et al*., 2002), indica que la prioridad debe ser controlar el flujo de individuos dispersantes que pueden fácilmente recolonizar las áreas donde se controla y elimina la especie. Esto implica realizar un esfuerzo (personal, trampeos y financiación) constante, así como la verificación continua de su ausencia desde las áreas donde se realiza el control.

La abundancia es un parámetro que permite dar respuestas a cuestiones más profundas sobre la dinámica poblacional (Mackenzie and Nichols, 2004), así que el capítulo 2 se ha dedicado a evaluar los cambios temporales y espaciales en la abundancia del visón europeo en la totalidad de su área de distribución.

Se ha detectado un lento declinar en la abundancia de esta población desde el año 2000, como revela el valor de la tasa finita de incremento, que es ligeramente inferior a 1 (0,994 ± 0,045). Según este parámetro, el número medio de los individuos per cuadrícula ha variado desde 6,9 ± 3,6 en el 2000 hasta 6,6 ± 3,6 en el 2010 (Fig. 3). Aunque este cambio pueda parecer no muy importante, el resultado indica que cada año el número de individuos reclutados gracias a nuevos nacimientos o a inmigración es inferior respecto al año anterior.

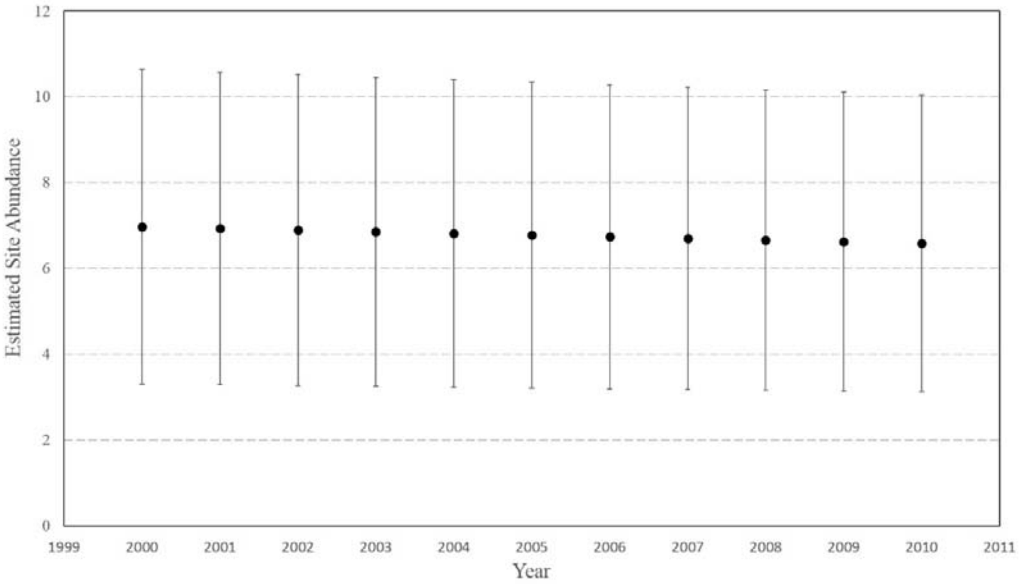


Figura 3. Estima de la abundancia media por cuadrícula del vison europeo en la totalidad de su área de distribución en el norte de la Península Ibérica, entre los años 2000 y 2010, calculada utilizando un modelo dinámico N-mixture.

La abundancia del vison europeo muestra una alta variabilidad espacial, estando concentrados los valores más elevados en la parte central de su área de distribución, concretamente en las regiones de Álava, el norte de La Rioja, el este de Burgos y el sur de la Navarra, área que corresponde a la parte alta de la cuenca del Ebro (Fig. 4).

Factores como la precipitación anual media, la proporción de la vegetación natural y el impacto antrópico no han resultado ser limitantes para la densidad de la población a la resolución espacial estudiada (cuadrículas 10x10 km) y la extensión (ocho provincias españolas) del análisis realizado. De hecho la abundancia ha resultado ser más elevada en las zonas de planicie a lo largo del río Ebro y sus afluentes, que son también las más afectadas por la presencia humana y donde la precipitación es muy inferior comparado por ejemplo con las cuencas atlánticas.

Este resultado necesita una importante aclaración: los factores ambientales evaluados en este análisis parecen no tener un efecto negativo en la abundancia del visón europeo a la escala espacial considerada, aunque esto no significa que no lo tengan a una escala más fina. De hecho, estudios realizados en España demuestran que variables como la amplitud de la vegetación de ribera, la calidad del agua y el grado de alteración del hábitat de río, pueden tener un efecto notable en determinar la presencia del visón europeo a micro-escala (Palazón *et al.*, 2006c; Zabala *et al.*, 2006).

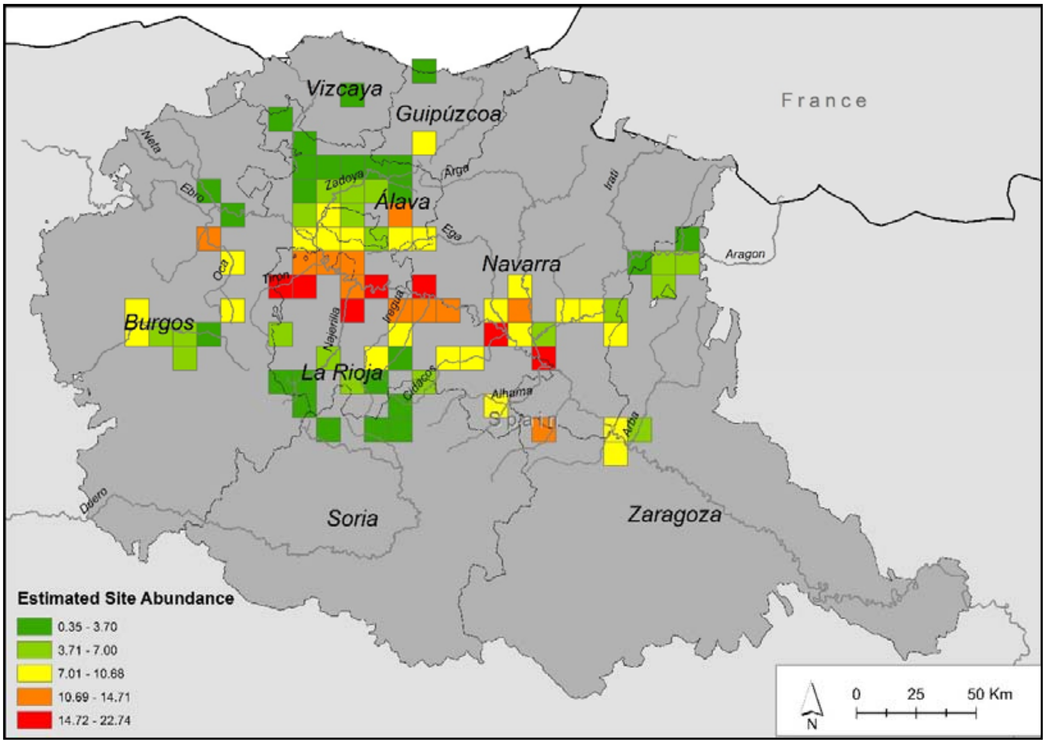


Figura 4. Distribución espacial de la estima de abundancia del vison europeo en las 86 cuadriculas (10x10 km UTM) muestreadas en las ocho provincias españolas donde se encuentra la especie.

Por otro lado, aparece clara la relación positiva entre la abundancia del visón europeo y la disponibilidad de ríos pequeños y, en menor medida, de tamaño mediano. En el área de estudio los ríos pequeños son principalmente los afluentes secundarios de los ríos medianos, los cuales representan los mayores afluentes del Ebro o del Duero. Aunque no se ha publicado mucha información sobre las dimensiones de los ríos seleccionados por el visón europeo, parece que las hembras reproductoras y los individuos jóvenes ocupan principalmente pequeños ríos con buena cobertura vegetal y calidad del agua, mientras los ríos grandes (como el río Ebro) actúan como corredores para la dispersión de los machos, lo cual puede explicar la baja densidad observadas en este tipo de ríos (MAGRAMA, 2009; Palazón and Ruiz-Olmo, 1998a).

La hipótesis que se defiende es que las cuencas atlánticas en el norte y la parte más al sur del área de distribución de la especie muestran valores de abundancia inferiores por causas diferentes: los ríos del País Vasco son cortos, escarpados, con corriente rápida y baja calidad de agua (Palazón *et al.*, 2003) y el área está invadida por el visón americano desde hace por lo menos dos décadas (Zabala *et al.*, 2006); en la parte meridional del área de distribución del visón europeo las bajas densidades pueden ser debidas a la presencia de la Sierra de la Demanda, que forma parte del Sistema Ibérico, alcanza los 2.230 msnm, y que puede actuar como una barrera geográfica para el visón autóctono.

En este capítulo no se detectó el efecto del visón americano en la abundancia del visón europeo. Una razón puede ser que en los ajustes del modelo N-mixture el único parámetro que se puede poner en función de la presencia del visón americano es la probabilidad de detección. Sin embargo, en el capítulo 1 se observa que la detección del visón europeo no está afectada por la detección del visón americano y que generalmente si las dos especies están presentes en una cuadrícula, las dos son detectadas, probablemente gracias a la eficacia del método de muestreo.

Otro motivo de este hecho puede ser que las 86 cuadrículas seleccionadas en el estudio representan el área donde se concentra el mayor esfuerzo de monitorización de la especie autóctona y de control de la especie invasora y, donde es posible que el efecto negativo de esta última sobre el visón europeo sea mitigado por mantener baja su densidad, como se indica en el capítulo 1.

En este estudio se revela que aunque las causas del declive del visón europeo no emergen claramente, el lento decremento del número de individuos reclutados cada año indica que los esfuerzos de conservación actuales no son suficientes para mantener una población viable a medio y largo plazo. Los esfuerzos de conservación de la especie deberían estar dirigidos a las áreas más estrictamente relacionas con los ríos y las riberas fluviales, y en la sub-población central, ya que esta puede ejercer de fuente suministradora de individuos para las subpoblaciones más pequeñas y con menor número de individuos, y puede generar una expansión de la especie.

Predicción de la expansión del visón americano e identificación de las áreas de conflicto potencial entre los dos visones

En el tercer capítulo de esta tesis se ha realizado una predicción a escala fina de la expansión potencial del visón americano en la Península Ibérica, correlacionando los factores ambientales que pueden incidir sobre su ecología con su distribución actual en el área de estudio.

La predicción de la distribución potencial de especies en "no equilibrio" con el ambiente, como las especies invasoras o las especies amenazadas de extinción, puede llevar a subestimar el área idónea, debido a toda una serie de condiciones ambientales que podrían incidir sobre la especie, pero que no están incluidas en la calibración de los modelos. Por este motivo en este capítulo se ha desarrollado un esquema analítico que incluye la mayor cantidad posible de información sobre la distribución global de la especie en una predicción a escala regional.

Se ha calibrado un modelo a resolución gruesa en todo el territorio de Norte América, el área de origen del visón americano, y en Europa, el área invadida por esta especie, utilizando variables climáticas. Además, se ha combinado con un modelo a resolución fina, calibrado en la Península Ibérica con variables del uso del suelo.

Se han testado las diferencias en las predicciones obtenidas utilizando una diferente cantidad de información procedente de: 1) solo del área invadida, 2) solo del área original y 3) de ambas áreas de distribución. Una vez proyectados a la escala de la Península Ibérica, estos modelos climáticos han dado predicciones muy diferentes (Fig. 5 e, 5 f, 5 g); diferencias que se ven reflejadas obviamente en la combinación con el modelo regional basado en el uso del suelo (Fig. 6).

El modelo que ha mostrado la mejor representación (en cuanto a proporción de presencias correctamente predichas) incluye la mayor cantidad de información sobre las condiciones ocupadas por el visón americano (en el área original y en el área invadida). El modelo calibrado sólo en Europa (área invadida), tiene el poder predictivo más bajo, probablemente debido al hecho que en esta área la especie invasora se encuentra lejos del estado de equilibrio (lejos de completar todo su nicho potencial).

El modelo con la mejor rendimiento indica que prácticamente toda la Península Ibérica tiene un clima idóneo para albergar la presencia del visón americano, revelando que la especie puede habitar en áreas áridas con veranos secos y cálidos, que es el clima prevalente en el sur de la Península, siempre y cuando existan cursos fluviales medianos y grandes.

El mapa derivado del modelo combinado (Fig. 6a) indica que la mayoría de las principales cuencas ibéricas pueden ser invadidas por la especie, especialmente ríos de dimensiones medianas y grandes.

Este estudio representa la primera predicción de la expansión del visón americano en la Península Ibérica y, aunque actualmente la especie está ocupando la mitad norte de la Península, nuestro modelo revela que las condiciones cálidas y secas del sur no son suficientes para parar su expansión.

El análisis muestra claramente los efectos de la calibración de los SDMs con datos de una especie en “no equilibrio”, y las consecuencias de confiar en una información incompleta sobre las condiciones ambientales ocupadas por una especie determinada.

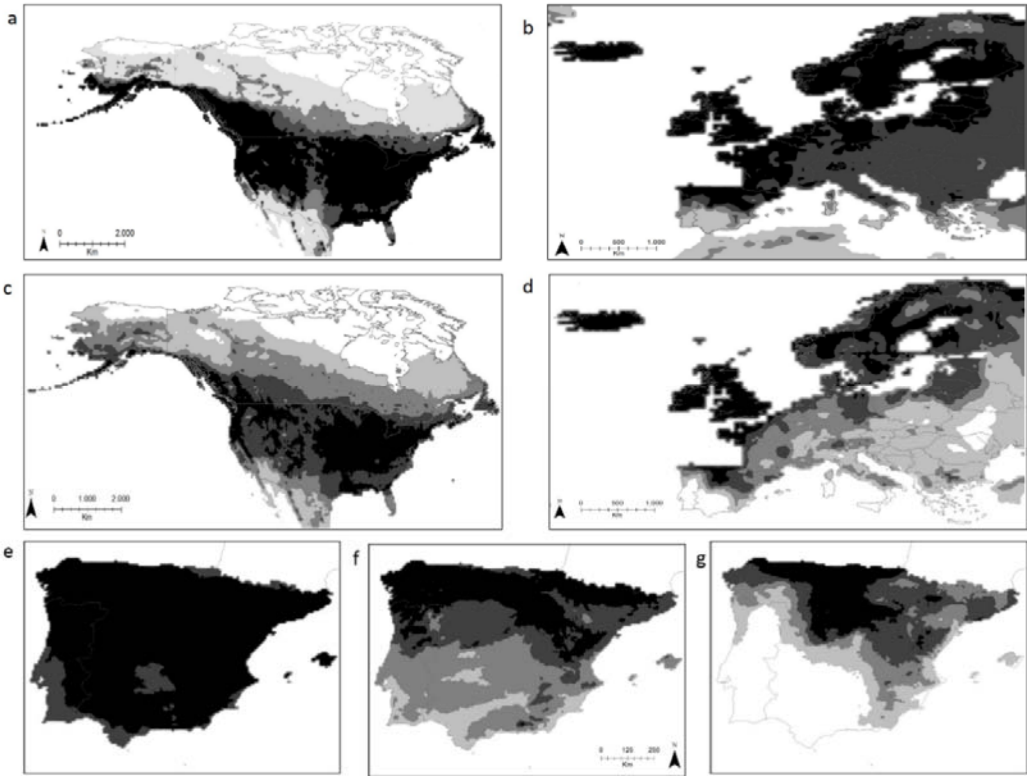


Figura 5. Mapas que representan la predicción de los modelos climáticos a escala gruesa calibrados en a) y b) ambos rangos de distribución, c) sólo en América del Norte, área de origen, d) sólo en Europa, área invadida. Los mapas de la fila inferior ilustran la proyección en la Península Ibérica de los modelos climáticos calibrados en e) ambas áreas, f) el área de origen y g) el área invadida. En todos los mapas los tonos más oscuros indican una mayor concordancia entre los cinco algoritmos utilizados en la calibración de los modelos.

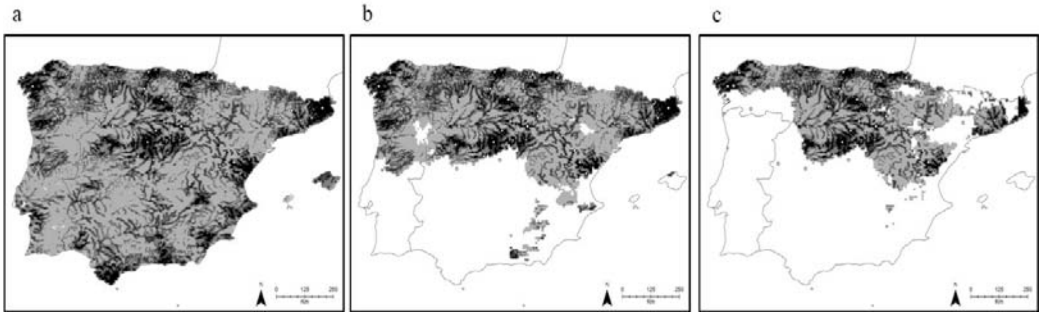


Figura 6. Mapas de la expansión potencial del vison americano en la Península Ibérica resultantes de la combinación multi-escala entre un modelo a escala fina calibrado utilizando variables del uso del suelo (modIP) con los modelos a escala gruesa calibrados en a) ambas áreas, de origen e invadidas (modNAEU), b) sólo el área de origen (modNA) y c) sólo el área invadida (modEU). Los puntos blancos representan una muestra del 10% de los datos utilizados para la evaluación independiente de los modelos. Todos los mapas los tonos más oscuros indican una mayor concordancia entre los cinco algoritmos utilizados en la calibración de los modelos.

El esquema analítico presentado en este capítulo puede ser utilizado para reducir el efecto negativo de los datos recogidos en “no equilibrio” y para mejorar la eficacia de los SDMs en la planificación de la prevención, gestión y control de las especies invasoras, a través de predicciones a escala fina basadas en la máxima cantidad de información disponible sobre las condiciones idóneas para la especie de interés.

En el capítulo 4 el mismo esquema ha sido aplicado para predecir las áreas potencialmente idóneas para la conservación del visón europeo en la Península Ibérica. Las especies en peligro crítico de extinción se encuentran comúnmente lejos del estado de equilibrio a causa de la extrema reducción de sus áreas de distribución y de sus efectivos poblacionales, por lo que predecir su área potencial presenta las mismas problemáticas que en las especies invasoras.

En este caso, la predicción ha sido el resultado de la combinación de un modelo climático calibrado en toda Europa con datos de la distribución histórica de la especie (antes de que desapareciera del 85% de su área original) y un modelo calibrado en la Península Ibérica utilizando variables de uso del suelo.

La predicción espacial obtenida se ha combinado con el modelo de expansión potencial del visón americano producido en el capítulo 3 (fila inferior en Fig. 7) para: 1) identificar las área de conflicto potencial entre el vison autóctono y el invasor y, 2) analizar la eficacia de la estrategia de las Comunidades Autónomas y del Gobierno de España sobre áreas protegidas en incluir áreas potencialmente idóneas para el visón europeo.

A pesar que las dos especies de visones tengan requerimientos de hábitat muy parecidos, los modelos obtenidos en el presente estudio generan predicciones muy diferentes (Fig. 7). Solo algunas cuencas del norte de la Península Ibérica son idóneas para el visón europeo, mientras que el visón americano puede ocupar ríos en casi todo el territorio ibérico, como se ha indicado en el capítulo 3.

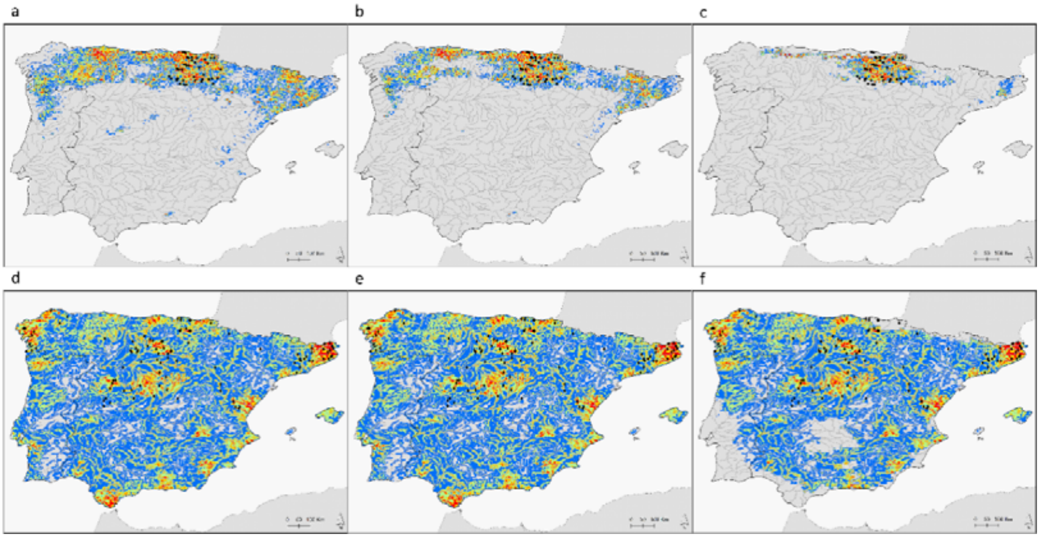


Figura 7. Mapas que representan la distribución potencial del visón europeo (fila de mapas superior) y del visón americano (fila de mapas inferior) en la Península Ibérica, obtenida con un enfoque jerárquico multi-escala. Se ha utilizado tres umbrales diferentes para combinar el modelo climático con los modelos regionales en ambas especies: 0,3 (a, d), 0,5 (b, e) y 0,7 (c, f). Los puntos negros en los mapas inferiores representan una muestra del 10% de los datos originales del modelo de calibración del visón europeo y el visón americano, respectivamente.

La diferencia en las predicciones se ha relacionado con diferencias en la biogeografía y en la biología de las dos especies. El visón americano muestra una plasticidad ecológica muy superior al visón europeo, que se manifiesta con una mayor capacidad de dispersión, una mayor adaptabilidad a condiciones adversas de hábitat, un nicho trófico más amplio y una mayor capacidad reproductora (Melero and Palazón, 2011; Sidorovich and Macdonald, 2001; Maran *et al.*, 1998b; Sidorovich *et al.*, 1997). Esta invasora se ha establecido en menos de un siglo en 20 países europeos (Bonesi and Palazón, 2007), aunque este proceso ha sido facilitado por la especie humana, mediante introducciones accidentales (desde granjas peleteras) o deliberadas (sueltas directas en el medio natural). El visón europeo es mucho menos adaptable ecológicamente, nunca ha colonizado los países del extremo norte y del sur Europa, aunque se expandió por el oeste de Francia en los siglos XIX y XX hasta llegar al norte de España recientemente en los años 1950s (Palazón *et al.*, 2003; Youngman, 1982; Rodríguez de Ondarra, 1955).

Del análisis realizado ha resultado que aproximadamente entre el 84% y el 93% del área de distribución potencial del visón europeo está en riesgo de ser invadida por el visón americano (Fig. 8). Esta es una observación preocupante si se tiene en cuenta que muchos otros factores amenazan la especies en el área de estudio, como son la perdida y la fragmentación del hábitat, la contaminación de los ríos (Zuberogoitia *et al.*, 2013; Palazón *et al.*, 2002), la aparición de enfermedades (Mañas *et al.*, 2003), los atropellos (Palazón *et al.*, 2012a), y otros tipos de mortalidad directa. Además menos de un cuarto del área ecológicamente idónea para el visón europeo se encuentra dentro de áreas protegidas, y la mayor parte de las áreas de conflicto (categorías de riesgo medio y alto) se encuentran en territorio sin ningún tipo de protección legal.

Para aumentar la eficacia de la conservación del visón europeo, las áreas prioritarias tendrían que ser la de riesgo medio y elevado, en particular en las áreas protegidas donde se espera que las actividades humanas se adapten a la conservación de las especies amenazadas (Araújo *et al.*, 2002).

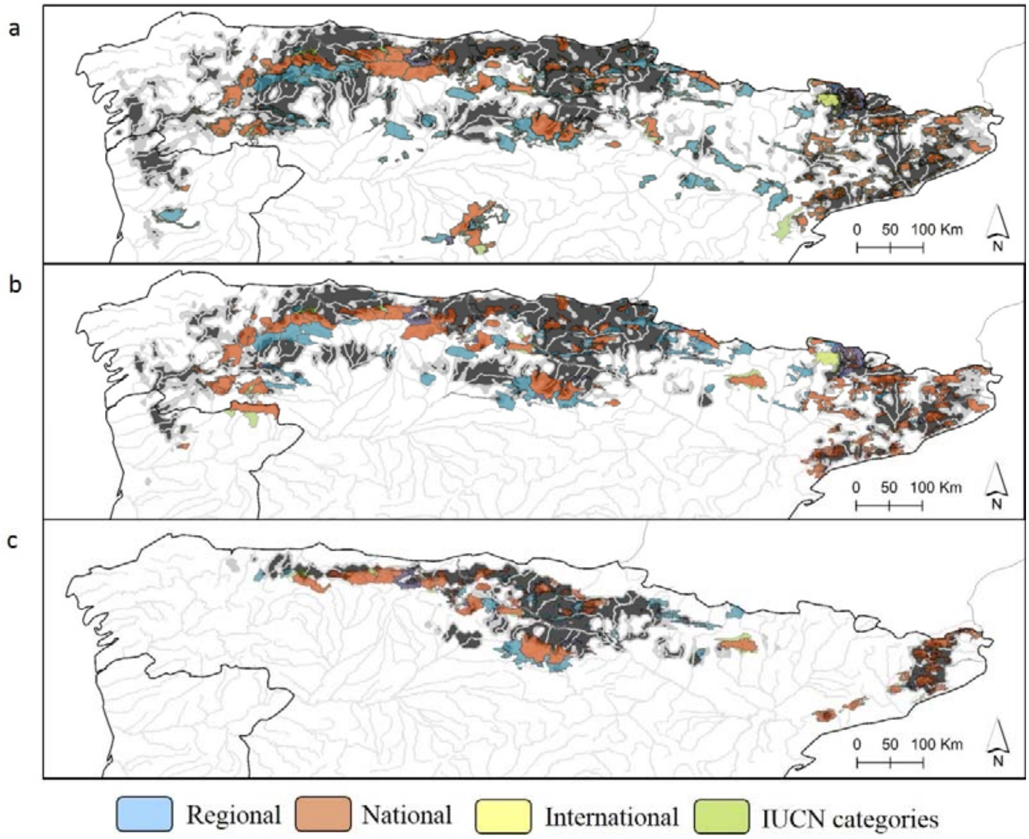


Figura 8. Mapas de las áreas con elevado (gris obscuro) y medio (gris claro) riesgo para la conservación del visón europeo, resultantes del solapamiento de la predicción de distribución potencial de las dos especies de visones en la Península Ibérica. En la figura se muestran las áreas protegidas (Regionales, Nacionales, Internacionales y las categorías IUCN de I a VI) que intersectan las áreas de conflicto. Estas últimas se han seleccionado usando tres umbrales diferentes para transformar la probabilidad continua en una predicción binaria: a) umbral conservador, b) mediano y c) estrecho.

La categoría más numerosa y extensa de áreas protegidas es la Regional que incluye principalmente Lugares de Importancia Comunitaria –LICs- (Directiva 92/43/CEE, “Hábitats”) y Áreas de Protección Especial para las aves (Directiva 79/409/CEE, “Aves”) gestionados por los gobiernos locales bajo la supervisión actual del Ministerio de Agricultura, Alimentación y Medio Ambiente. Sin embargo, centrar los esfuerzos de conservación solo dentro de las áreas protegidas llevaría al fracaso de cualquier estrategia cuyo objetivo fuera aumentar la viabilidad del visón europeo y frenar la expansión del americano, debido a que la mayor parte del área potencial de conflicto entre las dos especies no se halla actualmente protegida.

Los mapas de riesgo obtenidos, especialmente el escenario "estricto" que más se adapta al área de distribución actual del visón europeo, pueden dar indicaciones a los gestores para individualizar las áreas en las que es más urgente controlar la invasora o evitar su invasión; así como dónde centrar el monitoreo para detectar rápidamente su impacto, prevenir el conflicto con el visón europeo y ayudar a la expansión de la especie autóctona preservando la conectividad entre áreas idóneas.

Sin un esfuerzo eficaz de control en el área de conflicto en la que las dos especies están actualmente presentes, puede resultar difícil tener éxito en la conservación del visón europeo.

Implicaciones para la gestión y la conservación de las dos especies de visón

Del análisis desarrollado en esta tesis emerge que a pesar de los recursos (personal y financiero) y los esfuerzos invertidos en la conservación del visón europeo y en el control del visón americano en los últimos años (2000 - 2014), la actual estrategia no está teniendo el efecto esperado.

Una posible razón es la variabilidad espacial y temporal en el esfuerzo del control del visón americano, debido a unos recursos económicos variables e inconstantes en el tiempo y en el territorio, y a la falta de coordinación entre los gobiernos regionales, que permite el establecimiento de mecanismos compensatorios en la reproducción y la inmigración de la población de la especie invasora.

Debido a la elevada capacidad de recolonización del visón americano, es necesario un esfuerzo mucho más intenso para llegar a controlar y eliminar la especie invasora de la totalidad del área de distribución del visón europeo y de una oportuna “área de amortiguamiento” en sus alrededores.

Todas las cuencas fluviales de la Península Ibérica pueden ser invadidas por el visón americano, predicción que hace necesaria la monitorización de la expansión hacia el sur de esta especie, y la verificación de su ausencia/presencia de las áreas donde se aplica el control para comprobar el éxito/fracaso de los esfuerzos de control y erradicación.

La acción de protección del visón europeo tendría que estar centrada en las áreas más estrictamente relacionada con las zonas húmedas y ríos y sus riberas adyacentes; por ejemplo a través de la restauración de la vegetación de ribera allí donde se halla deteriorada o eliminada, y manteniendo la calidad del bosque de ribera y su conservación. Además, continuar manteniendo el agua a niveles aceptables de calidad (Estaciones Depuradoras de Aguas Residuales) para mantener la presencia de las poblaciones de visón europeo y otras especies de mamíferos semiacuáticos.

Solo una pequeña parte del área potencialmente idónea para el visón europeo está hoy legalmente protegida; aunque las áreas protegidas gestionadas por los gobiernos regionales pueden ser puntos importantes para la conservación de la especie, todas las áreas con riesgo de conflicto entre las dos especies de visón tendrían que ser constantemente monitorizadas para prevenir el impacto de la especie invasora sobre la especie autóctona.

La sub-población de visón europeo que ocupa la parte central de su área de distribución actual, en los afluentes de la cuenca alta del Ebro, es la que presenta una densidad más elevada y tendría que recibir una atención especial en los proyectos de conservación debido a que puede ser la fuente suministradora de individuos migrantes para la subpoblación de las cuencas atlánticas, y para su expansión hacías las zonas extremas del sureste y este de su área de distribución.

Se deben invertir mayores recursos económicos, materiales y de personal, en controlar las poblaciones de visón americano que se están expandiendo en Álava, en las cuencas Atlánticas (Vizcaya y Guipúzcoa), y la que se acerca por el suroeste (Burgos y La Rioja). Especialmente, el control debería resultar eficaz para mantener localmente bajas las densidades de la especie invasora.

En general, son necesarias una mejor coordinación entre las políticas regionales y una mayor constancia en la monitorización y el control de la especie invasora para mejorar la estrategia de conservación del visón europeo en España.

CONCLUSIONES

1. La expansión del visón americano, una especie invasora, está ocasionando el desplazamiento y la desaparición del visón europeo de su área de distribución original en el norte de España.

2. El visón americano coloniza preferentemente los territorios (cuadrículas) ocupados por el visón europeo, el cual tiene una mayor probabilidad de extinguirse en territorios ocupados por la especie invasora que en territorios donde este último está ausente.

3. Localmente, especialmente dentro del área de distribución del visón europeo, los esfuerzos de control de la especie invasora mantienen baja su densidad poblacional y ralentizan el proceso de sustitución de la especie autóctona. Pero globalmente el aumento de la ocupación del visón americano indica que los esfuerzos actuales de control no están teniendo éxito.

4. La abundancia del visón europeo está lentamente disminuyendo, y cada año la población se renueva a un ritmo más lento, debido a un menor nacimiento de nuevos individuos y una menor tasa de inmigración.

5. La estima de la dimensión de la población de visón europeo en España en el año 2000 fue de 599.75 individuos, y en el año 2010 de 566.52 individuos.

6. La abundancia del visón europeo presenta una gran variabilidad espacial y las mayores densidades poblacionales están localizadas en la parte central de su área de distribución, en los afluentes de la cuenca alta del rio Ebro - regiones de Álava, norte de La Rioja, este de Burgos y sur de Navarra.

7. El visón europeo es más abundante en los ríos de dimensiones pequeñas y medianas que en los ríos de grandes dimensiones. Las características de las áreas más estrictamente relacionadas con los ríos (calidad del agua, estado de la vegetación de ribera) son más importantes para la conservación de la especie autóctona que el hecho de mejorar el impacto humano o la proporción de vegetación natural a escala gruesa.

8. Casi todo el territorio ibérico es climáticamente idóneo para el visón americano. Debido a este hecho, la especie puede potencialmente invadir los ríos de casi todas las cuencas ibéricas. Por el contrario, sólo algunas cuencas del norte de España son idóneas para el visón europeo.

9. Menos de un cuarto del área potencialmente idónea para el visón europeo se encuentra en áreas protegidas; la gran mayoría (alrededor de 90%) de este territorio potencialmente idóneo se halla en riesgo de invasión por parte del visón americano y la mayoría del área de conflicto entre las dos especies de visones se encuentra en territorio no protegido legalmente.

10. Las acciones de conservación y gestión de las dos especies de visones tendría que centrarse no solo adentro si no también afuera de las áreas protegidas para preservar el hábitat idóneo para el visón europeo y mitigar o prevenir el conflicto entre las dos especies.

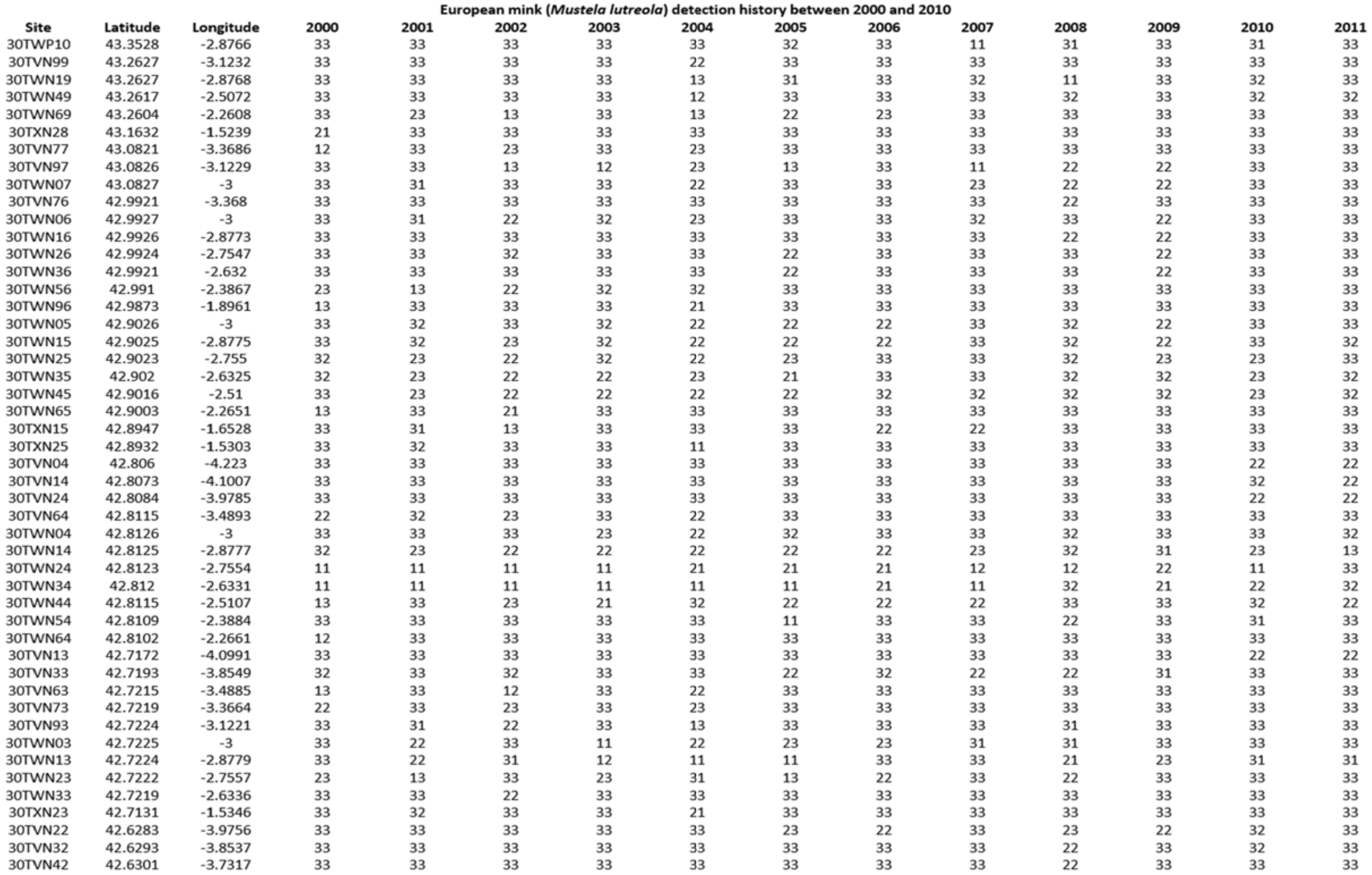
11. Son necesarias una mejor coordinación entre las políticas locales y una mayor constancia en la monitorización y el control del vison americano para mejorar la estrategia de conservación del visón europeo en España

Appendix

APPENDIX

In appendix we show the data used in Chapter 1, gathered from live-trapping surveys conducted between 2000 and 2011 in Northern Spain as part of the European mink conservation plan and the American mink control plan implemented by managers and technicians of regional governments coordinated by the Spanish Ministry of Agriculture, Food and Environment.

The data represent detection histories used in a two-species multi-season occupancy analysis (MacKenzie et al., 2006): the trapping events have been grouped into annual primary sampling occasions (each year from 2000 to 2011) that included two secondary periods (January - March and September - December). The sites surveyed were cells of 10x10km.



European mink (*Mustela lutreola*) detection history between 2000 and 2010

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TWP10	43.3528	-2.8766	33	33	33	33	33	32	33	11	31	33	31	33
30TVN99	43.2627	-3.1232	33	33	33	33	22	33	33	33	33	33	33	33
30TWN19	43.2627	-2.8768	33	33	33	33	13	31	33	32	11	33	32	33
30TWN49	43.2617	-2.5072	33	33	33	33	12	33	33	33	32	33	32	32
30TWN69	43.2604	-2.2608	33	23	13	33	13	22	23	33	33	33	33	33
30TXN28	43.1632	-1.5239	21	33	33	33	33	33	33	33	33	33	33	33
30TVN77	43.0821	-3.3686	12	33	23	33	23	33	33	33	33	33	33	33
30TVN97	43.0826	-3.1229	33	33	13	12	23	13	33	11	22	22	33	33
30TWN07	43.0827	-3	33	31	33	33	22	33	33	23	22	22	33	33
30TVN76	42.9921	-3.368	33	33	33	33	33	33	33	33	22	33	33	33
30TWN06	42.9927	-3	33	31	22	32	23	33	33	32	33	22	33	33
30TWN16	42.9926	-2.8773	33	33	33	33	33	33	33	33	22	22	33	33
30TWN26	42.9924	-2.7547	33	33	32	33	33	22	33	33	33	22	33	33
30TWN36	42.9921	-2.632	33	33	33	33	33	22	33	33	33	22	33	33
30TWN56	42.991	-2.3867	23	13	22	32	32	33	33	33	33	33	33	33
30TWN96	42.9873	-1.8961	13	33	33	33	21	33	33	33	33	33	33	33
30TWN05	42.9026	-3	33	32	33	32	22	22	22	33	32	22	33	33
30TWN15	42.9025	-2.8775	33	32	23	32	22	22	22	33	32	22	33	32
30TWN25	42.9023	-2.755	32	23	22	32	22	23	33	33	32	23	23	33
30TWN35	42.902	-2.6325	32	23	22	22	23	21	33	33	32	32	23	32
30TWN45	42.9016	-2.51	33	23	22	22	22	22	32	32	32	32	23	32
30TWN65	42.9003	-2.2651	13	33	21	33	33	33	33	33	33	33	33	33
30TXN15	42.8947	-1.6528	33	31	13	33	33	33	22	22	33	33	33	33
30TXN25	42.8932	-1.5303	33	32	33	33	11	33	33	33	33	33	33	33
30TVN04	42.806	-4.223	33	33	33	33	33	33	33	33	33	33	22	22
30TVN14	42.8073	-4.1007	33	33	33	33	33	33	33	33	33	33	32	22
30TVN24	42.8084	-3.9785	33	33	33	33	33	33	33	33	33	33	22	22
30TVN64	42.8115	-3.4893	22	32	23	33	22	33	33	33	33	33	33	33
30TWN04	42.8126	-3	33	33	33	23	22	32	33	33	32	33	33	32
30TWN14	42.8125	-2.8777	32	23	22	22	22	22	22	23	32	31	23	13
30TWN24	42.8123	-2.7554	11	11	11	11	21	21	21	12	12	22	11	33
30TWN34	42.812	-2.6331	11	11	11	11	11	11	21	11	32	21	22	32
30TWN44	42.8115	-2.5107	13	33	23	21	32	22	22	22	33	33	32	22
30TWN54	42.8109	-2.3884	33	33	33	33	33	11	33	33	22	33	31	33
30TWN64	42.8102	-2.2661	12	33	33	33	33	33	33	33	33	33	33	33
30TVN13	42.7172	-4.0991	33	33	33	33	33	33	33	33	33	33	22	22
30TVN33	42.7193	-3.8549	32	33	32	33	33	22	32	22	22	31	33	33
30TVN63	42.7215	-3.4885	13	33	12	33	22	33	33	33	33	33	33	33
30TVN73	42.7219	-3.3664	22	33	23	33	23	33	33	33	33	33	33	33
30TVN93	42.7224	-3.1221	33	31	22	33	13	33	33	33	31	33	33	33
30TWN03	42.7225	-3	33	22	33	11	22	23	23	31	31	33	33	33
30TWN13	42.7224	-2.8779	33	22	31	12	11	11	33	33	21	23	31	31
30TWN23	42.7222	-2.7557	23	13	33	23	31	13	22	33	22	33	33	33
30TWN33	42.7219	-2.6336	33	33	22	33	33	33	33	33	33	33	33	33
30TXN23	42.7131	-1.5346	33	32	33	33	21	33	33	33	33	33	33	33
30TVN22	42.6283	-3.9756	33	33	33	33	33	23	22	33	23	22	32	33
30TVN32	42.6293	-3.8537	33	33	33	33	33	33	33	33	22	33	32	33
30TVN42	42.6301	-3.7317	33	33	33	33	33	33	33	33	22	33	33	33

Sites from 1 to 50; 1=species detected; 2=species non detected; 3=site not surveyed

European mink (*Mustela lutreola*) detection history between 2000 and 2010

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVN52	42.6308	-3.6098	33	33	33	33	33	33	33	33	22	33	33	33
30TVN62	42.6314	-3.4878	31	33	11	33	21	33	32	33	33	31	33	33
30TVN92	42.6324	-3.122	33	33	33	33	33	33	33	33	21	33	33	33
30TWN02	42.6324	-3	31	33	12	11	11	22	11	23	11	11	11	33
30TWN12	42.6324	-2.878	31	13	11	11	13	22	31	33	21	33	13	13
30TWN22	42.6322	-2.7561	11	13	21	23	33	32	21	33	22	33	33	33
30TWN32	42.6319	-2.6341	13	33	22	33	23	12	32	33	33	33	33	33
30TWN42	42.6314	-2.5122	33	33	21	33	23	13	33	32	32	13	33	33
30TWN52	42.6308	-2.3902	31	33	21	33	13	33	33	33	31	13	33	13
30TWN72	42.6293	-2.1463	12	33	33	33	33	33	33	33	33	33	33	33
30TWN92	42.6272	-1.9024	33	31	33	11	33	33	33	33	33	33	33	33
30TXN62	42.6158	-1.0492	33	33	22	23	33	22	33	22	22	23	23	33
30TVN31	42.5392	-3.8525	33	33	33	33	33	32	22	32	23	32	33	33
30TVN61	42.5414	-3.4871	33	33	33	33	33	33	33	33	33	22	33	33
30TWN01	42.5424	-3	33	33	21	21	13	33	33	31	33	33	13	13
30TWN11	42.5423	-2.8782	33	33	11	21	12	13	23	13	13	11	13	11
30TWN21	42.5421	-2.7564	33	33	21	33	33	13	21	33	13	13	33	23
30TXN41	42.5297	-1.2953	33	33	33	23	33	22	33	31	22	33	13	33
30TXN51	42.5278	-1.1736	33	33	33	33	33	33	33	33	22	23	23	33
30TXN61	42.5258	-1.052	33	33	22	33	33	33	33	33	22	23	23	33
30TXN71	42.5237	-0.9303	33	33	22	33	33	33	33	33	22	23	23	33
30TVN30	42.4492	-3.8512	33	32	33	32	33	22	32	32	22	32	32	33
30TVN50	42.4507	-3.608	33	33	33	33	33	33	33	33	33	22	33	33
30TVN70	42.4518	-3.3648	33	31	11	13	33	33	31	33	33	33	33	33
30TVN80	42.4521	-3.2432	33	23	13	33	22	33	33	33	33	33	33	33
30TVN90	42.4523	-3.1216	33	31	13	31	11	33	33	31	31	33	13	13
30TWN20	42.4521	-2.7568	31	13	21	21	11	13	11	13	13	13	33	11
30TWN30	42.4518	-2.6352	31	33	11	22	13	13	33	13	33	31	33	12
30TWN40	42.4513	-2.5136	31	31	31	13	11	13	33	23	13	33	31	13
30TWN50	42.4507	-2.392	31	33	33	33	11	33	33	21	33	33	13	13
30TWN90	42.4471	-1.9056	33	32	33	33	11	33	23	22	22	22	33	33
30TXN50	42.4378	-1.1763	33	33	33	23	33	22	33	32	22	23	23	33
30TVM09	42.3558	-4.2143	33	33	33	33	32	33	23	32	23	33	32	22
30TVM29	42.3582	-3.9714	33	33	33	33	33	23	23	33	22	22	32	33
30TVM39	42.3591	-3.85	33	33	23	32	22	32	22	33	22	32	32	33
30TVM49	42.36	-3.7286	33	33	23	32	33	23	33	33	32	22	33	33
30TVM59	42.3607	-3.6072	33	33	33	33	32	33	33	33	33	22	32	33
30TVM69	42.3612	-3.4857	33	33	33	33	33	32	33	33	33	22	33	33
30TVM89	42.362	-3.2429	33	33	31	33	22	33	33	33	33	33	33	23
30TVM99	42.3622	-3.1214	33	33	33	33	33	33	33	33	22	33	33	33
30TWM09	42.3623	-3	33	33	33	33	33	33	33	32	31	31	23	22
30TWM29	42.362	-2.7571	32	13	21	11	11	33	11	13	13	11	13	13
30TWM49	42.3612	-2.5143	11	13	32	31	32	33	33	13	33	33	33	13
30TWM59	42.3607	-2.3928	33	33	22	31	32	33	33	12	33	33	33	13
30TWM69	42.36	-2.2714	31	33	31	33	11	13	33	31	33	33	33	13
30TWM99	42.3571	-1.9072	33	31	33	33	11	33	13	11	11	21	33	33
30TXM09	42.3558	-1.7857	33	33	33	33	11	33	13	33	31	33	33	33
30TXM19	42.3545	-1.6644	33	33	33	33	11	12	13	11	33	33	33	33
30TXM29	42.353	-1.543	33	31	33	33	11	33	13	11	33	33	33	33
30TXM39	42.3514	-1.4216	33	33	33	23	33	33	33	22	11	23	13	33

Sites from 51 to 100; 1=species detected; 2=species non detected; 3=site not surveyed

European mink (*Mustela lutreola*) detection history between 2000 and 2010

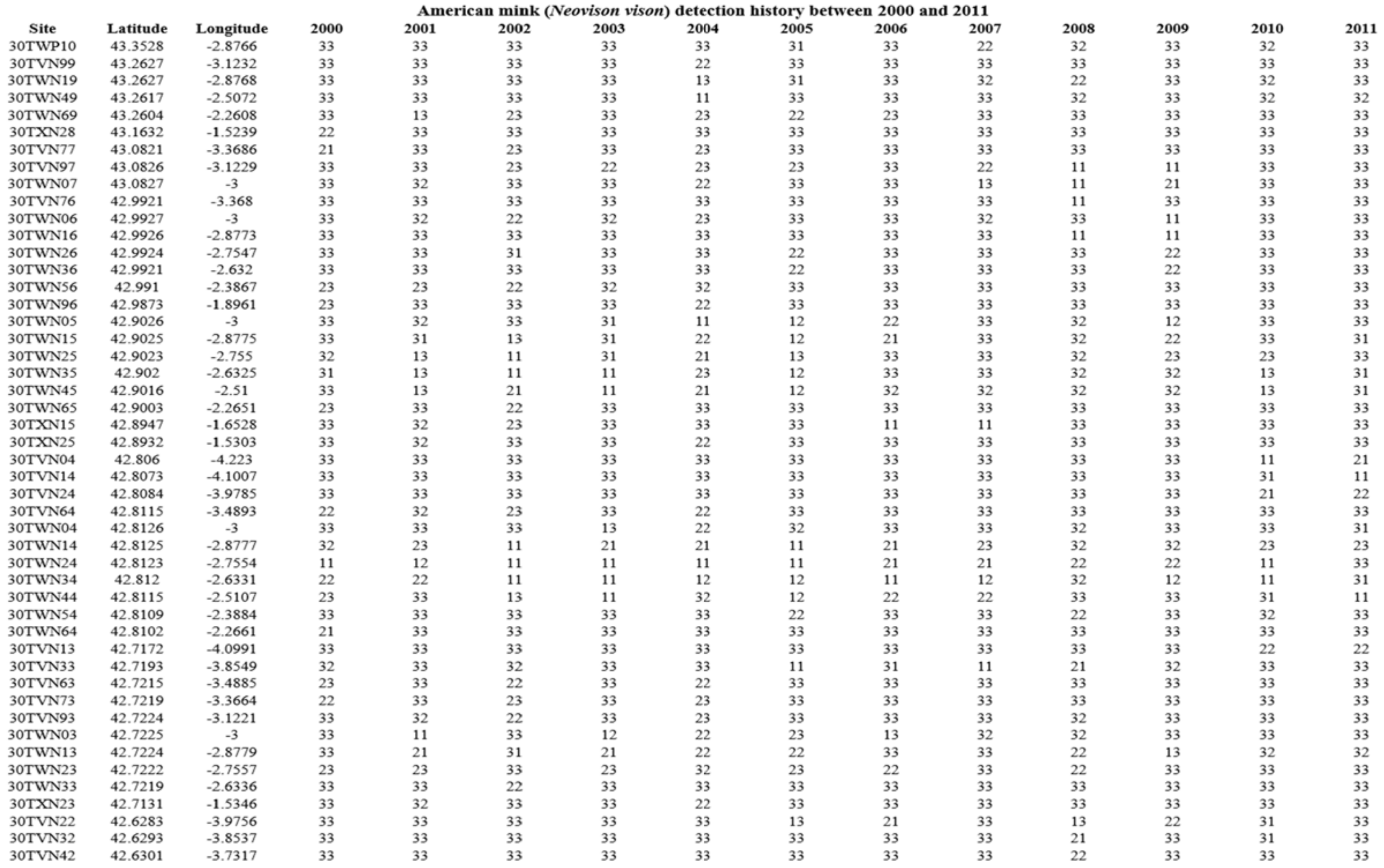
Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVM08	42.2658	-4.2125	33	33	33	23	32	33	22	32	22	32	33	33
30TVM28	42.2681	-3.9701	33	33	22	32	22	22	22	33	32	22	32	33
30TVM38	42.2691	-3.8488	33	23	22	22	22	32	22	22	22	22	32	33
30TVM48	42.2699	-3.7276	33	32	33	22	22	22	22	32	22	22	32	33
30TVM58	42.2706	-3.6063	33	32	33	22	22	22	21	32	22	22	32	33
30TVM68	42.2712	-3.4851	23	33	21	22	22	22	32	32	32	32	32	33
30TVM98	42.2721	-3.1213	33	33	13	33	31	22	33	32	31	31	33	12
30TWM08	42.2722	-3	33	33	33	23	23	22	33	32	32	32	33	32
30TWM18	42.2721	-2.8787	33	33	33	21	23	33	22	33	12	32	33	22
30TWM38	42.2716	-2.6362	33	23	31	33	11	33	33	13	33	33	33	13
30TWM88	42.2681	-2.0299	33	31	12	31	11	33	23	31	31	33	33	13
30TWM98	42.267	-1.9087	31	32	23	33	11	11	13	11	11	21	33	33
30TXM08	42.2658	-1.7875	32	33	33	33	11	11	13	11	13	31	33	33
30TXM18	42.2645	-1.6663	33	31	33	33	33	11	33	11	33	33	33	33
30TXM38	42.2614	-1.4238	33	33	33	33	13	33	33	21	22	13	13	33
30TVM07	42.1758	-4.2108	33	33	33	23	33	23	23	33	33	22	33	33
30TVM17	42.177	-4.0897	33	33	22	22	22	23	23	33	32	33	33	33
30TVM27	42.1781	-3.9687	33	33	32	32	22	22	33	33	32	32	32	33
30TVM37	42.179	-3.8476	32	33	33	32	23	33	23	32	32	33	22	32
30TVM47	42.1798	-3.7265	33	33	33	22	22	32	33	32	33	33	32	22
30TVM57	42.1805	-3.6054	33	33	33	23	22	22	22	32	32	22	32	33
30TVM67	42.1811	-3.4844	33	33	33	33	32	23	33	33	33	32	33	22
30TVM87	42.1819	-3.2422	33	33	33	22	23	22	32	23	33	23	33	22
30TVM97	42.1821	-3.1211	33	31	33	33	31	32	33	22	32	33	33	23
30TWM07	42.1821	-3	33	33	22	23	23	23	23	22	32	33	33	22
30TWM17	42.1821	-2.8789	32	33	33	32	23	33	33	22	31	23	33	22
30TWM37	42.1816	-2.6367	13	33	31	33	13	13	33	23	33	32	33	23
30TWM47	42.1811	-2.5156	21	33	32	33	22	33	33	23	33	33	33	23
30TWM67	42.1798	-2.2735	31	33	23	33	31	33	33	21	33	33	33	23
30TWM77	42.179	-2.1524	32	33	13	33	12	33	33	21	33	33	33	13
30TWM97	42.177	-1.9103	33	33	31	13	13	33	23	21	33	33	33	13
30TXM07	42.1758	-1.7892	31	31	21	31	11	33	23	13	33	33	33	23
30TXM57	42.1678	-1.184	33	33	33	33	33	33	33	33	22	23	33	33
30TVM16	42.0869	-4.0882	33	33	22	23	33	23	23	33	32	33	33	33
30TVM36	42.089	-3.8464	33	33	32	33	21	32	33	33	32	33	23	23
30TVM76	42.0915	-3.3628	33	33	32	33	23	32	22	32	32	32	33	23
30TVM86	42.0918	-3.2418	33	33	23	22	22	33	22	21	33	23	33	23
30TVM96	42.092	-3.1209	33	33	33	23	22	22	22	22	33	33	33	22
30TWM06	42.0921	-3	32	13	12	33	33	33	22	22	31	32	33	22
30TWM16	42.092	-2.8791	33	32	33	33	23	33	33	33	32	33	33	22
30TWM26	42.0918	-2.7582	33	32	31	23	12	32	23	23	33	33	33	13
30TWM56	42.0905	-2.3954	33	31	33	23	13	33	23	22	33	33	33	23
30TWM66	42.0898	-2.2745	33	33	33	31	33	33	33	21	33	33	33	33
30TXM06	42.0857	-1.7909	31	33	33	32	23	33	33	33	33	33	11	33
30TXM16	42.0844	-1.67	12	33	33	31	13	33	33	33	33	33	33	33
30TXM56	42.0778	-1.1866	33	33	33	33	33	33	33	22	33	33	23	33
30TVM15	41.9969	-4.0867	33	33	33	23	22	22	23	23	33	23	33	33
30TVM25	41.998	-3.9659	33	33	33	22	32	22	22	32	22	32	33	33
30TVM35	41.9989	-3.8452	33	33	32	32	22	22	32	32	32	32	32	22
30TVM45	41.9997	-3.7245	32	33	22	32	22	32	32	22	33	23	33	33

Sites from 101 to 150; 1=species detected; 2=species non detected; 3=site not surveyed

European mink (*Mustela lutreola*) detection history between 2000 and 2010

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVM55	42.0004	-3.6037	32	33	33	23	32	32	22	23	33	22	32	32
30TVM65	42.001	-3.483	33	33	33	22	22	22	33	32	32	22	32	23
30TVM75	42.0014	-3.3622	32	33	23	22	22	22	22	22	32	22	32	22
30TVM85	42.0018	-3.2415	33	23	33	22	33	33	32	33	33	33	33	32
30TVM95	42.002	-3.1208	33	33	33	23	33	23	22	32	33	33	22	33
30TWM05	42.002	-3	23	23	32	23	22	32	22	22	33	33	33	32
30TWM25	42.0018	-2.7585	21	33	33	33	33	33	33	33	33	33	33	33
30TWM45	42.001	-2.517	33	31	33	23	22	33	23	22	33	33	33	33
30TWM65	41.9997	-2.2755	33	32	33	23	23	33	33	33	32	33	33	33
30TWM75	41.9989	-2.1548	33	33	33	33	33	33	23	22	33	33	33	33
30TWM85	41.998	-2.0341	33	32	23	33	32	33	33	13	33	33	33	11
30TVM34	41.9088	-3.844	33	33	33	33	22	23	33	32	33	33	33	33
30TVM44	41.9097	-3.7235	33	33	32	32	22	32	33	32	33	33	32	23
30TVM54	41.9104	-3.6029	33	33	33	33	33	22	33	32	33	33	33	33
30TVM64	41.9109	-3.4823	33	23	33	32	23	22	33	32	33	22	22	32
30TVM74	41.9114	-3.3617	33	33	33	33	32	22	33	32	22	33	33	22
30TVM84	41.9117	-3.2412	22	23	23	23	22	22	22	22	33	23	32	22
30TVM94	41.9119	-3.1206	33	33	33	22	32	22	33	23	33	23	32	23
30TWM04	41.9119	-3	33	33	33	33	33	33	23	23	33	33	33	22
30TWM14	41.9119	-2.8794	33	33	33	23	22	33	23	23	33	33	33	33
30TWM34	41.9114	-2.6383	32	33	33	23	22	33	23	23	33	33	33	33
30TWM44	41.9109	-2.5177	33	32	33	23	22	33	23	22	33	33	33	33
30TWM74	41.9088	-2.156	33	33	33	33	33	33	23	22	33	31	33	33
30TXM04	41.9056	-1.7943	33	33	33	33	33	33	33	22	13	13	13	33
30TXM34	41.9013	-1.4327	33	33	33	23	33	22	33	21	11	13	12	22
30TXM44	41.8995	-1.3122	33	33	33	23	33	22	33	33	23	23	23	22
30TVM13	41.8168	-4.0836	33	33	33	33	22	33	33	33	33	33	33	33
30TVM73	41.8213	-3.3612	33	33	33	32	33	22	23	33	23	33	23	23
30TVM83	41.8216	-3.2408	33	33	33	22	33	33	32	23	33	32	33	23
30TWM43	41.8209	-2.5184	32	33	33	33	33	33	33	22	33	33	33	33
30TWM63	41.8196	-2.2776	23	33	33	33	33	33	23	22	33	33	33	33
30TWM93	41.8168	-1.9164	33	32	33	33	33	33	23	22	33	33	33	33
30TXM33	41.8112	-1.4349	33	33	33	23	33	22	33	22	22	33	13	22
30TXM43	41.8095	-1.3146	33	33	33	23	33	22	33	33	22	33	33	33
30TVM12	41.7267	-4.0821	33	23	23	23	23	32	33	33	33	22	33	33
30TVM22	41.7278	-3.9619	33	23	22	23	33	33	33	33	33	23	33	32
30TVM72	41.7312	-3.3607	33	33	33	23	33	22	32	22	33	32	32	22
30TVM82	41.7316	-3.2405	33	33	33	33	33	22	33	33	33	33	33	33
30TWM32	41.7312	-2.6393	32	33	33	33	33	33	33	22	33	33	33	33
30TWM42	41.7308	-2.519	32	33	33	23	22	33	33	22	33	33	33	33
30TXM52	41.7177	-1.1968	33	33	33	33	33	33	33	33	23	23	23	22
30TXM62	41.7157	-1.0766	33	33	33	33	33	33	33	33	23	22	23	22
30TVM11	41.6367	-4.0806	33	33	33	23	22	33	33	33	33	33	33	33
30TVM21	41.6377	-3.9605	33	33	32	22	32	32	22	32	33	32	32	33
30TVM31	41.6387	-3.8405	33	32	32	23	32	22	32	32	33	22	32	33
30TVM51	41.6402	-3.6004	33	23	23	32	32	22	32	32	33	33	33	33
30TVM91	41.6417	-3.1201	33	33	23	33	33	33	33	22	22	32	33	33
30TXM71	41.6236	-0.9593	33	33	33	33	33	33	33	33	23	32	22	33
30TVM30	41.5486	-3.8393	33	33	33	33	33	33	22	33	33	23	32	33
30TVM50	41.5501	-3.5995	33	33	32	22	33	22	32	33	33	33	33	33
30TVM60	41.5507	-3.4796	33	33	33	23	32	33	33	23	22	33	33	33
30TVM70	41.5511	-3.3597	33	33	33	23	33	33	33	23	22	33	33	33
30TVM80	41.5514	-3.2398	33	33	33	33	33	33	33	22	32	33	33	33
30TVM90	41.5516	-3.1199	33	33	33	33	33	33	33	32	22	33	33	33
30TWM20	41.5514	-2.7602	33	33	33	23	22	33	33	33	33	33	33	33
30TVL89	41.4613	-3.2395	33	33	33	33	33	33	33	23	22	33	33	33

Sites from 151 to 204; 1=species detected; 2=species non detected; 3=site not surveyed



American mink (*Neovison vison*) detection history between 2000 and 2011

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TWP10	43.3528	-2.8766	33	33	33	33	33	31	33	22	32	33	32	33
30TVN99	43.2627	-3.1232	33	33	33	33	22	33	33	33	33	33	33	33
30TWN19	43.2627	-2.8768	33	33	33	33	13	31	33	32	22	33	32	33
30TWN49	43.2617	-2.5072	33	33	33	33	11	33	33	33	32	33	32	32
30TWN69	43.2604	-2.2608	33	13	23	33	23	22	23	33	33	33	33	33
30TXN28	43.1632	-1.5239	22	33	33	33	33	33	33	33	33	33	33	33
30TVN77	43.0821	-3.3686	21	33	23	33	23	33	33	33	33	33	33	33
30TVN97	43.0826	-3.1229	33	33	23	22	23	23	33	22	11	11	33	33
30TWN07	43.0827	-3	33	32	33	33	22	33	33	13	11	21	33	33
30TVN76	42.9921	-3.368	33	33	33	33	33	33	33	33	11	33	33	33
30TWN06	42.9927	-3	33	32	22	32	23	33	33	32	33	11	33	33
30TWN16	42.9926	-2.8773	33	33	33	33	33	33	33	33	11	11	33	33
30TWN26	42.9924	-2.7547	33	33	31	33	33	22	33	33	33	22	33	33
30TWN36	42.9921	-2.632	33	33	33	33	33	22	33	33	33	22	33	33
30TWN56	42.991	-2.3867	23	23	22	32	32	33	33	33	33	33	33	33
30TWN96	42.9873	-1.8961	23	33	33	33	22	33	33	33	33	33	33	33
30TWN05	42.9026	-3	33	32	33	31	11	12	22	33	32	12	33	33
30TWN15	42.9025	-2.8775	33	31	13	31	22	12	21	33	32	22	33	31
30TWN25	42.9023	-2.755	32	13	11	31	21	13	33	33	32	23	23	33
30TWN35	42.902	-2.6325	31	13	11	11	23	12	33	33	32	32	13	31
30TWN45	42.9016	-2.51	33	13	21	11	21	12	32	32	32	32	13	31
30TWN65	42.9003	-2.2651	23	33	22	33	33	33	33	33	33	33	33	33
30TXN15	42.8947	-1.6528	33	32	23	33	33	33	11	11	33	33	33	33
30TXN25	42.8932	-1.5303	33	32	33	33	22	33	33	33	33	33	33	33
30TVN04	42.806	-4.223	33	33	33	33	33	33	33	33	33	33	11	21
30TVN14	42.8073	-4.1007	33	33	33	33	33	33	33	33	33	33	31	11
30TVN24	42.8084	-3.9785	33	33	33	33	33	33	33	33	33	33	21	22
30TVN64	42.8115	-3.4893	22	32	23	33	22	33	33	33	33	33	33	33
30TWN04	42.8126	-3	33	33	33	13	22	32	33	33	32	33	33	31
30TWN14	42.8125	-2.8777	32	23	11	21	21	11	21	23	32	32	23	23
30TWN24	42.8123	-2.7554	11	12	11	11	11	11	21	21	22	22	11	33
30TWN34	42.812	-2.6331	22	22	11	11	12	12	11	12	32	12	11	31
30TWN44	42.8115	-2.5107	23	33	13	11	32	12	22	22	33	33	31	11
30TWN54	42.8109	-2.3884	33	33	33	33	33	22	33	33	22	33	32	33
30TWN64	42.8102	-2.2661	21	33	33	33	33	33	33	33	33	33	33	33
30TVN13	42.7172	-4.0991	33	33	33	33	33	33	33	33	33	33	22	22
30TVN33	42.7193	-3.8549	32	33	32	33	33	11	31	11	21	32	33	33
30TVN63	42.7215	-3.4885	23	33	22	33	22	33	33	33	33	33	33	33
30TVN73	42.7219	-3.3664	22	33	23	33	23	33	33	33	33	33	33	33
30TVN93	42.7224	-3.1221	33	32	22	33	23	33	33	33	32	33	33	33
30TWN03	42.7225	-3	33	11	33	12	22	23	13	32	32	33	33	33
30TWN13	42.7224	-2.8779	33	21	31	21	22	22	33	33	22	13	32	32
30TWN23	42.7222	-2.7557	23	23	33	23	32	23	22	33	22	33	33	33
30TWN33	42.7219	-2.6336	33	33	22	33	33	33	33	33	33	33	33	33
30TXN23	42.7131	-1.5346	33	32	33	33	22	33	33	33	33	33	33	33
30TVN22	42.6283	-3.9756	33	33	33	33	33	13	21	33	13	22	31	33
30TVN32	42.6293	-3.8537	33	33	33	33	33	33	33	33	21	33	31	33
30TVN42	42.6301	-3.7317	33	33	33	33	33	33	33	33	22	33	33	33

Sites from 1 to 50; 1=species detected; 2=species non detected; 3=site not surveyed

American mink (*Neovison vison*) detection history between 2000 and 2011

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVN52	42.6308	-3.6098	33	33	33	33	33	33	33	33	12	33	33	33
30TVN62	42.6314	-3.4878	32	33	22	33	22	33	32	33	33	32	33	33
30TVN92	42.6324	-3.122	33	33	33	33	33	33	33	33	22	33	33	33
30TWN02	42.6324	-3	32	33	11	11	22	12	22	13	12	22	22	33
30TWN12	42.6324	-2.878	32	23	21	22	23	22	32	33	22	33	23	23
30TWN22	42.6322	-2.7561	22	23	22	23	33	32	22	33	22	33	33	33
30TWN32	42.6319	-2.6341	23	33	22	33	13	22	32	33	33	33	33	33
30TWN42	42.6314	-2.5122	33	33	22	33	23	23	33	32	32	23	33	33
30TWN52	42.6308	-2.3902	32	33	22	33	23	33	33	33	32	23	33	23
30TWN72	42.6293	-2.1463	22	33	33	33	33	33	33	33	33	33	33	33
30TWN92	42.6272	-1.9024	33	32	33	22	33	33	33	33	33	33	33	33
30TXN62	42.6158	-1.0492	33	33	22	23	33	22	33	22	22	23	23	33
30TVN31	42.5392	-3.8525	33	33	33	33	33	31	21	31	13	31	33	33
30TVN61	42.5414	-3.4871	33	33	33	33	33	33	33	33	33	22	33	33
30TWN01	42.5424	-3	33	33	22	22	23	33	33	32	33	33	23	23
30TWN11	42.5423	-2.8782	33	33	12	12	22	23	23	13	13	22	13	22
30TWN21	42.5421	-2.7564	33	33	22	33	33	23	22	33	23	13	33	23
30TXN41	42.5297	-1.2953	33	33	33	23	33	22	33	32	22	33	23	33
30TXN51	42.5278	-1.1736	33	33	33	33	33	33	33	33	22	23	23	33
30TXN61	42.5258	-1.052	33	33	22	33	33	33	33	33	22	23	23	33
30TXN71	42.5237	-0.9303	33	33	22	33	33	33	33	33	22	23	23	33
30TVN30	42.4492	-3.8512	33	31	33	31	33	11	31	31	11	31	31	33
30TVN50	42.4507	-3.608	33	33	33	33	33	33	33	33	33	11	33	33
30TVN70	42.4518	-3.3648	33	32	22	23	33	33	32	33	33	33	33	33
30TVN80	42.4521	-3.2432	33	23	23	33	22	33	33	33	33	33	33	33
30TVN90	42.4523	-3.1216	33	32	23	32	22	33	33	32	31	33	13	23
30TWN20	42.4521	-2.7568	32	23	22	22	12	23	22	23	23	13	33	12
30TWN30	42.4518	-2.6352	32	33	22	22	23	23	33	13	33	32	33	22
30TWN40	42.4513	-2.5136	32	32	32	23	22	23	33	23	23	33	32	23
30TWN50	42.4507	-2.392	32	33	33	33	22	33	33	22	33	33	23	23
30TWN90	42.4471	-1.9056	33	32	33	33	22	33	23	22	22	22	33	33
30TXN50	42.4378	-1.1763	33	33	33	23	33	22	33	32	22	23	23	33
30TVM09	42.3558	-4.2143	33	33	33	33	32	33	13	31	13	33	31	11
30TVM29	42.3582	-3.9714	33	33	33	33	33	13	13	33	21	11	31	33
30TVM39	42.3591	-3.85	33	33	23	31	11	31	21	33	11	31	31	33
30TVM49	42.36	-3.7286	33	33	13	31	33	13	33	33	31	11	33	33
30TVM59	42.3607	-3.6072	33	33	33	33	32	33	33	33	33	11	31	33
30TVM69	42.3612	-3.4857	33	33	33	33	33	31	33	33	33	21	33	33
30TVM89	42.362	-3.2429	33	33	32	33	22	33	33	33	33	33	33	13
30TVM99	42.3622	-3.1214	33	33	33	33	33	33	33	33	11	33	33	33
30TWM09	42.3623	-3	33	33	33	33	33	33	33	31	32	32	13	11
30TWM29	42.362	-2.7571	32	13	22	22	22	33	22	23	23	22	23	23
30TWM49	42.3612	-2.5143	22	23	32	32	32	33	33	23	33	33	33	23
30TWM59	42.3607	-2.3928	33	33	22	32	32	33	33	22	33	33	33	23
30TWM69	42.36	-2.2714	32	33	32	33	22	23	33	32	33	33	33	23
30TWM99	42.3571	-1.9072	33	32	33	33	22	33	13	22	22	12	33	33
30TXM09	42.3558	-1.7857	33	33	33	33	22	33	23	33	32	33	33	33
30TXM19	42.3545	-1.6644	33	33	33	33	22	22	23	22	33	33	33	33
30TXM29	42.353	-1.543	33	32	33	33	22	33	23	22	33	33	33	33
30TXM39	42.3514	-1.4216	33	33	33	23	33	33	33	22	22	23	23	33

Sites from 51 to 100; 1=species detected; 2=species non detected; 3=site not surveyed

American mink (*Neovison vison*) detection history between 2000 and 2011

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVM08	42.2658	-4.2125	33	33	33	23	31	33	11	31	11	31	33	33
30TVM28	42.2681	-3.9701	33	33	11	31	21	11	21	33	31	11	31	33
30TVM38	42.2691	-3.8488	33	13	11	11	11	31	11	11	11	11	31	33
30TVM48	42.2699	-3.7276	33	31	33	11	12	11	12	31	11	11	31	33
30TVM58	42.2706	-3.6063	33	31	33	22	12	12	21	31	21	11	31	33
30TVM68	42.2712	-3.4851	23	33	12	21	21	22	32	31	31	31	31	33
30TVM98	42.2721	-3.1213	33	33	23	33	31	11	33	31	31	32	33	21
30TWM08	42.2722	-3	33	33	33	13	13	11	33	31	31	31	33	31
30TWM18	42.2721	-2.8787	33	33	33	12	13	33	11	33	21	31	33	11
30TWM38	42.2716	-2.6362	33	13	32	33	22	33	33	23	33	33	33	13
30TWM88	42.2681	-2.0299	33	32	21	32	22	33	13	32	32	33	33	23
30TWM98	42.267	-1.9087	32	31	23	33	22	22	13	22	22	12	33	33
30TXM08	42.2658	-1.7875	32	33	33	33	22	22	23	22	23	32	33	33
30TXM18	42.2645	-1.6663	33	32	33	33	33	22	33	22	33	33	33	33
30TXM38	42.2614	-1.4238	33	33	33	33	23	33	33	22	22	23	23	33
30TVM07	42.1758	-4.2108	33	33	33	23	33	13	13	33	33	11	33	33
30TVM17	42.177	-4.0897	33	33	11	11	21	13	13	33	31	33	33	33
30TVM27	42.1781	-3.9687	33	33	31	31	21	21	33	33	31	31	31	33
30TVM37	42.179	-3.8476	31	33	33	31	13	33	13	31	31	33	11	31
30TVM47	42.1798	-3.7265	33	33	33	11	11	31	33	31	33	33	31	11
30TVM57	42.1805	-3.6054	33	33	33	13	11	11	21	31	31	21	31	33
30TVM67	42.1811	-3.4844	33	33	33	33	31	13	33	33	33	31	33	11
30TVM87	42.1819	-3.2422	33	33	33	21	13	11	31	13	33	13	33	11
30TVM97	42.1821	-3.1211	33	32	33	33	32	31	33	11	32	33	33	23
30TWM07	42.1821	-3	33	33	11	13	13	13	13	21	31	33	33	11
30TWM17	42.1821	-2.8789	32	33	33	32	23	33	33	22	32	13	33	12
30TWM37	42.1816	-2.6367	23	33	32	33	23	23	33	23	33	31	33	23
30TWM47	42.1811	-2.5156	22	33	32	33	12	33	33	23	33	33	33	23
30TWM67	42.1798	-2.2735	32	33	23	33	32	33	33	22	33	33	33	23
30TWM77	42.179	-2.1524	32	33	23	33	22	33	33	22	33	33	33	23
30TWM97	42.177	-1.9103	33	33	32	23	23	33	13	12	33	33	33	23
30TXM07	42.1758	-1.7892	32	32	22	32	22	33	13	23	33	33	33	23
30TXM57	42.1678	-1.184	33	33	33	33	33	33	33	33	22	23	33	33
30TVM16	42.0869	-4.0882	33	33	11	13	33	13	13	33	31	33	33	33
30TVM36	42.089	-3.8464	33	33	31	33	11	31	33	33	31	33	13	13
30TVM76	42.0915	-3.3628	33	33	31	33	13	31	11	31	31	31	33	13
30TVM86	42.0918	-3.2418	33	33	13	21	12	33	21	11	33	13	33	13
30TVM96	42.092	-3.1209	33	33	33	23	11	11	22	11	33	33	33	12
30TWM06	42.0921	-3	31	23	21	33	33	33	22	12	32	31	33	22
30TWM16	42.092	-2.8791	33	31	33	33	13	33	33	33	32	33	33	12
30TWM26	42.0918	-2.7582	33	32	32	23	22	31	23	23	33	33	33	23
30TWM56	42.0905	-2.3954	33	32	33	23	23	33	23	22	33	33	33	23
30TWM66	42.0898	-2.2745	33	33	33	32	33	33	33	22	33	33	33	33
30TXM06	42.0857	-1.7909	32	33	33	32	23	33	33	33	33	33	22	33
30TXM16	42.0844	-1.67	22	33	33	32	23	33	33	33	33	33	33	33
30TXM56	42.0778	-1.1866	33	33	33	33	33	33	33	22	33	33	23	33
30TVM15	41.9969	-4.0867	33	33	33	13	11	11	13	13	33	13	33	33
30TVM25	41.998	-3.9659	33	33	33	12	31	11	11	31	11	31	33	33
30TVM35	41.9989	-3.8452	33	33	31	31	21	11	31	31	31	31	31	11
30TVM45	41.9997	-3.7245	31	33	11	31	21	31	31	11	33	13	33	33
30TVM55	42.0004	-3.6037	31	33	33	13	31	31	11	13	33	11	31	31

Sites from 101 to 150; 1=species detected; 2=species non detected; 3=site not surveyed

American mink (*Neovison vison*) detection history between 2000 and 2011

Site	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
30TVM65	42.001	-3.483	33	33	33	12	11	11	33	31	31	11	31	13
30TVM75	42.0014	-3.3622	31	33	13	21	21	11	21	11	31	11	31	11
30TVM85	42.0018	-3.2415	33	13	33	11	33	33	31	33	33	33	33	31
30TVM95	42.002	-3.1208	33	33	33	23	33	13	11	32	33	33	11	33
30TWM05	42.002	-3	23	13	32	23	21	31	11	11	33	33	33	31
30TWM25	42.0018	-2.7585	22	33	33	33	33	33	33	33	33	33	33	33
30TWM45	42.001	-2.517	33	32	33	23	22	33	23	22	33	33	33	33
30TWM65	41.9997	-2.2755	33	32	33	23	23	33	33	33	31	33	33	33
30TWM75	41.9989	-2.1548	33	33	33	33	33	33	23	22	33	33	33	33
30TWM85	41.998	-2.0341	33	32	23	33	32	33	33	23	33	33	33	22
30TVM34	41.9088	-3.844	33	33	33	33	21	13	33	31	33	33	33	33
30TVM44	41.9097	-3.7235	33	33	31	31	22	31	33	31	33	33	31	13
30TVM54	41.9104	-3.6029	33	33	33	33	33	22	33	31	33	33	33	33
30TVM64	41.9109	-3.4823	33	13	33	32	13	12	33	31	33	11	11	31
30TVM74	41.9114	-3.3617	33	33	33	33	32	22	33	31	11	33	33	11
30TVM84	41.9117	-3.2412	11	13	13	23	11	22	11	11	33	13	31	11
30TVM94	41.9119	-3.1206	33	33	33	22	32	21	33	23	33	13	31	13
30TWM04	41.9119	-3	33	33	33	33	33	33	13	13	33	33	33	11
30TWM14	41.9119	-2.8794	33	33	33	23	22	33	13	23	33	33	33	33
30TWM34	41.9114	-2.6383	32	33	33	23	22	33	23	23	33	33	33	33
30TWM44	41.9109	-2.5177	33	31	33	23	22	33	23	22	33	33	33	33
30TWM74	41.9088	-2.156	33	33	33	33	33	33	23	22	33	32	33	33
30TXM04	41.9056	-1.7943	33	33	33	33	33	33	33	22	23	23	23	33
30TXM34	41.9013	-1.4327	33	33	33	23	33	22	33	22	22	23	22	22
30TXM44	41.8995	-1.3122	33	33	33	23	33	22	33	33	23	23	23	22
30TVM13	41.8168	-4.0836	33	33	33	33	11	33	33	33	33	33	33	33
30TVM73	41.8213	-3.3612	33	33	33	31	33	11	13	33	13	33	13	13
30TVM83	41.8216	-3.2408	33	33	33	21	33	33	31	13	33	31	33	13
30TWM43	41.8209	-2.5184	32	33	33	33	33	33	33	22	33	33	33	33
30TWM63	41.8196	-2.2776	13	33	33	33	33	33	23	22	33	33	33	33
30TWM93	41.8168	-1.9164	33	32	33	33	33	33	23	22	33	33	33	33
30TXM33	41.8112	-1.4349	33	33	33	23	33	22	33	22	22	33	23	22
30TXM43	41.8095	-1.3146	33	33	33	23	33	22	33	33	22	33	33	33
30TVM12	41.7267	-4.0821	33	13	13	13	13	31	33	33	33	11	33	33
30TVM22	41.7278	-3.9619	33	13	11	13	33	33	33	33	33	13	33	31
30TVM72	41.7312	-3.3607	33	33	33	23	33	11	31	11	33	31	31	11
30TVM82	41.7316	-3.2405	33	33	33	33	33	11	33	33	33	33	33	33
30TWM32	41.7312	-2.6393	31	33	33	33	33	33	33	22	33	33	33	33
30TWM42	41.7308	-2.519	32	33	33	23	22	33	33	22	33	33	33	33
30TXM52	41.7177	-1.1968	33	33	33	33	33	33	33	33	23	23	23	22
30TXM62	41.7157	-1.0766	33	33	33	33	33	33	33	33	23	22	23	22
30TVM11	41.6367	-4.0806	33	33	33	13	22	33	33	33	33	33	33	33
30TVM21	41.6377	-3.9605	33	33	31	11	32	31	21	31	33	31	31	33
30TVM31	41.6387	-3.8405	33	31	31	13	32	11	31	31	33	11	31	33
30TVM51	41.6402	-3.6004	33	13	13	31	32	21	32	31	33	33	33	33
30TVM91	41.6417	-3.1201	33	33	13	33	33	33	33	11	22	31	33	33
30TXM71	41.6236	-0.9593	33	33	33	33	33	33	33	33	23	32	22	33
30TVM30	41.5486	-3.8393	33	33	33	33	33	33	22	33	33	13	31	33
30TVM50	41.5501	-3.5995	33	33	31	21	33	21	31	33	33	33	33	33
30TVM60	41.5507	-3.4796	33	33	33	13	31	33	33	13	11	33	33	33
30TVM70	41.5511	-3.3597	33	33	33	13	33	33	33	23	22	33	33	33
30TVM80	41.5514	-3.2398	33	33	33	33	33	33	33	22	32	33	33	33
30TVM90	41.5516	-3.1199	33	33	33	33	33	33	33	31	22	33	33	33
30TWM20	41.5514	-2.7602	33	33	33	23	22	33	33	33	33	33	33	33
30TVL89	41.4613	-3.2395	33	33	33	33	33	33	33	23	22	33	33	33

Sites from 151 to 204; 1=species detected; 2=species non detected; 3=site not surveyed