UNIVERSIDADE DE ÉVORA

ESCOLA DE CIÊNCIAS E TECNOLOGIA

DEPARTAMENTO DE BIOLOGIA

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INSTITUTO SUPERIOR DE AGRONOMIA

Modeling the factors limiting the distribution and abundance of the European rabbit (*Oryctolagus cuniculus*) in SE Portugal

Ana Marta Serronha

Orientação: Pedro Monterroso

Paulo Célio Alves

Mestrado em Gestão e Conservação de Recursos Naturais

Dissertação

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AGRADECIMENTOS

Em primeiro lugar quero agradecer ao meu orientador, Doutor Pedro Monterroso e ao meu co-orientador, Professor Doutor Paulo Célio Alves, por me terem recebido e orientado durante todo este percurso. Obrigado pela amizade, ensinamentos e apoio constante em todas as fases da realização da tese, e ainda pela exigência e pelo incentivo no seu término.

Agradeço ao Instituto da Conservação da Natureza e das Florestas pelo fornecimento de dados relativos à abundância de coelho-bravo.

Agradeço também à Direção-Geral de Agricultura e Desenvolvimento Rural, e em especial ao Dr. Nuno do Rosário pelo fornecimento da Carta de Solos para o Alentejo e Algarve.

Agradeço à Direcção-Geral dos Recursos Florestais, por me terem cedido as Cartas de Zonas de Caça para as regiões do Alentejo e Algarve.

Ao Neftalí Sillero que, apesar de o trabalho com ele desenvolvido não estar directamente representado na tese, teve um importante contributo nos ensinamentos e desenvolvimento do inicial do trabalho.

A todos os que permitiram a conclusão desta tese, com a sua indispensável ajuda e incentivo, em especial ao Luís Tinoco Faria, Miguel Salgado, Cátia Matos, Fátima Sanches, Sónia Ferreira e Sofia Vaz um muito e sincero obrigado!

Um obrigado muito especial à minha amiga, colega e companheira de secretária Helena Santos, que sem ela a última etapa de conclusão da tese não teria sido ultrapassada. Obrigada pelas correcções, incentivo e ânimo!

A todos os meus amigos, colegas e familiares que contribuíram indirectamente com incentivo e boa disposição um muito obrigada.

A minha irmã Lígia, por todo o apoio, compreensão desde o início desta etapa um muito obrigada.

Por fim agradeço aos meus pais, pelo incentivo e apoio incondicional não só na conclusão desta tese mas em todo o meu percurso académico, profissional e pessoal. Sem eles sem dúvida alguma que não teria alcançado esta meta.

Modelação dos factores que limitam a distribuição e abundância do Coelho-bravo (Oryctolagus cuniculus) no SE de Portugal

RESUMO

O Coelho-bravo (*Oryctolagus cuniculus*) é uma espécie com um papel-chave nos ecossistemas Ibéricos. A sua distribuição e abundância são influenciadas por um elevado números de factores, que conjuntamente com a sua plasticidade, tornam a gestão das suas populações uma tarefa complexa. Este estudo tem como objectivo identificar os factores que limitam a distribuição e abundância das populações de Coelho-bravo no SE de Portugal, uma região que é prioritária para a conservação do Lince-ibérico. Os dados de campo consistiram num Índice Quilométrico (latrinas) de Abundância (IQA), ao qual modelos univariados e multivariados de regressão de quantis foram ajustados, usando diversas variáveis. Os resultados obtidos revelaram que as populações de Coelho-bravo são limitadas por factores ecológicos, climáticos e de gestão, e que variam de acordo com as áreas em estudo. Este estudo fornece informação relevante para a recuperação da população de Coelho-bravo, contribuindo consequentemente para o sucesso das reintroduções do Lince-ibérico.

ABSTRACT

The European rabbit (*Oryctolagus cuniculus*) plays a key role in Iberian ecosystems. This species' distribution and abundance is affected by a combination of several factors, and its high plasticity makes population management a challenging task. The main goal of this study is to identify the factors limiting the distribution and abundance of European rabbit populations in SE Portugal, a priority region for the Iberian lynx conservation. Field data consisted of a Kilometric Index of (latrine) Abundance (KIA), to which univariate and multivariate quantile regression models were fitted, using a diversity of variables. The obtained results revealed that European rabbits populations are limited by ecological, climatic and management factors, which varied across sampling areas. This study provides highly relevant information for European rabbit population recovery, consequently contributing for the success of Iberian lynx reintroductions.

INDEX

LIST OF FIGURES

GENERAL INTRODUCTION AND STUDY AREA

SCIENTIFIC PAPER: Modeling the factors limiting the distribution and abundance of the European rabbit (*Oryctolagus cuniculus*) in SE Portugal

LIST OF TABLES

SCIENTIFIC PAPER: Modeling the factors limiting the distribution and abundance of the European rabbit (*Oryctolagus cuniculus*) in SE Portugal

GENERAL INTRODUCTION AND STUDY AREA

The European rabbit (*Oryctolagus cuniculus*) is a native species to the Iberian Peninsula in southwestern Europe (Monnerot et al. 1994, Ferrand and Branco 2007). In the Quaternary glaciations, this lagomorph was confined in two areas of the Iberian Peninsula, one in the northeast and other in the southwest, after which recolonized the entire Peninsula and Europe (Branco et al. 2000, Branco et al. 2002). Molecular evidences show that two subspecies, *Oryctolagus cuniculus cuniculus* and *Oryctolagus cuniculus algirus* occur in the northeast and in the southwest of the Iberian Peninsula, respectively (Branco et al. 2000, Ferrand and Branco 2007). Geographically, these two subspecies' distributions follow a northwest-southeast direction dividing the Iberian Peninsula, with a small contact area in the middle (Branco et al. 2000, Ferrand and Branco 2007). In the Middle Age the European rabbit was introduced in the north of Europe, Africa, Australia, New Zealand, South America and in several islands, for food and hunting purposes (Ferrand and Branco 2007, Lees and Bell 2008). However, where the species was initially introduced, its' high adaptability, reproduction rate, and the absence of predators turned the European rabbit into a pest, capable of causing damages in agriculture and natural vegetation, and endangering native plants and animals (Cooke 2008, Lees and Bell 2008).

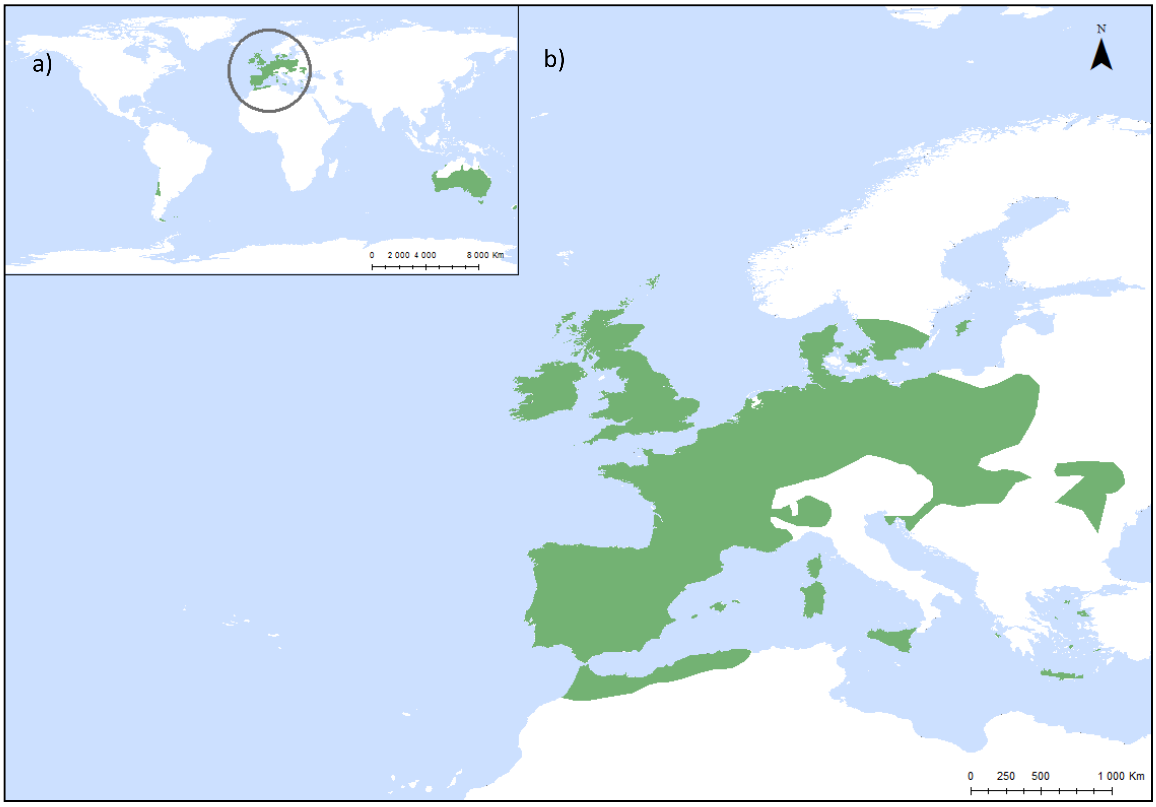

Figure 1 – a) World European rabbit distribution. b) European and North African distribution of the European rabbit. The spatial data for European rabbit distribution was obtained from IUCN 2010.

The European rabbit is considered as an ecosystem engineer in the Mediterranean ecosystem (Delibes et al. 2007, Delibes et al. 2008a). It plays an important role affecting flora diversity and landscape structure through grazing and seed dispersal, and also soil fertilization through latrines (Willot et al. 2000, Dellafiore et al. 2006, Dellafiore et al. 2010). The European rabbit also affects animal biodiversity providing refuges for other species that use their warrens (e.g. Galante and Cartagena 1999, Bravo et al. 2009, Grillet et al. 2010). Moreover, one of its main roles in the Mediterranean ecosystems is as a staple prey in vertebrate predator-prey dynamics. The species represents a large part of the diet of several predators (Jaksic and Soriguer 1981, Delibes-Mateos et al 2007), including two of the most endangered species in the Iberian Peninsula, the Imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*), whose survival depend on abundant and stable European rabbit populations (Ferrer and Negro, 2004). In addition to its high ecological importance, the European rabbit has a high economic value being one of the most appreciated small game species in Portugal and Spain (Angulo and Villafuerte 2003, Alves and Ferreira 2004, Delibes-Mateos et al. 2014).

The European rabbit's populations have been declining since the 20th century. The decline started in the first half of the century apparently as a result of habitat loss and fragmentation (Delibes-Mateos et al. 2010), which was a consequence of the agriculture intensification and of the abandonment of traditional agricultural practices (Myers et al. 2000). Furthermore, the arrival of the Myxomatosis disease during the 1950s, and of the Rabbit Hemorrhagic Disease in the 1980s (RHD) accentuated the declined (Ratcliffe et al. 1952, Villafuerte et al. 1995, Calvete et al. 2002, Delibes-Mateos et al. 2008). Myxomatosis is an endemic disease to the South American rabbits (*Syvilagus sp.*) and was introduced in France in 1952 as a pest control for the European rabbits. The disease spread away quickly and was detected for the first time in the Iberian Peninsula in 1953 (reviewed in Kerr 2012). Although information about the initial outbreak of Myxomatosis in the Iberia Peninsula is scarce, the disease probably had the same catastrophic effect as in England and France, killing about 99% of the European rabbit population (Fenner and Fantini 1999). The RHD was detected for the first time in the People's Republic of China in 1984 and in the Iberian Peninsula in 1989. Initial mortality rates were estimated in 55–75% of the European rabbit population (Villafuerte et al. 1994, Villafuerte et al. 1995). After the initial outbreaks, both Myxomatosis and RHD mortality rates started to decline as a consequence of higher physiological disease resistance of the European rabbit. However, both diseases continue to play an important role in the European rabbit's mortality (Calvete et al. 2002). As a result of this decline, the European rabbit was classified as Near-Threatened and Vulnerable in the Portuguese and Spanish Red List of Vertebrates, respectively (Cabral et al. 2005, Villafuerte and Delibes-Mateos 2007). The species was also classified with the Near-Threatened status at the international level (Red List of the IUCN; Smith and Boyer 2008).

A new variant of the Rabbit Hemorrhagic Disease Virus (RHDV2) was recently detected in Europe exhibiting high mortality rates (Marchandeau 2014, personal communication). This new variant was detected for the first time in April 2010 in France, May 2011 in Spain and June 2011 in Italy (Le Gall-Reculé et al. 2013). In November 2012 the new variant of the RHDV was detected in Portugal (Alves 2014, personal communication). This variant differs from the traditional strain because it affects the young rabbit population, causing mortality in kits <30 days of age (Dalton et al. 2012) and in juveniles <2 months of age (Abrantes et al. 2013). Therefore, the recruitment of new individuals to the population becomes highly constrained, compromising the persistence of several European rabbit populations. The new variant of RHDV spread rapidly and with stronger outbreaks than the classic RHDV (Abrantes et al. 2013, Le Gall-Reculé et al. 2013). Le Gall-Reculé et al. (2013) suggested that this new variant is a new member of *Lagovirus*, producing disease with different duration, mortality rates, and higher occurrence of subacute/chronic forms, and recommended the RHDV2 name. As a consequence, the Iberian European rabbit population has been declining, causing high impacts on the ecological and socio-economic levels (Garrote 2014, personal communication).

Native to the Iberian Peninsula, the Iberian lynx is considered the most endangered feline on earth, and has suffered a steep decline in the second half of the 20th century (Simón et al. 2012). This decline is a consequence of intensive human persecutions, habitat loss, and decrease in European rabbit populations (Simón et al. 2012). Presently, the Iberian lynx is only found in two isolated native populations in southern Spain. Therefore, an important conservation program has been developed to preserve its populations, but also the Iberian lynx historical areas of distribution. In this context, the LIFE+ Iberlince (LIFE10 NAT/ES/000570/IBERLINCE) program for the recovery of the Iberian lynx's historical distribution range was approved for Portugal and Spain in 2011. The present program aims to re-establish extinct populations through habitat and prey management, followed by reintroduction in areas with high priority level for Iberian lynx conservation. Therefore, promoting the recovery of rabbit populations is of utmost importance for the successful restocking of the Iberian lynx populations.

In this context, the main goal of this study is to assess which factors are limiting the distribution and abundance of European rabbit population in SE Portugal, an important area for Iberian lynx reintroduction by:

a) Identifying the factors limiting the abundance and distribution of European rabbits in a high-priority region for Iberian lynx conservation in Portugal;

b) Evaluating the effectiveness of quantile regression techniques in a wildlife conservation scenario, when compared to traditional regression methods;

c) Predicting the spatial distribution of the most suitable areas for European rabbits in the SE of Portugal, by projecting the developed models;

d) Proposing specific management guidelines for the conservation of the European rabbit.

The study area is encompassed in the Alentejo and Algarve regions, which are included in the historical range of the Iberian lynx. It comprises five protected natural areas with high conservation level for the Iberian lynx (LIFE10 NAT/ES/000570/IBERLINCE, ICNF 2006a, ICNF 2006b): the Guadiana Valley Natural Park (GVNP), the Natura 2000 Network Site Moura-Barrancos (PTCON0053), the Natura 2000 Network Site Guadiana (PTCON0036), the Natura 2000 Network Site Caldeirão (PTCON0057) and the Natura 2000 Network Site Monchique (PTCON0037) (figure 2). Due to overlapping, and similarity, the GVNP and Natura 2000 Network Site Guadiana were merged in the present study, for analyses purposes.

The study area comprises a total of 773,600ha and is included in the biogeographic Mediterranean region in the Mariânico-Monchiquense sector (Costa et al. 1998). The climate is Mediterranean with annual mean temperature between 17.5° and 20°C, and with a mean annual precipitation between 400 and 1000 mm (ICA 2011). The soils are dominated by lithosols over the entire study area. The topography is heterogeneous with altitudes ranging from 2 to 706m a.s.l. Lower altitudes are mostly represented in northwest, and higher altitudes in southwest of the study area. At flat areas the landscape is mainly characterized by the agroforestry system commonly known as "montado", an open tree layer with Cork oak (*Quercus suber*) and/or Holm oak (*Q. rotundifolia*) (Joffre et al. 1999), included in the Annex 1 Habitat type 6310 (Habitat Directive 92/43/EEC). Patches of cereal croplands, permanent crops (e.g. olive groves *Olea europaea*, vineyards *Vitus vinifera*) and forested mosaics of Stone pine (*Pinus pinea;* mainly directed to forestry) are also represented. Natural vegetation patches are mostly present in steep slopes and ridges, represented by Mediterranean scrublands, and in valleys associated with watercourses represented by riparian vegetation. In the southwestern region, the landscape is mainly occupied by forestry mosaics of Maritime pine (*Pinus pinaster*) and Eucalyptus (*Eucalyptus globulus*).

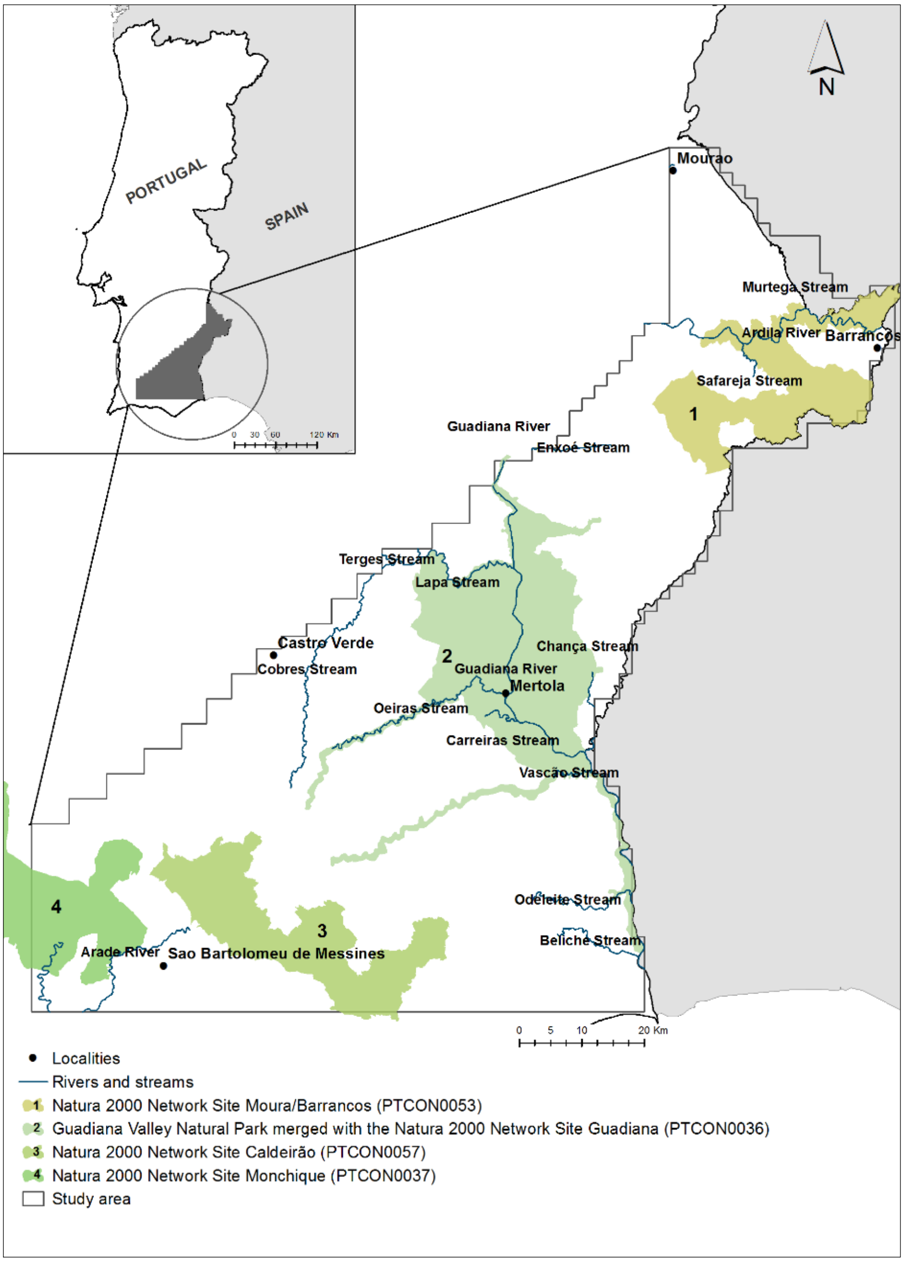

Figure 2 – Map of the study area with the Natural Protected Areas with importance for Iberian lynx reintroduction.

The study area is also included in the Mediterranean basin biodiversity hotspot (Myers et al. 2000, Pascual et al. 2013), and includes the most important ecological corridor of southern Portugal, the Guadiana River basin, harboring more than 220 species of breeding vertebrates (WWF international). The hunting activity has an important socio-economic role in the study area, where hunting estates are present in 88% of the study area. The Red-partridge (*Alectoris rufa*) and the European rabbit are the most appreciate small game species in the area.

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Modeling the factors limiting the distribution and abundance of the European rabbit (*Oryctolagus cuniculus*) in SE Portugal

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ABSTRACT: The European rabbit (*Oryctolagus cuniculus*) plays a key role in Iberian ecosystems. This species' distribution and abundance is affected by a combination of several factors, and its high plasticity makes population management a challenging task. The main goal of this study is to identify the factors limiting the distribution and abundance of European rabbit populations in SE Portugal, a priority region for the Iberian lynx conservation (*Lynx pardinus*). Field data consisted of a Kilometric Index of (latrine) Abundance (KIA), to which univariate and multivariate quantile regression models were fitted, using a diversity of variables. The obtained results revealed that rabbits populations are limited by ecological, climatic and management factors, varying across sampling areas. This study provides highly relevant information for European rabbit population recovery, consequently contributing for the success of Iberian lynx reintroductions.

KEYWORDS: *Oryctolagus cuniculus*, quantile regression model, limiting factors, *Lynx pardinus.*

INTRODUCTION

The European rabbit (*Oryctolagus cuniculus*) is a native species to the Iberian Peninsula (Monnerot et al. 1994, Ferrand and Branco 2007) and plays a key role in the Mediterranean ecosystem (Delibes-Mateos et al. 2007, Delibes-Mateos et al. 2008a). It is responsible for flora diversity and landscape structure through grazing and seed dispersal (e.g. Dellafiore et al. 2006, Dellafiore et al. 2010). Moreover, European rabbits affect animal biodiversity providing nest sites and shelter for other species that use their warrens (e.g. Bravo et al. 2009, Grillet et al. 2010). The European rabbit is also considered a key species in the vertebrate predator-prey dynamics, constituting a large part of the diet of a diversity of predators (Jaksic and Soriguer 1981, Delibes-Mateos et al. 2007), including the two most endangered species, the Imperial eagle (*Aquila adalberti*) and Iberian lynx (*Lynx pardinus*), whose survival depend on abundant and stable populations of this species (Ferrer and Negro 2004).

Since the last century, the European rabbit populations have declined significantly across the Iberian Peninsula. Two major factors have been responsible for this steep reduction, the habitat loss and fragmentation (Delibes-Mateos et al. 2010) and the diseases Myxomatosis and Rabbit Haemorrhagic Disease (RHD) (Ratcliffe et al. 1952, Villafuerte et al. 1995). As a result of this decline, the European rabbit was classified as Near-Threatened and Vulnerable in the Portuguese and Spanish Red List of Vertebrates, respectively (Cabral et al. 2005, Villafuerte and Delibes-Mateos 2007). The species was also classified with the Near-Threatened status at the international level (Red List of the IUCN; Smith and Boyer 2008).

Currently, another viral disease was identified in Europe with high impacts on European rabbit populations. The disease is a new variant of Rabbit Hemorrhagic Disease Virus (RHDV) and was detected for the first time in 2012 in Spain and in 2013 in Portugal. This new variant of RHDV, differs from the traditional strain since it affects the young rabbit population, causing mortality in kits <30 days of age (Dalton et al. 2012) and in juveniles <2 months of age (Abrantes et al. 2013), which compromises the recruitment of new individuals to the population. The new variant of RHDV also spreads more rapidly and produces stronger outbreaks than the classic RHDV (Abrantes et al. 2013, Le Gall-Reculé et al. 2013).

Several factors other than epizootic outbreaks contribute to the distribution and abundance of the European rabbit populations. In general, European rabbit distribution and abundance is affected by a combination of factors such as soil features, climate, landscape vegetation patterns, topography, hunting, and predation pressure (Trout et al. 2000, Lombardi et al. 2003, Monzón et al. 2004). However, the high plasticity of European rabbits and the diversity of factors that affect it make the management of their populations a challenging task.

Several authors have developed ecological models of European rabbits' distribution in introduced (e.g. Trout et al. 2000) and native areas (e.g. Virgos et al. 2003, Calvete et al. 2004), attempting to identify the environmental factors that shape the observed spatial patterns. However, such models revealed limited performance due to the limited explained variability (e.g. Virgos et al. 2003, Calvete et al. 2004), or small spatial extent, preventing their transferability (e.g. Moreno and Villafuerte 1995, Fa et al. 1999, Martins et al. 2003, Monzón et al. 2004, Beja et al. 2007).

An alternative to the most commonly used statistical methods in ecological modeling (e.g. PCA, linear regression, general linear models) is the quantile regression (Koenker and Basset 1978), which provides a different view of the factors influencing distribution and abundance (Cade and Noon 2003, Austin 2007). Quantile regression has been described as an useful tool in several research fields such as medicine, financial and economics, as well as in environmental modeling (reviewed in Yu et al. 2005). However, in spite of being suitable in providing a more complete view of the data distribution and detecting missing relationships between the response and explanatory variables (Cade et al.

1999, Cade and Noon 2003), this statistical approach is still scarcely applied in ecological research (e.g. Cade and Guo 2000, Haire et al. 2000, McClain and Rex 2001, Dunham et al. 2002, Eastwood et al. 2001, 2003, Schröder et al. 2005, Vaz et al. 2008, Fleeger et al. 2010). Conventional statistic methods only focus on the mean (central tendency) response of the relationship between the dependent and explanatory variables. Therefore, they may underestimate the effect of the explanatory variables and only provide a general direction of the response (Thomson et al. 1996, Scharf et al. 1998, Cade et al. 1999). In contrast, quantile regression is a method used to model the relation between the dependent variable and the explanatory variables along the entire dataset, where a trendline is adjusted for each τ quantile [0, 1] of the data distribution (Cade et al. 1999). This method is useful for finding relationships that other regression methods, which focus in the center of the data distribution, cannot detect (Koenker and Bassett 1978, Cade and Noon 2003). Additional advantages of quantile regression models include the fact that variance homogeneity of the error distribution is not needed and it is robust to outliers (Cade et al. 1999, Cade and Noon 2003). Since quantile regression is useful to assess data distributions with heterogeneous variance, this method can be used to account for possible interactions between measured and unmeasured factors (Cade and Noon 2003). This is particularly valuable in the case of European rabbits because their traits are often affected by unmeasured factors (Trout et al. 2000). For regressions for higher quantiles (50^{th} to 99^{th}), it is possible to model the upper limit of the data distribution, and understand the maximum biological response of the dependent variable. With this information it is possible to detect which variables are limiting the distribution of the data range (Cade et al 1999, Cade and Noon 2003). The limiting factor cannot be assessed by conventional statistic methods with focus on central tendency and, therefore, the regression quantile is a proper method to address such ecological questions (Thomson et al. 1996). Moreover, upper quantile regression models are able to predict species' spatial patterns (Eastwood et al. 2001, Vaz et al. 2008), providing a representation of the potential suitable or unsuitable areas for the target species.

In addition to its high ecological importance as a key species in the Mediterranean ecosystems, the European rabbit has also a high socioeconomic value being one of the most appreciate small game species in Iberian Peninsula (Angulo and Villafuerte 2003, Alves and Ferreira 2004, Delibes-Mateos et al. 2014). Due to its steep decline in the last decades, population management of the European rabbit abundance and distribution has increased, serving both conservation and socioeconomic roles. With this purpose, understanding which variables are limiting the distribution and abundance of European rabbit populations in the Iberian Peninsula is an important goal.

Considered as a super-specialist predator, Iberian lynx survival depends on abundant and stable European rabbit populations. This prey abundance should be at least 4 rabbits/ha in during breeding season (spring) and 1 rabbit/ha in the autumn to support an Iberian lynx population (Palomares

2001). A conservation program to recover the Iberian lynx natural populations is currently ongoing in the Iberian Peninsula, LIFE+ Iberlince (*Recovering the historic distribution range of the Iberian lynx (Lynx pardinus) in Spain and Portugal* - LIFE10 NAT/ES/000570/IBERLINCE). That program aims to recover extinct populations through habitat and prey management followed by reintroduction in areas with high priority level for Iberian lynx conservation. In southeast Portugal, an extent target area includes four areas with high-priority level. Each of these high-priority areas include several hunting estates where European rabbit is one of the most appreciate small game species. In order to avoid conflict between hunters and conservationists, increasing European rabbit abundance is of utmost importance (Delibes-Mateos et al. 2014). Therefore, promoting the recovery of rabbit populations is a major concern for successful restocking of the Iberian lynx. The first step is to understand which factors are limiting the European rabbit distribution and abundance, and identify the areas with highest constrains to population recovery in order to implement locally adjusted management actions. In this context, the main goal of this study is to assess which factors are limiting the distribution and abundance of the European rabbit populations in SE Portugal, an important area for the Iberian lynx reintroduction, trough: a) identifying the factors limiting the abundance and distribution of European rabbits in a high-priority region for Iberian lynx conservation in Portugal; b) evaluating the effectiveness of quantile regression techniques in a wildlife conservation scenario, when compared to traditional regression methods; c) predicting the spatial distribution of the most suitable areas for European rabbits in the SE of Portugal, by projecting the developed models; d) proposing specific management guidelines for the conservation of the European rabbit.

METHODS

Study area

The study was carried out in southeast Portugal (38°25'16''N, 7°15'31''W to 37°11'22''N, 8°31'36''W; figure 1) in an area of 773,600ha. The area is included in the Mediterranean biogeographic region in the Mariânico-Monchiquense sector (Costa et al. 1998), with mean annual temperature between 17.5° and 20°C, and mean annual precipitation between 400 and 1000mm (ICA 2011).

The soils are dominated by lithosol soils over the entire study area. The topography is heterogeneous with altitudes ranging from 2m to 706m a.s.l. Lower altitudes are mostly represented in northwest, and higher altitudes in southwest of the study area. At flat areas the landscape is mainly characterized by the agroforestry system commonly known as “montado”, an open tree layer with Cork oak (*Quercus suber*) and/or Holm oak (*Q. rotundifolia*) (Joffre et al. 1999), included in the Annex 1 Habitat type 6310 (Habitat Directive 92/43/EEC). Patches of cereal croplands, permanent crops (e.g. olive groves *Olea europaea*, vineyards *Vitus vinifera*) and forested mosaics of Stone pine (*Pinus pinea;* mainly directed to forestry) are also represented.

Natural vegetation patches are mostly present in steep slopes and ridges, represented by Mediterranean scrublands, and in valleys associated with water courses represented by riparian vegetation. At the southwestern region, the landscape is mainly occupied by forestry mosaics of Maritime pine (*Pinus pinaster*) and Eucalyptus (*Eucalyptus globulus*).

The study area is included in the Mediterranean basin biodiversity hotspot (Myers et al. 2000, Pascual et al. 2013), where the European rabbit is an important prey for more than 30 species (Jaksic & Soriguer 1981, Delibes-Mateos et al. 2007), including the endangered Imperial eagle (*Aquila adalberti*) and Iberian lynx (*Lynx pardinus*) (Ferrer and Negro 2004). Given the study area's strategic importance for wildlife conservation in the south of the Iberian Peninsula, particularly for the conservation of the Iberian lynx, it was included as a target region for the reintroduction program in the LIFE+ Iberlince (*Recovering the historic distribution range of the Iberian lynx (Lynx pardinus) in Spain and Portugal* - LIFE10 NAT/ES/000570/IBERLINCE). The study area includes five classified areas with high conservation level for this species (LIFE10 NAT/ES/000570/IBERLINCE, ICNF 2006a, ICNF 2006b): the Guadiana Valley Natural Park (GVNP), the Natura 2000 Network Site Moura/Barrancos (PTCON0053), the Natura 2000 Network Site Guadiana (PTCON0036), the Natura 2000 Network Site Caldeirão (PTCON0057) and the Natura 2000 Network Site Monchique (PTCON0037). Due to overlapping, and similarity, the GVNP and Natura 2000 Network Site Guadiana were merged in the present study, for analyses purposes.

Apart from its ecological importance, the European rabbit plays an important socio-economic role, since it is one of the most appreciated small game species in the Iberian Peninsula (Delibes-Mateos 2014) particularly in this study area, where hunting estates are present in 88% of the study area.

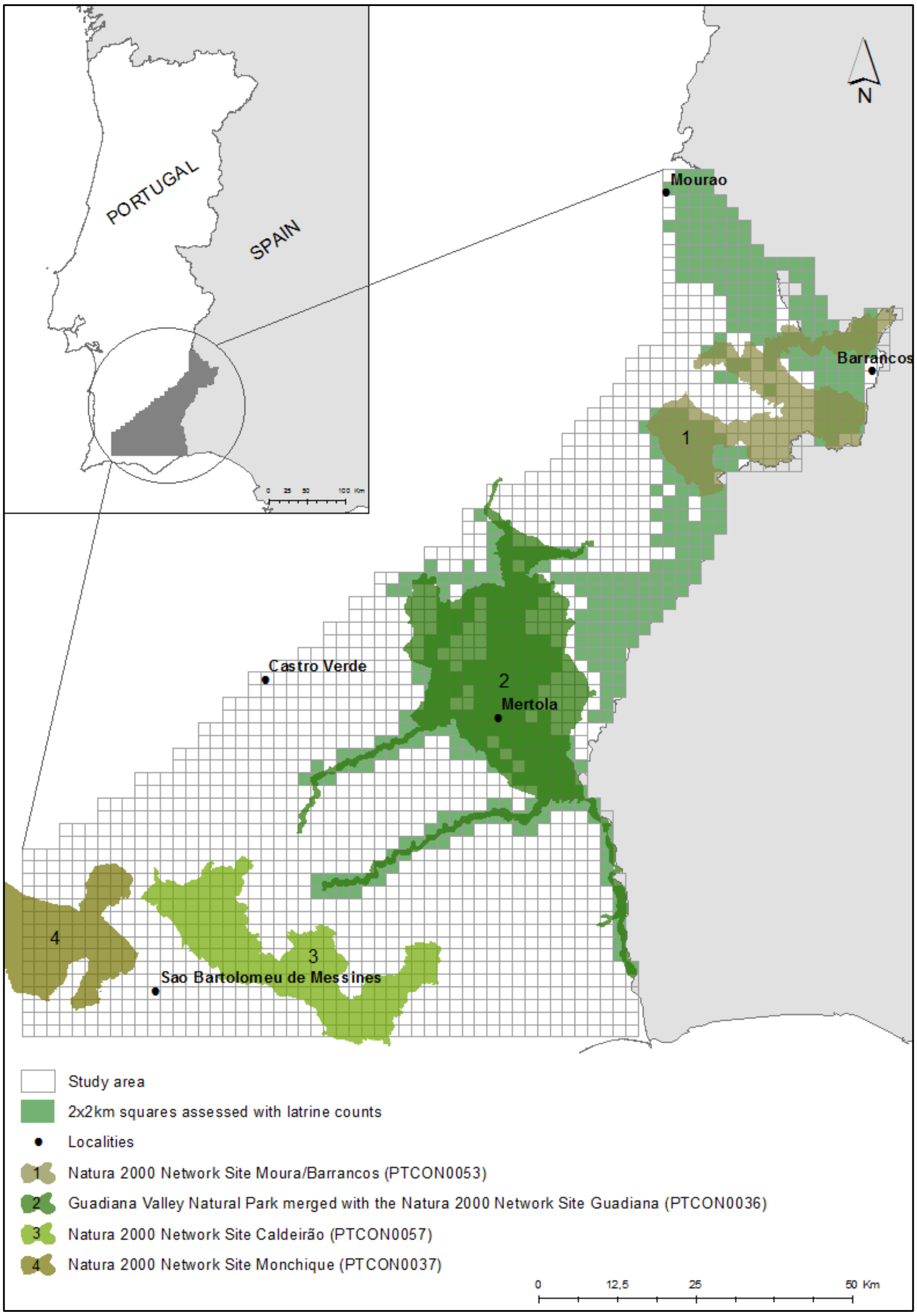

Figure 1 – Map of the study area with the 2x2 square units assessed with latrine counts and with the Natural Protected Areas with importance for Iberian lynx reintroduction.

Field sampling

Distribution and abundance of the European rabbit's study followed the Portuguese monitoring methodology, developed by the project "INCOB – Information System for European Rabbit Populations". The INCOB project was part of the *Wild Rabbit Recovery Program* (in Portuguese, PRECOB; Portuguese Law issue nº 296/2007, 8-01) which aimed to create a standard method for collecting data to assess the abundance and distribution of European rabbit populations in Portugal (Ferreira and Delibes-Mateos 2010). The method is based on latrine counts, which is commonly used to evaluate the distribution and abundance of European rabbits (reviewed in Ferreira and Delibes-Mateos 2010). This method can be efficiently applied to large areas in a short period of time, producing satisfactory abundance estimates, highly correlated to other estimation methods (Iborra and Lumaret 1997, Campbel et al. 2004). Latrines have a territorial and social function in rabbit ecology and can be deposited by single individuals or family groups (Sneddon 1991). Latrine was defined as any group of > 20 pellets in a circle with a <30cm^2 area (Virgós et al. 2003).

A sampling grid of 2×2km UTM (*Universal Transverse Mercator*) square units (Sarmento et al. 2012), with a total of 1934 squares, was superimposed over the study area, and approximately 25% of these squares were sampled. The sampled squares were selected to include the 4 natural protected areas referred above. Four 500m long transects were defined in each sampled square (one per quadrant). All transects were selected in areas with suitable habitat for the European rabbit, along trails (Delibes-Mateos et al. 2008b). Two observers walked the transect side-by-side, and counted the number of latrines within a 6-m-wide band (3 m on each side covered by each observer) along the transect. The geographic location of all transects and of each latrine was registered in a handheld portable GPS (global positioning system) navigator.

A Kilometric Index Abundance (KIA) was calculated for each transect and for each sampled square using the following formula:

$$Formula\ 1: \qquad KIAt = \frac{lat \times 1000}{tl}$$

$$Formula\ 2: \qquad KIAs = \frac{\sum_{i=1}^{n} KIAt}{n}$$

where KIAt - Kilometric Index Abundance for each transect; KIAs - Kilometric Index Abundance for each samples square; lat - number of rabbit latrines detected in a transect; tl – transect length (500m); n – number of transects in each sampled square.

The field sampling was conducted during June and July 2010, a period that corresponds to the highest density of European rabbit, at the end of the breeding season (Gonçalves et al. 2002); before the seasonal outbreaks of myxomatosis and rabbit viral hemorrhagic disease (Calvete et al. 2002, Calvete et al. 2006); and before the hunting period (Decree-Law n. º 2/2011 of January 6).

Explanatory variables

Six sets of potential variables related to European rabbit distribution and abundance were evaluated: aspect, topographic, climatic, land cover, soil, and hunting management (table 1). Aspect and topographic variables provide different microclimatic conditions and can act as a movement barrier (Trout et al. 2000, Calvete et al. 2004). Climate conditions can affect the physiological conditions of the European rabbit, the vegetation structure and the water availability (reviewed in Delibes-Mateos et al. 2009). Land cover is related with food and shelter availability (Virgos et al. 2003, Delibes et al. 2008b). Soil type can influence the digging capacity (Virgos et al. 2003, Delibes-Mateos et al. 2008b) and the type of vegetation for food and shelter (Virgos et al. 2003, Ferreira and Alves 2009). Hunting management can directly affect the abundance of the species but also the availability of food, shelter and abundance of predators (Delibes-Mateos et al. 2008b).

Aspect variables

To calculate the aspect (slope direction), the global digital elevation model (GDEM) grid was first obtained from the ASTER (Advanced Spaceborne Thermal Emission and Reflection radiometer; http://gdem.ersdac.jspacesystems.or.jp/) with a resolution of 30x30m. The aspect grid was created over the GDEM grid with the extension DEM Surface Tools for ArcGIS10, and was classified into nine categorical directions with 45°, plus one class with no direction corresponding to flat areas (table 1) (Jenness 2012). The total area (ha) occupied by each aspect class within each sampled 2x2 square was calculated with ArcGIS10 tools.

Topographic variables

Topographic variables were obtained using the previously described GDEM grid. A topographic position index (TPI) grid was calculated as the difference between each cell's elevation and the average elevation of the surrounding cells (Jenness et al. 2012). This calculation was performed with the extension Land Facet Corridor for ArcGIS10 with a 60m circular neighborhood (Jenness et al. 2012). The TPI grid was classified in six topographic classes (table 1) according to Jenness et al. (2012). The total area occupied by each TPI class within each sampled 2x2 square was calculated with ArcGIS10 tools.

Climatic variables

Six climatic grids were obtained from the Digital Climatic Atlas of the Iberian Peninsula (http://opengis.uab.es/wms/iberia/en_index.htm) with a resolution of 300x300m. Precipitation, radiance, annual mean, annual maximum and annual minimum temperatures corresponded to the mean values for 2010 (table 1). Maximum temperature for July was also taken as a variable, representing the highest values registered for this month. The mean value by each climatic variable within each sampled 2x2 square was estimated with ArcGIS10 tools.

Land cover variables

Land cover variables were obtained from the land cover vector dataset (COS 2007 level 2; IGEOE 2010, http://www.igeo.pt) with 15 classes and a minimum mapping unit of 1ha (IGEOE 2010). The original dataset was reclassified into 8 ecologically relevant classes for the European rabbit, based on the published literature (Moreno et al. 1996, Lombardi et al. 2003, Virgos et al. 2003, Calvete et al. 2004, Ferreira and Alves 2009): artificial areas, represented by humanized areas; temporary crops, represented by crops with rotation system; permanent crops, represented by crops without a rotation system (e.g. olive groves, vineyards); pastures, represented by herbaceous species; heterogeneous agricultural areas, represented by annual crops with permanent crops on the same area, mixed with pastures and natural vegetation; forests, represented by forests and woodlands composed by coniferous and/or deciduous trees; open forest with shrub and/or herbaceous vegetation association, and open areas with little and/or sparse vegetation, represented by open areas with shrubs and herbaceous cover. The total area occupied by each land cover class within each sampled 2x2 square was calculated with ArcGIS10 tools.

Soil variables

Soil variables were obtained from a 1:25,000 scale vector, provided by the Portuguese General Direction of Agriculture and Rural Development (DGADR; http://www.dgadr.mamaot.pt) and follow the Portuguese soils classification (ISA, 2014). The classes recorded for the study area were reclassified into 13 classes, according to hardness, compaction and deepness soil features: rock outcrop, represented by areas of rocky formation exposed above the surface of the surrounding land; aluviosoils, represented by young and moist soils, formed on the slopes by deposition with a groundwater course bellow; clays, represented by mature, compacted, and easily collapsed; lithosols, represented by young soils with less than 10cm deep; calcareous soils, represented by low mature acid soils, with a median-high texture; halomorphic, hydromorphic and turfs, represented by wet or moist soils, temporarily or permanently flooded by water; litholic soils, represented by young soils with humus; mediterranean soils, represented by five classes of mature soils with different compositions (calcareous, clays or hydromorphic); and artificial areas, represented by humanized areas. The total area occupied by each soil class within each sampled 2x2 square was calculated with ArcGIS10 tools.

Hunting estates variables

Hunting estates variables were obtained from a 1:25,000 scale vector, provided by the Portuguese Directorate-General of Forest Resources (DGFR). Six classes of hunting management were considered for the study: unmanaged, associative hunting estates, municipal hunting estates, national hunting estates, tourist hunting estates and non-hunting estates. The national and municipal hunting estates are managed by Portuguese Government and municipalities, respectively. The associative and touristic hunting areas have private management, by local hunting associations and by private stakeholders, respectively. The non-hunting class represents the areas were the hunting activity is prohibited, and the unmanaged class represents areas without hunting management. The vector was converted into a grid format with a resolution of 300x300m. The total area occupied by hunting class within each sampled 2x2 square was calculated with ArcGIS10 tools.

Table 1 – Variables extracted and used for statistical analysis. *variables selected after Spearman's rank correlation.

Type	**Variable**	**range**	**% in the study area**	**Code**
Aspect	flat*	-1	1.50%	A1
	northeast*	22.5 – 67.5	3.16%	A2
	north*	0 – 22.5	22.80%	A3
	north2	337.5 – 359.7	16.15%	A4
	northwest*	292.5 – 337.5	2.76%	A5
	southeast	112.5 – 157.5	2.80%	A6
	east	67.5 – 112.5	21.80%	A7
	south*	157.5 – 202.5	4.14%	A8
	southwest*	202.5 – 247.5	3.14%	A9
	west*	247.5 – 292.5	21.74%	A10
Topography	valleys*	TPI <= -1	10.42%	T1
	lower slopes	-1 < TPI < -0.5	15.78%	T2
	gentle slopes	-0.5 < TPI < 0.5 and slope <= 5	2.34%	T3
	steeps slopes	-0.5 < TPI < 0.5 and slope > 5	45.04%	T4
	uppers slopes*	0.5 < TPI < 1	16.55%	T5
	ridges	TPI >= 1	9.87%	T6

Climatic	annual mean precipitation (mm)	3538 – 11926		C1
	annual maximum temperature (°C)*	20.5 – 24.3		C2
	July maximum temperature (°C)*	30.9 – 36.4		C3
	annual mean temperature (°C)*	15.0 – 18.4		C4
	annual minimum temperature (°C)*	8.2 – 12.9		C5
	annual mean radiance (kWh m^{-2} day^{-1})	1552 –2297		C6
Land cover	artificial areas		0.92%	L1
	temporary crops		15.09%	L2
	permanent crops		6.51%	L3
	pastures		4.64%	L4
	heterogeneous agricultural areas*		15.27%	L5
	coniferous and deciduous forests		12.05%	L6
	open forest with shrub and/or herbaceous vegetation association, and open areas with little and/or sparse vegetation*		41.53%	L7
	water bodies		1.35%	L8
Soil	rock outcrop		0.89%	S1
	aluviosoils		0.98%	S2
	clays*		1.46%	S3
	lithosols soils*		60.27%	S4
	calcareous soils*		2.76%	S5
	halomorphic, hydromorphic and turf soils*		0.74%	S6
	Litholic soils		1.52%	S7
	mediterranean brown calcareous semi-clay and mediterranean red calcareous semi-clay soils*		1.10%	S8
	mediterranean browns non-calcareous normal and mediterranean reds non-calcareous normal soils*		23.43%	S9
	mediterranean browns non-calcareous semi-brown and mediterranean red non-calcareous semi-brown soils		0.40%	S10
	mediterranean brown non-calcareous semi-hidromorphic and mediterranean red non-calcareous semi-hidromorphic soils*		0.93%	S11
	mediterranean reds calcareous normal soils*		2.30	S12
	artificial areas		0.69%	S13
Hunting estates	unmanaged estates*		1.18%	H1
	associative hunting estates		51.19%	H2
	municipal hunting estates		7.75%	H3
	national hunting estates*		0.60%	H4
	tourist hunting estates*		29.37%	H5
	non-hunting estates		0.96%	H6

Data analysis

Preliminary analyses

In order to reduce the possible correlation effect between the extracted variables (48 variables), the Spearman's rank correlation was calculated (Zar 1999) between explanatory variables. For each significantly correlated (p<0.05) pair of variables, the one with the highest correlation with the dependent variable (KIA) was selected. To further reduce the number of explanatory variables, and to construct independent sets of variables that characterize the landscape structure (Trout et al. 2000), a principal component analysis (PCA) was performed. The most contributive components (i. e., the ones that explain most of the variability of the data) were retained for further analyses, following the Kaiser Criterion, where components with eigenvalue greater than 1.0 were retained. A rotation of the principal component matrix was carried on to identify the most contributive set of variables for each component. The variables with the highest loadings (>0.3) for each component were considered as the most contributive for that particular component.

Quantile regression models

Quantile regression (QR) is a regression method used to model the relation between the dependent variable and the explanatory variables along the entire dataset, where a trendline is adjusted for each τ quantile [0, 1] of the data distribution (Cade et al. 1999). For regressions for higher quantiles (50^{th} to 99^{th}), it is possible to model the upper limit of the data distribution, and understand the maximum biological response of the dependent variable. With this information it is possible to detect which variable (or set of variables) is limiting the distribution of the data range (Cade et al 1999, Cade and Noon 2003).

To assess the individual relationship between each explanatory variable and the dependent variable, univariate regression quantile models were fitted. A multivariate regression model was assessed to identify the most significant set of variables with the KIA.

Univariate models

Linear quantile regressions were performed for the dependent variable KIA using each principal component (PC) as explanatory variable. In order to assess the relationships at different levels of the data distribution, the regression was computed for thirteen quantiles: 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.75, 0.80, 0.85, 0.90, 0.95 and 0.99. A rank-inversion test was performed to generate the confidence intervals of the regressions (Koenker, 2012). It was considered that the explanatory variable influenced the response variable when the rate of change (slope) was significantly different from zero. The significance of the relationships between KIA and PC for each quantile were tested

(H0: slope=0) with the rank-score test with the probabilities evaluated as the χ^2 distribution (Koenker and d'Orey 1994).

The quantile regression models were evaluated with the coefficient goodness-of-fit R^1 , which is based on minimizing the sum of weighted distances for each quantile, using the formula:

$$Formula\ 3) \qquad R^1 = 1 - F(\tau)/R(\tau)$$

where, $F(\tau)$ is the weighted sum of absolute deviations minimized in a full model, $R(\tau)$ is the weighted sum of absolute deviations minimized in a null model, for a τ quantile.

Limiting factors (the principal components) were identified at the highest significant quantile ($p < 0.05$), in each set of regression quantile.

An ordinary univariate least squares regression model was also fitted between KIA and each PCA components for comparative purposes with quantile regression. These models were assessed using the coefficient of determination (R^2; e.g. Baur et al. 2004, Munir et al. 2012).

Multivariate models

Multivariate quantile regression models were performed between the dependent variable (KIA) and explanatory variables (PCs) for each quantile of the data distribution. Multivariate models were performed for upper quantiles (≥0.7), with the main goal of assessing the factors limiting European rabbit populations (KIA).

An initial full model was fitted with the most contributive principal components (principal components with eigenvalue greater than 1.0) as explanatory variables, for each quantile separately (0.7, 0.75, 0.8, 0.85, 0.9, 0.95 and 0.99). Then, it was applied a backward stepwise elimination procedure, whereby the principal component with the highest non-significant $p - value$ was removed in each step, until all variables in the model had significant effect (Vaz et al. 2008). The variables' significance was tested with the rank-score test (Koenker and d'Orey 1994).

From the seven final models (one for each quantile), only one was selected as the multivariate final model to assess the limiting factors for the European rabbit populations (KIA). Since the currently existing goodness-of-fit tests did not correctly apply to our study, was selected the model for the highest quantile, in which all the variables were statistically significant ($p < 0.05$) in univariate models.

Models' validation was performed with a Spearman correlation rank between the selected model and the KIA dataset.

The selected model was projected for the entire study area using ArcGIS 10 (®ESRI). For each protected area, the limiting set of variables was assessed through the principal components mean values.

All analyses were performed in R (R Development Core Team 2008). Spearman correlation and PCA were performed using the *stats* package. Quantile regressions and rank inversion tests were performed using the *quantreg* package, a library for quantile regression analyses (Koenker 2008).

RESULTS

Preliminary analyses

A total of 26 variables (51.4% of the initial set) was selected for further analyses after the Spearman's rank correlation test (table 1).

The first eight components of the PCA, eigenvalues>1 (figure 2), explained a total of 68% of the variability of the dataset. The first component (PC1) had the highest contribution, accounting for 18% of the total variability, followed by the second and third components, which explained 11% and 10%, respectively. The following components (PC4 to PC8) have the lowest contributions (less than 10%).

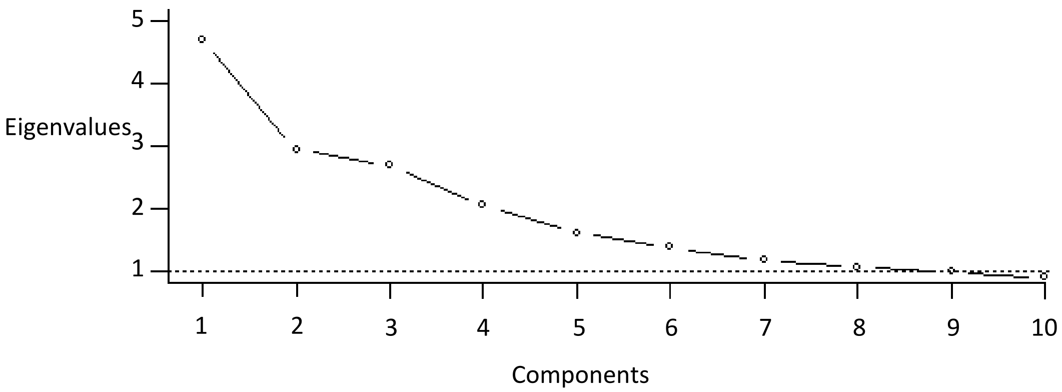

Figure 2 – Screeplot representing the variability explained (eigenvalues) by the first 10 components of the Principal Components Analysis. The 1st to the 8th component have eigenvalues >1. Dashed line – eigenvalue =1.

The variables that contributed the most for PC1 (figure 3, table 2) had all positive loadings in the component structure, and comprise three climatic variables: annual minimum temperature (C5), annual mean temperature (C4) and annual maximum temperature (C2); one land cover variable: open forest with shrub and/or herbaceous vegetation association and open areas with little and/or sparse vegetation (L7); and one soil type: lithosol soils (S4). The second component (PC2) also consists in two climatic variables: annual maximum temperature, annual mean temperature (C2 and C4); and one aspect variable: flat (A1), all with positive loadings (table 2), whereas the hunting estate variable, national hunting area (H4), showed negative loadings for this component (figure 3). The composition of the remaining components is described in the table 2.

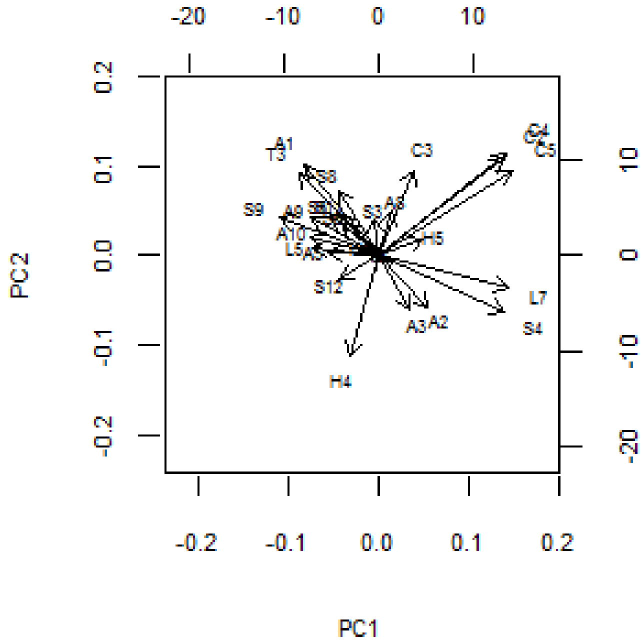

Figure 3 – Biplot of principal component analysis between the first component (PC1) and the second (PC2).

<u>Univariate quantile regression models</u>

The univariate quantile regression models showed that the principal components have different effects on the relative abundance of European rabbit (KIA), and that also this effect changes between different quantiles (figure 4 and 5).

In all principal components (PC1 to PC8) the regressions along the quantiles have different intercept values and different slopes (see figure 1 to 8 of Appendix), suggesting that the included variables did not explain all the data variability by themselves.

For PC1 (figure 4 and 5), the slopes of quantile regressions were significantly positive ($p < 0.05$) for all quantiles up to the 99^{th} quantile, and the rate of change (slope) increased towards the higher quantiles (see also table 4 to 11 of Appendix). This suggests that European rabbit relative abundance progressively increased in areas with higher temperatures (C2, C4 and C5), higher availability of open forest with shrub and herbaceous cover (L7) and with the presence of lithosol soils. The upper limit of European rabbit relative abundance appears to be limited in areas with low values of these variables, because the slope of the regression was significantly different from zero for the the 95th quantile.

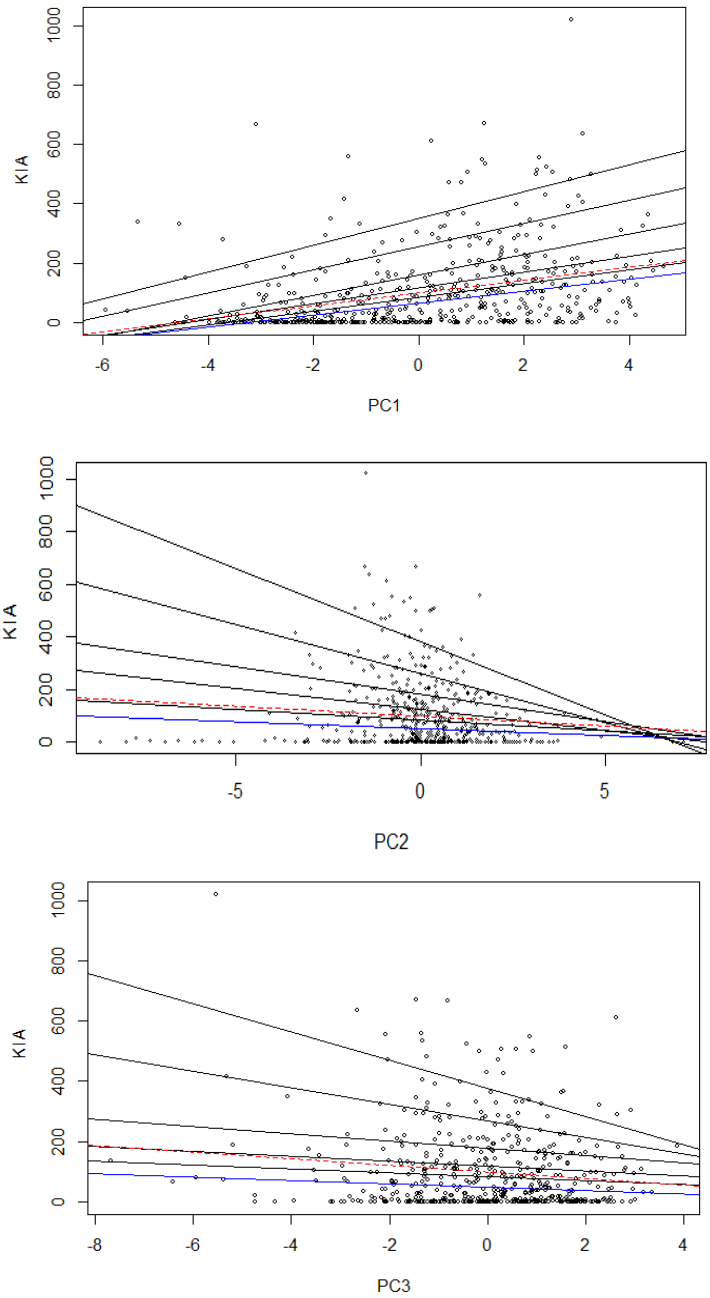

Figure 4 – Quantile regression plots for the first three principal components (PC1, PC2 and PC3). Regression lines are represented for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles in black, the 0.50 quantile in blue and the ordinary least squares estimates of the conditional mean function as the dashed red line.

For both PC2 and PC3 the quantile regressions had negative slopes. That implies a negative effect on European rabbit relative abundance, when the variables of each component had positive loadings and a positive effect when variables had negative loadings. Therefore, variables with negative influence on component were limiting the upper limit of the data distribution by low presence in the area; and the variables with positive influence on component were limiting by high presence in the area.

For PC2, the slopes of quantile regressions were only significantly negative ($p < 0.05$) only for quantiles ≥ 0.70 (table 5 of Appendix), suggesting that the European rabbit relative abundance was potentially limited in areas with little presence of national hunting estates, and with a high availability of flat ground and high annual temperatures.

Table 2 – First eight components (PC1 to PC8) from principal component analysis with loadings of the most contributive variables

	Variables	Loadings		Variables	Loadings
PC1	C5 annual minimum temperature	0.360	**PC5**	S8 mediterranean brown calcareous semi-clay soil, mediterranean red calcareous semi-clay soil	-0.441
	L7 Open forest with shrub and/or herbaceous vegetation association, open areas with little and/or sparse vegetation	0.349		L5 heterogeneous agricultural areas	0.428
	C4 annual mean temperature	0.340		S9 mediterranean brown non-calcareous normal, mediterranean red non-calcareous normal	0.420
	C2 annual maximum temperature	0.345		S5 calcareous	-0.362
	S4 lithosol soils	0.337		S11 mediterranean brown non-calcareous semi-hidromorphic, mediterranean red non-calcareous semi-hidromorphic	-0.310
PC2	C4 annual mean temperature	0.348	**PC6**	H5 touristic hunting reserve	-0.524
	H4 national hunting area	-0.340		S12 mediterranean red calcareous normal soil	-0.433
	C2 annual maximum temperature	0.333		T5 uppers slopes	0.421
	A1 flat	0.312		H1 unmanaged areas	0.360
PC3	A2 northeast	-0.475	**PC7**	C3 July maximum temperature	0.378
	A3 north	-0.422		S12 mediterranean red calcareous normal soil	0.364
	A9 southwest	0.370		T3 gentles	-0.355
	A8 south	0.321		A1 flat	-0.336
PC4	A5 northwest	-0.581	**PC8**	S3 clay soil	-0.607
	A8 south	0.482		S6 halomorphic, hydromorphic and turf soil	0.515
	A10 west	-0.447		H1 unmanaged areas	-0.321

For PC3, the slopes were only significantly negative ($p < 0.05$) for quantiles ≥ 0.85. The upper limit of the European rabbit relative abundance was, in this case, potentially limited by low presence of areas with northeast and north ground exposition and high presence of areas with southwest and south ground exposition.

The ordinary least square regression was significant for all principal components, however values for R^2 were low ($R^2 \leq 0.1$; table 3) with a reduced explained variability of the data distribution.

Quantile regression shows different values of R^1 for each quantile, however, higher values were all above the quantile 0.5 (see Appendix – quantile regression results). For PC2, PC3, PC5, PC6 and PC8 the highest R^1 value was for the upper significant quantile (see table 4 to 11 of Appendix).

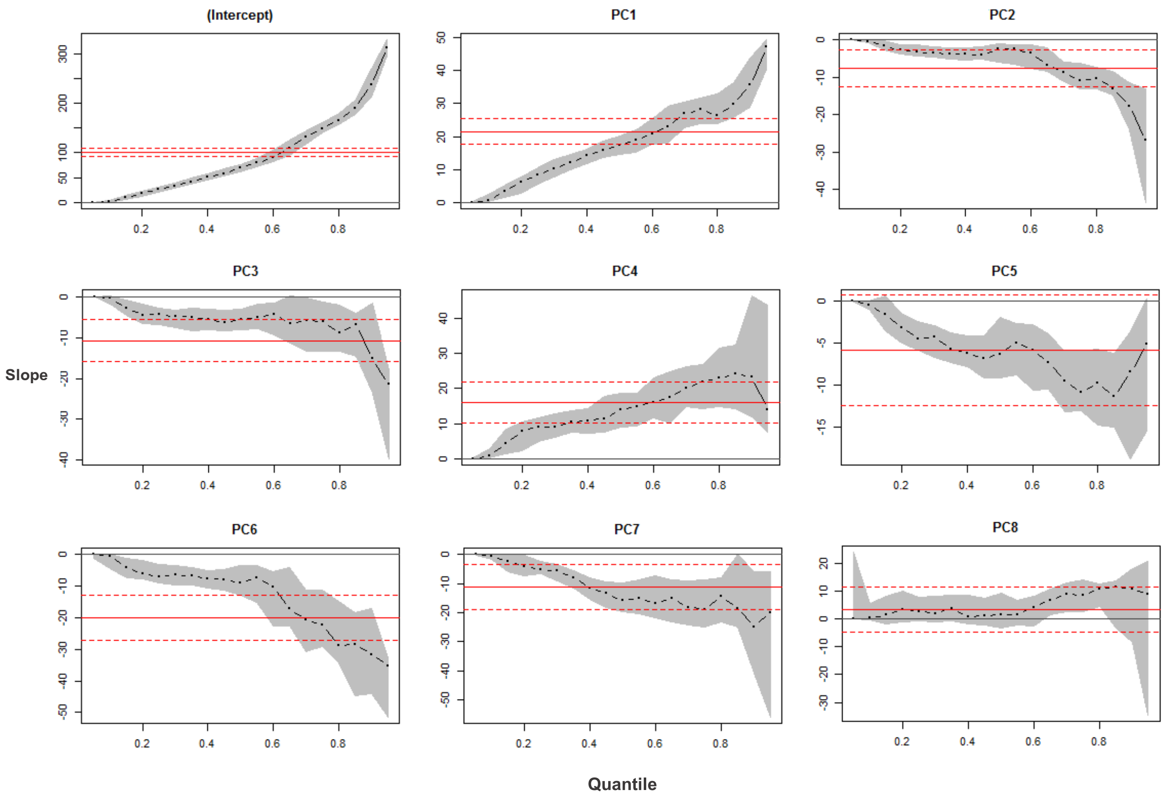

Figure 5 – Slope of quantile regression (dashed dotted black line) between each predictor variable (principal components 1 to 8) and the response variable KIA for 50th to 99th quantiles with 95% confidence interval (gray shaded) to test the H_0: slope=0 (gray solid line). Ordinary least square (solid red line) regression for the same variables with 95% confidence interval (dashed red line). See the different scale for y-axis.

Table 3 – Univariate quantile regressions for the highest significant quantiles, and ordinary least square regressions for each KIA-principal component combination.

	Regression type	Model	Std. Error	p-value	Goodness-of-fit
PC1	95th QR	351,36 + 45,40x	15,84	0.004	R^1=0.073
	OLS	100.18 + 21.57x	4.17	0.000	R^2=0.117
PC2	99th QR	541.28 - 76.26x	11.60	0.000	R^1=0.086
	OLS	100.18 -7.53x	3.512	0.032	R^2=0.007
PC3	99th QR	574.63 - 80.66x	33.74	0.017	R^1=0.111
	OLS	100.18 -10.78x	3.659	0.003	R^2=0.015
PC4	85th QR	210.48 + 22.20x	9.47	0.013	R^1=0.023
	OLS	100.18 + 15.95x	3.659	0.003	R^2=0.026
PC5	95th QR	377.41 - 85.11x	11.00	0.000	R^1=0.027
	OLS	100.18 -20.11x	5.062	0.000	R^2=0.029
PC6	95th QR	384.50 - 51.28x	18.45	0.005	R^1=0.048
	OLS	100.18 -11.29x	5.507	0.040	R^2=0.029
PC7	80th QR	183.21 - 9.48x	9.48	0.028	R^1=0.006
	OLS	100.18 -11.29x	5.507	0.040	R^2=0.029
PC8	99th QR	560.96 + 51.95x	10.69	0.000	R^1=0.020
	OLS	100.18 -11.29x	5.507	0.040	R^2=0.029

Multivariate regression quantile model

The best multivariate model included three explanatory variables (PC1, PC3 and PC6), fitted for the 95th quantile. As described in the univariate results, the selected model had a positive effect of PC1 and a negative effect of PC3 on European rabbit relative abundance distribution. PC6 had also a negative effect on European rabbit relative abundance distribution (table 4).

Table 4 – Estimates of highest significant quantiles for each KAI-principal component regression.

	Value	Std. Error	p-value
Intercept	355.167	35.323	0.000
PC1	47.236	10.842	0.000
PC3	-34.851	15.316	0.023
PC6	-60.316	13.956	0.000

The multivariate approach revealed that the European rabbit relative abundance was limited by low temperature values, low presence of lithosol soil and mediterranean red calcareous normal soil, reduced area of touristic hunting estates, low presence of areas with south and southwest exposition and low availability area of open shrubs and herbaceous cover. The multivariate regression also revealed that the rabbit abundance was limited by high presence of areas with northeast and north ground exposition, high presence of upper slopes areas, and high presence of unmanaged areas.

The best multivariate quantile regression model had the form of,

$$Equation\ 4: \quad y = 355.167 + 47.236\ PC1 - 34.851\ PC3 - 60.316\ PC6$$

and revealed a highly significant correlation with KIA values ($r_s = 0.495, p < 0.01$).
The model projection for the entire study area (figure 6) showed that the central area had the biggest extent with the lowest values of limiting factors. Geographically, this area is situated on the Guadiana river basin and corresponds partially to the Guadiana protected area (Guadiana Valley Natural Park and Natura 2000 Network Site Guadiana; figure 6). Two other small areas in the north had low limiting factors for European rabbit relative abundance, both included on the Moura-Barrancos protected area (Natura 2000 Network Site Moura-Barrancos). Throughout the remaining study area, high values of limiting factors were represented, including the Monchique and Caldeirão protected areas (Natura 2000 Network Site Monchique and the Natura 2000 Network Site Caldeirão, respectively).
The model projection for the four natural protected areas showed that the Monchique and Caldeirão had the biggest extent with the highest influence of limiting factors. In contrast, the Guadiana natural protected area which had the biggest extent with the lowest influence of limiting factors. However, Guadiana protected area registered the highest and the lowest values of limiting factors, as well as in the Moura-Barrancos protected area (figure 6).
When analyzing the limiting factors, the univariate quantile regression results for the four protected areas showed the European rabbit abundance was more limited by high presence of areas with upper slopes and unmanaged areas, and by low presence of mediterranean red calcareous normal soil and touristic hunting reserves in the Monchique and Caldeirão than in the other protected areas. Areas with high north and northeast exposition and low presence of south and southwest expositions also seemed to be more limited in the Monchique and Caldeirão protected areas. In turn, areas with low presence of high temperatures, low area with lithosol soils, and open areas with shrub and herbaceous cover seemed to limit more the abundance of European rabbits in Moura-Barrancos than in the other areas. In the Guadiana protected area, the European rabbit abundance seemed to be limited through low presence of lithosol soils, low presence of open areas with shrubs and herbaceous cover, low presence of high temperatures, and low presence of areas with south exposure.

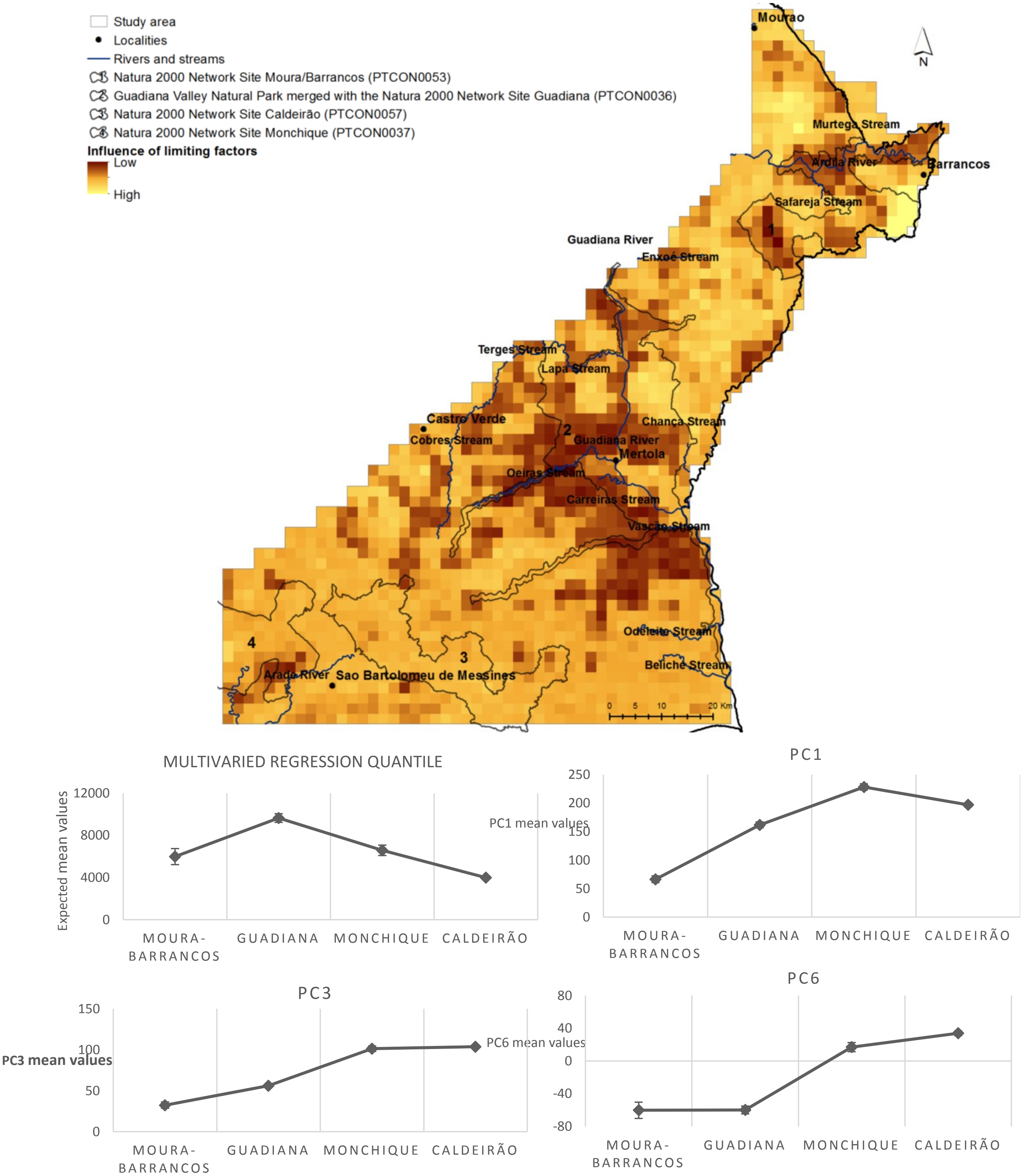

Figure 6 – Projection of predictive KIA distribution with higher limiting areas (light color) and lower limiting areas (dark color) for European rabbit abundance. For each protected area, was represented the expected mean values from the multivaried regression quantile and the mean values of each principal component, PC1, PC3 and PC6.

DISCUSSION

The European rabbit is a species with high adaptability to a number of environmental and ecological conditions, making it a successful colonist. Due to this characteristic, its distribution and abundance can be affected by several different factors. In fact, the present study showed that the distribution and abundance of this species is limited by numerous ecological, environmental and management factors. Moreover, the factors shaping the species' distribution and abundance showed to be variable between the different distribution areas, supporting this species' plasticity in colonizing different habitats. Even though the distribution areas studied have different characteristics, the method used was able to identify which factors were limiting the European rabbit's distribution range and abundance in each of the different areas. The use of this new approach can aid in conservation and management measures, allowing an efficient and reliable identification of the factors affecting the European rabbit's distribution and abundance. Even though this method is not widely used in ecology, this study showed that it can be highly useful not only for the European rabbit's conservation management, but also could be used for other species of conservation interest.

Environmental factors limiting the European rabbit's population

The present study demonstrated that the European rabbit's abundance was limited by land cover, soil, climatic, topographic and hunting management factors. From this set of factors, the distribution and abundance of the European rabbit seemed to be more limited in areas with low availability of open areas with shrubs and herbaceous vegetation cover, low presence of high temperatures and of lithosol soils. This means that high abundance of European rabbits seemed to be more frequent in areas where these factors' are present. Open areas with shrubs and herbaceous vegetation are composed by a mixed matrix of croplands, natural vegetation patches and scrublands. This landscape structure can provide both feeding and shelter areas in proximity of each other. Previous studies have also described that the European rabbit is a species mainly associated with sites containing a mixture of shrub cover and open areas in Mediterranean ecosystems (Moreno et al. 1996, Lombardi et al. 2003, Calvete et al. 2004, Fernández 2005). This area also comprised soils with less than 10cm deep over hard continuous rock. This contrasts with other studies, where soft and deep soils are selected by European rabbits to construct warrens (Gea-Izquierdo et al. 2005). The selection of this type of soil seemed to be related with the land cover type associated with it and not necessarily with the advantages for the European rabbits' presence. The lithosol soils cover more than 60% of the study area, while the soft and deep soils are occupied by extensive areas of crops and forestry, which are not the suitable vegetation for European rabbits' presence. Therefore, the European rabbit likely preferred the areas with the less suitable soil for warrens, but with the shrubs and herbaceous cover.

Besides the soil and land cover type, the areas with higher abundance also had high temperatures. High temperatures can be an advantage against diseases since they decrease the RHD virus survival (Tablado et al. 2012, McColl et al. 2002) and the presence of the *Spilopsyllus cuniculi* flea, a vector of European rabbit's diseases (Osacar-Jimenez et al. 2001). Nevertheless, previews studies have demonstrated that temperature is directly correlated with European rabbit abundance in areas with Atlantic climate and inversely correlated in Mediterranean areas (reviewed in Delibes-Mateos et al. 2009).

The present study also showed that the factors shaping the European rabbits' distribution and abundance showed to be variable between the different distribution areas. The four protected areas within the study area showed that the studied factors had different impacts on local European rabbit populations. The geographic proximity between Monchique and Caldeirão protected areas caused these areas to have similar influencing factors on European rabbits' population. Both Monchique and Caldeirão protected areas had the lowest extent of suitable areas for European rabbits' presence. This species abundance seemed to be limited in areas with high north and northeast exposition in upper slopes, with low availability of Mediterranean red calcareous soil and touristic hunting reserves. Areas with north and northeast exposition have less solar exposure and consequently are more wet and cold, limiting this species' presence. Similar findings for the same area were reported by Godinho et al. (2013) that stated that the presence of European rabbits had negative relationship with both slope directions. This species probably avoids these topographic directions (Godinho et al. 2013) since it seems to reduce litters' survival (Rödel et al. 2009) and allow the presence of some diseases like RHD and the *Spilopsyllus cuniculi* flea, a vector of diseases (Osacar-Jimenez et al. 2001, McColl et al. 2002). Moreover, the abundance of European rabbit seems to be limited by the reduced availability of the opposite aspect (south and southwest), highlighting the importance of warm and dry areas.

Topography and altitude has been reported by some researchers as an important factor for European rabbit's distribution and abundance (e.g Calvete et al. 2004, Fárfan et al. 2008). This study shows that the high availability of upper slopes seems to limit the abundance of European rabbit in Monchique and Caldeirão protected areas. This finding is coherent with other studies where high topography is negatively related with abundance (Calvete et al. 2004, Fárfan et al. 2008). The Mediterranean red calcareous soil is a deep and soft soil (ISA, 2014), which can facilitates the construction of warrens (Gea-Izquierdo et al. 2005). The absence of this type of soil could limit the availability of shelter. Areas with soft soils have been demonstrated by others studies as an important factor for European rabbit's distribution and abundance (e.g. Trout et al. 2000, Calvete et al. 2004, Williams et al. 2007). Limited occupancy of touristic hunting reserve is also related to constraints in the abundance of European rabbits in the Monchique and Caldeirão protected areas. This lagomorph is one of the most appreciated small-game species in the south of Portugal, therefore high densities of European rabbits for hunting purposes is a common goal in hunting estates. Touristic hunting estates are the only estates with private management by stakeholders and are managed with the objective of profiting from hunting. Therefore, with more financial resources and target management, the European rabbit can have more suitable conditions, increasing its abundance and distribution in these estates. Similar findings were reported by Delibes et al. (2008c) where a higher abundance was found in intensively managed hunting areas than in protected areas and other non-protected areas. In accordance with these findings, the results of this study also suggest that abundance is limited by the presence of unmanaged areas, since there are no significant implementation efforts to increase the number of European rabbits.

The European rabbit abundance in the Moura-Barrancos protected area seemed to be limited by the low presence of open areas with shrubs and herbaceous vegetation cover, of high temperatures and of lithosol soils. These factors had also different influences along the protected area, in which the most and the less suitable areas for the European rabbit's presence were represented.

Guadiana protected area had the largest suitable area for European rabbit's presence, geographically surrounded in the south by the high-suitability area of the Guadiana river basin partially enclosed within the protected area (figure 6). However, this protected area had also unsuitable areas, where the European rabbit's abundance is limited by the low presence of lithosol soils, open areas with shrubs and herbaceous cover, low presence of high temperatures and low presence of areas with low sun exposition.

Quantile regression models

Despite the fact that quantile regression is still little used in ecology, this method revealed to be a useful tool to detect the factors limiting the European rabbit population. Some other studies have demonstrated that quantile regression is a useful tool in ecological studies for detecting limiting factors (reviewed in Cade and Noon 2003). In fact, since it is a very plastic species, modelling the European rabbit is a challenge and the statistical models always have little variability explained (e.g. Virgos et al. 2003, Calvete et al. 2004). With the use of regression quantile models, it was possible to identify different limiting factors for different particular areas with the general features of the extent area. This is highly useful since it provides different information at the global and local level, making it more easy and efficient to implement specific management actions. By being able to give information at both scales, it also undermines the need to build different studies for the different scales, minimizing the overall cost of the study.

The statistical properties of regression quantiles provide advantages over the ordinary least-square (OLS) estimates (Cade and Noon 2003). One of the advantages was the possibility to explore other parts of the response distribution, and, in this case, model the upper quantiles, rather than just the mean response. Low variability explained in the OLS regressions shows that this is not the most suitable method to understand which factors are influencing the abundance of European rabbits.

The spatial projection of the regression quantile multivariate model of the higher limit of the data distribution, provides a visual representation of the suitable areas that the European rabbit can occupy. The spatial representation includes the influence of measured and unmeasured factors that are influencing the species distribution and abundance (Eastwood et al. 2003, Vaz et al. 2008). With this representation it is possible to make a more accurate management plan for unsuitable areas and to identify the best areas in terms of prey abundance, in this particularly case for the Iberian lynx reintroduction.

Implications for Iberian lynx conservation

As the most endangered feline species in the world, the Iberian lynx has been a target of several conservation programs in the Iberia Peninsula (Simón et al. 2012). The ongoing reintroduction program, carried out in the scope of the LIFE+ IBERLINCE (LIFE10 NAT/ES/000570/IBERLINCE), is an example of one of the various conservation programs for this species and aims to recover the Iberian lynx populations in Portugal and Spain through habitat and prey management, as well as lynx reintroductions. For a successful reintroduction program for the Iberian lynx, stable and abundant prey resources are identified as one of the most important factors (Simón et al. 2009, 2012). Therefore, the increase in abundance and distribution of the populations of this species' preferred prey, the European rabbit, is one of the priorities of this program. The present study provides useful information regarding which factors are influencing the abundance of European rabbits and which should be managed to increase this species' population.

From the four priority areas in southeast Portugal, Moura-Barrancos and the Guadiana protected areas have largest extent of unconstrained conditions for European rabbit populations. Due to the geographical position of these two priority areas, management efforts are recommended to create a corridor of favorable conditions for the European rabbit's occurrence between these two areas.

Even though the different protected areas within the study area present some distinct limiting factors affecting the distribution and abundance of the European rabbit, there are many concordant factors between them. The presence of this species seems to be favoured by warmer habitats, represented by south and southeast exposure and high temperatures in the study area. Moreover, despite not being present as a limiting factor in all the protected areas, the presence of deep and soft soils also seems to favour this species' occurrence. Although these features cannot be directly managed, the management measures hereafter proposed will be more successful if these factors are taken into account. Habitat management is recommended, as the land cover that seems to favour the presence of European rabbit are open areas with shrubs and herbaceous cover. Clearing of the shrubland in order to create a matrix of open spaces with herbaceous is an efficient way to increase habitat availability for this species. Touristic hunting estates showed to be the areas with better habitat management, presenting higher European rabbit abundance. Other hunting estates should consider incorporating these types of management practices, in order to increase suitable areas for this species.

The present study provides useful information regarding which variables are influencing the distribution and abundance of European rabbit in the extent area in southwest Portugal and in four small areas with high importance for Iberian lynx reintroduction. Moreover, this study provides managers and conservationists with specific information on which management efforts should be applied to each area, while also providing general information on how to manage all the extent area. These efforts are particularly urgent, since a new variant of the RHD virus is currently affecting the European rabbit's populations, and a stable and abundant population of these species is highly important for a successful reintroduction of the Iberian lynx.

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MAIN CONCLUSIONS

The present study provides useful information regarding which factors are influencing the distribution and abundance of European rabbit in the extent area in the southwest Portugal, encompassing four protected areas with high importance for Iberian lynx reintroduction. The European rabbits' abundance showed to be limited by land cover, soil, climatic, topographic and hunting management factors. However, the factors shaping the European rabbits' distribution and abundance showed to be variable between the different protected areas and in the extent study area. With this information managers and conservationists are able to apply specific management actions in each of the protected areas, by also obtaining general information on how to manage the whole of the extent area.

The limiting factors were analyzed using quantile regression models. This method revealed to be a useful and reliable tool in identifying the factors that are shaping the European rabbit's population. One of the advantages over the ordinary least-square (OLS) was the possibility to explore other parts of the response distribution and model the upper quantiles, rather than just the mean response. Low variability explained in the OLS regressions showed that this is not the most suitable method for our goal.

The spatial projection of the regression quantile multivariate model provided a visual representation of the suitable areas for the European rabbit. The spatial representation included the influence of measured and unmeasured factors affecting the species' distribution and abundance. With this representation it's possible to make more accurate management plans and to identify the best areas in terms of prey abundance, in this particular case for the Iberian lynx reintroduction. In this context, the Moura-Barrancos and Guadiana protected areas had the largest suitable area for European rabbit presence. For these reasons, management efforts are recommended to create a single extent and unconstrained area for the European rabbits' occurrence.

This study is particularly important at a time when the European rabbits are affected by the new variant of RHD, and to have a stable and abundant population of European rabbit is imperative for a successful Iberian lynx restocking.

Appendix

Sperman rank correlation results

Table 1 – Spearman rank correlation results between the KIA (Kilometric Index of Abundance) and the 49 independent variables.

	IKA	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	C1	C2	C3	C4	C5	C6	L1	L2	L3	L4	L5	L6	L7
IKA	1,000																							
A1	-,126**	1,000																						
A2	,172**	-,085	1,000																					
A3	,116**	-,072	,574**	1,000																				
A4	-,035	-,223**	,056	,640**	1,000																			
A5	-,259**	-,014	-,386**	,085	,586**	1,000																		
A6	,067	,022	-,101*	-,487**	-,540**	-,444**	1,000																	
A7	,077	-,107*	,506**	-,051	-,334**	-,500**	,510**	1,000																
A8	,131**	,065	-,398**	-,533**	-,573**	-,490**	,398**	-,134**	1,000															
A9	-,166**	,169**	-,571**	-,500**	-,329**	,016	-,219**	-,477**	,378**	1,000														
A10	-,335**	,043	-,555**	-,312**	,104*	,654**	-,345**	-,468**	-,211**	,472**	1,000													
C1	-,060	-,110*	,009	,096*	,128**	,126**	-,098*	-,040	-,210**	-,007	,082	1,000												
C2	,260**	-,205**	,075	,003	,010	-,148**	,203**	,141**	,101*	-,229**	-,185**	-,472**	1,000											
C3	-,225**	,010	-,120**	-,096*	,000	,057	,022	-,032	-,009	,072	,114*	-,247**	,439**	1,000										
C4	,267**	-,149**	,133**	,049	,028	-,152**	,153**	,144**	,050	-,232**	-,211**	-,581**	,909**	,491**	1,000									
C5	,401**	-,178**	,161**	,089*	,039	-,161**	,126**	,121**	,109*	-,263**	-,252**	-,658**	,865**	,186**	,849**	1,000								
C6	,078	,127**	-,347**	-,678**	-,667**	-,418**	,507**	,098*	,719**	,384**	-,066	-,214**	,044	,030	,018	,024	1,000							
L1	,011	,274**	-,041	-,038	-,073	,005	,101*	,016	,050	-,035	-,031	-,009	-,045	-,056	-,031	-,006	,066	1,000						
L2	,090*	,462**	,000	,053	-,092*	-,030	-,012	-,032	,033	,021	-,053	-,210**	-,081	-,022	-,037	,073	,044	,262**	1,000					
L3	-,061	,331**	-,035	-,009	-,064	,043	,018	-,047	-,056	,019	,023	,222**	-,254**	-,034	-,222**	-,313**	-,023	,095*	,178**	1,000				
L4	-,113*	,096*	-,056	-,022	-,001	,100*	,062	-,012	-,014	-,017	,078	,020	-,066	-,034	-,060	-,060	,025	,086	-,013	,149**	1,000			
L5	-,308**	,163**	-,172**	-,054	-,004	,141**	-,006	-,108*	,013	,116**	,178**	,279**	-,156**	,056	-,255**	-,305**	,021	,198**	,010	,180**	,206**	1,000		
L6	-,050	-,325**	,074	,004	,058	-,080	,078	,094*	-,026	-,084	-,061	,196**	,118**	-,030	,015	,004	-,063	-,121**	-,371**	-,124**	-,006	,047	1,000	
L7	,467**	-,419**	,133**	,111*	,136**	-,121**	,082	,109*	,106*	-,260**	-,216**	-,224**	,492**	-,154**	,454**	,633**	,004	-,093*	-,161**	-,324**	-,055	-,392**	,069	1,000
L8	,023	-,102*	,005	-,021	,070	,054	,035	-,032	-,028	-,062	,019	-,340**	,330**	,161**	,425**	,389**	,000	,005	-,103*	-,061	,135**	-,113*	,080	,232**
S1	-,034	-,158**	-,010	-,088*	-,014	,026	,020	,070	-,032	-,024	,053	-,028	,199**	,206**	,198**	,130**	-,020	-,069	-,054	-,073	-,028	-,006	,103*	,141**
S2	-,037	,034	,086	,052	,057	-,022	,038	,120**	-,056	-,129**	-,103*	,059	-,087	-,038	-,029	-,084	-,071	,116**	,006	,213**	-,002	,111*	,040	-,118**
S3	-,126**	,181**	-,100*	-,083	-,074	,046	,082	-,032	,007	,064	,051	-,138**	,021	,168**	,067	-,028	,043	,089*	,149**	,223**	,083	-,076	-,052	-,167**
S4	,311**	-,514**	,116**	,097*	,165**	-,078	,028	,095*	,043	-,175**	-,108*	-,139**	,357**	-,100*	,392**	,471**	-,026	-,121**	-,268**	-,417**	,052	-,189**	,210**	,711**
S5	-,135**	,349**	-,088*	-,088*	-,146**	,026	,023	-,005	-,064	,114*	,082	,030	-,185**	,107*	-,099*	-,262**	,045	,060	,229**	,524**	,010	,018	-,139**	-,418**
S6	-,129**	,345**	,099*	,064	-,041	,038	-,126**	-,040	-,113*	,022	,020	-,119**	-,110*	,112*	-,019	-,128**	-,053	,029	,225**	,178**	,048	,035	-,155**	-,293**
S7	-,103*	,172**	-,005	,059	,014	,027	-,035	-,071	-,018	,045	,035	-,058	-,066	,064	-,026	-,086	-,037	-,023	,091*	,143**	,062	,122**	-,143**	-,174**
S8	-,204**	,297**	-,133**	-,079	-,056	,114*	,031	-,051	-,062	,114*	,131**	-,150**	-,067	,244**	,038	-,127**	,039	,075	,298**	,341**	,028	,016	-,191**	-,295**
S9	-,175**	,526**	-,118**	,000	-,074	,104*	-,048	-,171**	,031	,104*	,067	,145**	-,288**	-,041	-,372**	-,340**	-,013	,239**	,424**	,367**	,143**	,429**	-,122**	-,463**
S10	-,042	,034	-,030	-,035	-,072	-,074	,075	,001	,070	,030	-,076	,074	,005	,041	-,011	-,071	,054	,071	,036	,108*	,108*	,128**	,038	-,095*
S11	-,187**	,301**	-,050	-,046	-,075	,102*	-,024	-,051	-,071	,082	,085	-,081	-,141**	,184**	-,042	-,182**	-,010	,057	,257**	,359**	,012	,036	-,194**	-,320**
S12	,168**	,140**	,096*	,014	-,111*	-,077	-,139**	-,054	-,100*	,096*	-,040	,279**	-,281**	-,172**	-,276**	-,298**	-,061	-,078	,033	,378**	-,153**	-,013	,093*	-,304**
S13	-,084	-,033	,043	-,064	-,038	-,070	,061	,056	,002	-,032	-,029	-,168**	,369**	,450**	,414**	,254**	-,001	,227**	-,111*	-,076	-,038	,009	,126**	,001
T1	-,152**	,731**	-,113*	-,022	-,149**	,077	,020	-,124**	,037	,106*	,068	-,014	-,250**	,030	-,202**	-,239**	,053	,297**	,431**	,282**	,124**	,221**	-,313**	-,428**
T2	,035	,016	,015	,009	,026	,017	,021	,029	-,025	-,005	-,035	,058	-,019	-,015	,005	-,013	,107*	,048	-,026	,059	,062	-,025	,043	-,053
T3	-,095*	,011	-,040	-,050	-,102*	-,126**	-,049	-,065	,121**	,164**	,005	,058	-,173**	-,017	-,200**	-,233**	-,052	-,101*	-,059	,036	-,117**	,018	,076	-,178**
T4	,016	,211**	-,013	,043	-,040	,091*	-,042	-,048	-,032	-,015	,025	,014	-,164**	-,060	-,146**	-,082	,001	,184**	,319**	,077	,058	,110*	-,226**	-,124**
T1	-,136**	-,051	-,080	-,079	-,043	-,021	,074	,036	,078	,041	,087	-,058	,017	,038	-,038	-,035	-,049	-,093*	-,069	-,047	-,022	,073	,042	,053
T2	,049	-,319**	,012	-,021	,136**	,031	,113*	,094*	-,057	-,146**	-,024	-,111*	,391**	,147**	,404**	,330**	,049	-,109*	-,330**	-,141**	,070	-,145**	,187**	,302**
H1	,120**	-,021	-,115*	-,118**	-,098*	-,123**	,186**	,017	,230**	,011	-,081	,097*	,090*	,032	-,043	,076	,212**	,068	,101*	,191**	,070	,105*	-,031	,140**
H2	,034	,080	-,087	-,063	-,067	-,023	,135**	,007	,125**	,011	-,027	,018	,020	-,157**	-,070	,097*	,115**	,131**	,205**	,161**	,122**	,135**	-,024	,107*
H3	-,113*	,232**	-,044	-,014	,002	,097*	-,031	-,034	-,043	,026	,073	-,022	-,068	,099*	-,060	-,111*	,021	,101*	,141**	,214**	,029	,162**	-,047	-,218**
H4	-,167**	-,177**	,040	,162**	,200**	,020	-,150**	-,050	-,089*	-,023	,025	,292**	-,282**	-,212**	-,291**	-,294**	-,155**	-,106*	-,198**	-,134**	-,019	-,050	,211**	,023
H5	,247**	-,036	,098*	,065	-,001	-,062	-,047	-,021	-,015	-,057	-,076	-,080	,180**	,058	,253**	,186**	-,081	-,039	-,011	-,046	-,043	-,059	,070	,129**
H6	-,098*	,055	-,163**	-,028	,023	,004	-,116**	-,207**	,155**	,218**	,071	,157**	-,141**	-,003	-,158**	-,176**	,068	,000	-,046	,090*	,118**	,224**	-,017	-,113*

	L8	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	T1	T2	T3	T4	T1	T2	H1	H2	H3	H4	H5	H6
L8	1,000																									
S1	,199**	1,000																								
S2	,079	,051	1,000																							
S3	,078	,045	-,024	1,000																						
S4	,305**	,071	-,093*	-,173**	1,000																					
S5	,012	-,031	,137**	,404**	-,432**	1,000																				
S6	-,024	-,021	,109*	,220**	-,278**	,248**	1,000																			
S7	,002	-,062	,097*	,063	-,210**	,148**	,160**	1,000																		
S8	,075	-,041	,116**	,401**	-,293**	,627**	,366**	,222**	1,000																	
S9	-,291**	-,107*	-,011	,058	-,734**	,249**	,160**	,185**	,112*	1,000																
S10	,067	,092*	,110*	,070	-,082	,164**	-,038	,044	,025	,088*	1,000															
S11	-,001	-,021	,140**	,243**	-,346**	,527**	,477**	,232**	,633**	,163**	-,037	1,000														
S12	-,193**	-,029	,088*	-,043	-,345**	,378**	,121**	-,056	-,032	,234**	-,030	,158**	1,000													
S13	,386**	,287**	,109*	,087	,011	,005	,036	,034	,045	-,135**	,088*	-,005	-,126**	1,000												
T1	-,188**	-,159**	-,027	,181**	-,478**	,298**	,288**	,147**	,270**	,566**	,069	,281**	,109*	-,101*	1,000											
T2	,191**	,007	,217**	-,033	,025	,054	,006	,002	,023	-,079	,103*	,018	,074	,126**	-,126**	1,000										
T3	-,184**	-,031	-,027	,024	-,218**	,053	,046	,018	,006	,100*	-,050	,064	,100*	-,056	-,088*	-,483**	1,000									
T4	-,244**	-,110*	-,102*	,067	-,147**	,072	,076	-,025	,055	,316**	-,010	,074	,073	-,180**	,524**	-,190**	-,413**	1,000								
T1	-,176**	-,037	-,125**	,030	,006	-,062	-,035	,037	,032	,036	-,091*	-,049	-,193**	-,138**	-,065	-,722**	,535**	-,145**	1,000							
T2	,486**	,195**	,107*	-,031	,372**	-,140**	-,133**	-,011	-,040	-,475**	,035	-,107*	-,228**	,291**	-,465**	,492**	-,316**	-,596**	-,356**	1,000						
H1	-,143**	-,068	-,042	-,039	,000	-,035	-,153**	-,056	-,038	,136**	,022	-,054	-,031	-,077	-,011	-,052	-,050	,013	,115**	-,002	1,000					
H2	-,078	-,044	-,036	-,062	-,005	,027	-,049	-,049	,012	,118**	-,029	,074	,001	-,113*	,021	-,042	-,033	,013	,109*	-,005	,362**	1,000				
H3	-,082	-,056	,249**	,119**	-,188**	,181**	,262**	,163**	,220**	,175**	,032	,213**	,072	-,017	,219**	-,011	-,013	,099*	,022	-,095*	,021	-,102*	1,000			
H4	-,014	-,047	-,077	-,032	,161**	-,068	-,053	-,041	-,048	-,135**	-,022	-,051	-,042	-,124**	-,121**	,052	,055	-,091*	-,025	,052	-,088*	-,145**	-,078	1,000		
H5	,190**	,137**	-,019	,071	,135**	,025	-,052	,005	-,069	,018	,038	-,083	,104*	,086	,018	,032	-,080	,085	-,141**	-,022	-,202**	-,598**	-,216**	-,162**	1,000	-,138**
H6	-,043	-,014	-,028	,033	-,073	,040	-,034	,036	-,019	,127**	,081	-,001	-,002	,004	,042	-,078	,112*	-,037	,073	-,062	,062	,052	,012	,178**	-,138**	1,000

KIA – Kilometric index of abundance; **Aspect variables**: A1 – flat, A2 – northeast, A3 – north, A4 – north2, A5 – northwest, A6 – southeast, A7 – east, A8 – south, A9 – southwest, A10 – west; **Climatic variables**: C1 – annual mean precipitation, C2 – annual maximum temperature, C3 - July maximum temperature, C4 - annual mean temperature, C5 – annual minimum temperature, C6 – annual mean radiance, **Land cover variables**: L1 – artificial areas, L2 – temporary crops, L3 – permanent crops, L4 – pastures, L5 – heterogeneous agricultural areas, L6 – coniferous and deciduous forests, L7 – open forest with shrub and/or herbaceous vegetation association + open areas with little and/or sparse vegetation, L8 – Water bodies; **Soil variables**: S1 – rocky outcrop, S2 – aluviosoils, S3 – clays, S4 – lithosoils, S5 – calcareous, S6 – halomorphic, hydromorphic and turfs, S7 – litholic, S8 – mediterranean brown calcareous semi-clay + mediterranean red calcareous semi-clay, S9 - mediterranean browns non-calcareous normal + mediterranean reds non-calcareous normal, S10 - mediterranean browns non-calcareous semi-brown + mediterranean red non-calcareous semi-brown, S11 - mediterranean brown non-calcareous semi-hidromorphic + mediterranean red non-calcareous semi-hidromorphic, S12 – mediterranean reds calcareous normal S13 – artificial areas, **Topographic variables**:T1 – valleys, T2 – lower slopes, T3 – gentle slopes, T4 – steeps slopes, T5 – uppers slopes, T6 – ridges, **Hunting areas variables**: H1 – unmanaged estates , H2 – associative hunting estates, H3 – municipal hunting estates, H4 – national hunting estates, H5 – tourist hunting estates, H6 – non-hunting estates

Principal components analyses results

Table 2 – Principal eight components results from PCA analysis.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard deviation	2.164	1.715	1.639	1.431	1.2718	1.177	1.094	1.038
Proportion of Variance	0.180	0.113	0.103	0.079	0.0622	0.053	0.046	0.041
Cumulative Proportion	0.180	0.293	0.397	0.475	0.5376	0.591	0.637	0.678
Eigenvalue	4.68	2.94	2.69	2.05	1.62	1.38	1.20	1.08

Table 3 – Eigenvalues of the eight principal components for the analysed variables.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
A1	-0,20121	0,311877	-0,20786	0,051301	-0,05286	0,081709	-0,3364	0,06459
A2	0,133007	-0,17655	-0,47536	0,113655	-0,00732	-0,0351	0,137793	0,052936
A3	0,083004	-0,18543	-0,42243	-0,17638	0,122108	0,087439	0,001136	-0,09521
A5	-0,14025	0,009162	0,079663	-0,58065	0,14036	0,008421	-0,011	-0,04867
A8	0,035756	0,15088	0,320546	0,482336	-0,09335	0,01384	-0,14697	0,030012
A9	-0,18359	0,128619	0,369705	0,089184	-0,1192	-0,23095	0,009387	0,130857
A10	-0,18794	0,065705	0,292366	-0,44685	0,032957	-0,09856	0,060261	0,04487
C2	0,339767	0,333219	-0,00713	-0,05106	0,117478	0,019324	0,070338	0,018232
C3	0,09486	0,291966	0,0123	-0,07979	0,079162	0,021937	0,377681	-0,01608
C4	0,345063	0,347862	-0,05077	-0,07867	0,028905	-0,0269	0,060366	0,077558
C5	0,359866	0,292311	-0,03057	-0,02337	0,080366	0,017345	-0,04773	0,032104
L5	-0,18109	0,023853	0,046771	-0,01872	0,42807	0,018398	-0,04611	0,057738
L7	0,349425	-0,10727	0,083147	-0,03124	-0,0904	0,093506	-0,20101	-0,05447
S3	-0,01123	0,125041	-0,06988	-0,03214	-0,14988	-0,13565	-0,17901	-0,60723
S4	0,337262	-0,19247	0,16182	-0,11312	-0,09547	0,027528	-0,21108	0,065114
S5	-0,13001	0,139949	-0,10223	-0,01695	-0,36231	-0,0982	0,281844	-0,12995
S6	-0,09499	0,10975	-0,20767	0,007182	-0,01238	0,094608	-0,20686	0,514854
S8	-0,1105	0,224824	-0,09468	-0,12234	-0,44141	0,124803	-0,03067	-0,15916
S9	-0,26955	0,133817	-0,11622	0,140322	0,419657	0,012161	-0,00847	-0,14702
S11	-0,10492	0,138517	-0,11514	-0,09931	-0,31003	0,256413	0,209993	0,232834
S12	-0,10757	-0,07984	-0,15023	0,201151	-0,06457	-0,43257	0,363539	0,09976
T1	-0,21829	0,285006	-0,19957	0,016148	-0,00772	0,046591	-0,3551	-0,05852
T5	-0,00148	0,003825	0,116442	0,018839	0,003977	0,421488	0,269332	-0,17666
H1	-0,03852	0,022226	0,062905	0,236403	0,178919	0,359759	0,142408	-0,32096
H4	-0,08031	-0,33973	0,006629	-0,02562	-0,2283	0,140867	-0,18469	-0,05851
H5	0,119278	0,056415	-0,08933	-0,05074	0,036097	-0,52415	-0,13133	-0,20123

Aspect variables: A1 – flat, A2 – northeast, A3 – north, A4 – north2, A5 – northwest, A6 – southeast, A7 – east, A8 – south, A9 – southwest, A10 – west; **Climatic variables**: C1 – annual mean precipitation, C2 – annual maximum temperature, C3 - July maximum temperature, C4 - annual mean temperature, C5 – annual minimum temperature, C6 – annual mean radiance, **Land cover variables**: L1 – artificial areas, L2 – temporary crops, L3 – permanent crops, L4 – pastures, L5 – heterogeneous agricultural areas, L6 – coniferous and deciduous forests, L7 – open forest with shrub and/or herbaceous vegetation association + open areas with little and/or sparse vegetation, L8 – Water bodies; **Soil variables**: S1 – rocky outcrop, S2 – aluviosoils, S3 – clays, S4 – lithosoils, S5 – calcareous, S6 – halomorphic, hydromorphic and turfs, S7 – litholic, S8 – mediterranean brown calcareous semi-clay + mediterranean red calcareous semi-clay, S9 - mediterranean browns non-calcareous normal + mediterranean reds non-calcareous normal, S10 - mediterranean browns non-calcareous semi-brown + mediterranean red non-calcareous semi-brown, S11 - mediterranean brown non-calcareous semi-hidromorphic + mediterranean red non-calcareous semi-hidromorphic, S12 – mediterranean reds calcareous normal S13 – artificial areas , **Topographic variables**:T1 – valleys, T2 – lower slopes, T3 – gentle slopes, T4 – steeps slopes, T5 – uppers slopes, T6 – ridges, **Hunting areas variables**: H1 – unmanaged estates , H2 – associative hunting estates, H3 – municipal hunting estates, H4 – national hunting estates, H5 – tourist hunting estates, H6 – non-hunting estates

Quantile regression results

Univarite models

Table 4 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC1).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
	10th	0,00 + 0,00*x*	0,00	1,000	0,0000
	20th	5,74 + 2,67*x*	1,08	0,014	0,0116
	30th	21,24 + 8,48*x*	1,44	0,000	0,0463
	40th	39,36 + 14,16*x*	1,60	0,000	0,0805
	50th	65,04 + 20,26*x*	1,79	0,000	0,1063
	60th	84,78 + 23,01*x*	2,45	0,000	0,1171
PC1	70th	116,66 + 26,47*x*	2,96	0,000	0,1128
	75th	133,68 + 29,94*x*	3,70	0,000	0,1066
	80th	160,40 + 34,71*x*	5,33	0,000	0,0966
	85th	194,85 + 38,80*x*	6,85	0,000	0,0877
	90th	255,78 + 39,17*x*	8,49	0,000	0,0817
	95th	351,36 + 45,40*x*	15,84	0,004	0,0731
	99th	525,99 + 35,20*x*	41,80	0,400	0,0250
Least-square Regression		Model *y*=100.18 + 21.57*x*	Std. Error = 4.17	*p*-value = 0.000	R^2 = 0.117

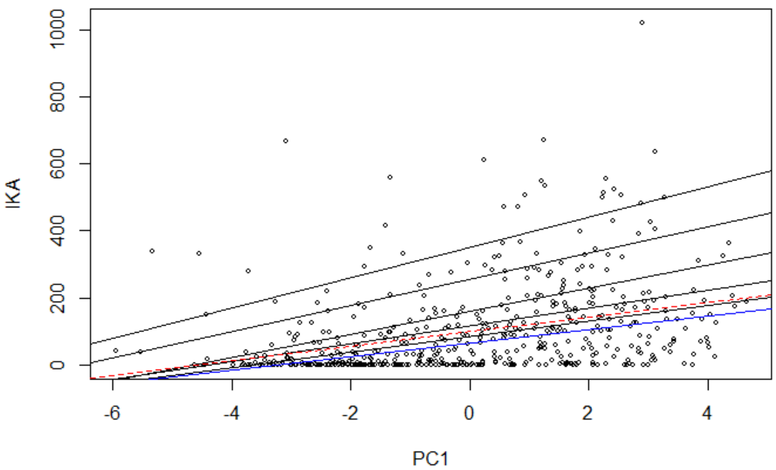

Figure 1 – Regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC1 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 5 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC2).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
PC2	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.00	1.000	0,0000
	30th	5.45 -0.39*x*	0.97	0.688	0,0001
	40th	21.63 + 1.81*x*	1.74	0.298	0,0004
	50th	50.77 -5.11*x*	2.85	0.073	0,0022
	60th	82.16 -8.03*x*	5.15	0.120	0,0054
	70th	124.65 -16.10*x*	4.43	0.000	0,0084
	75th	146.80 -18.75*x*	5.93	0.002	0,0116
	80th	181.81-20.77*x*	8.30	0.013	0,0172
	85th	224.56 -29.77*x*	5.73	0.000	0,0339
	90th	259.75 -37.17*x*	13.68	0.007	0,0420
	95th	379.90 -55.64*x*	5.41	0.000	0,0547
	99th	541.28 -76.26*x*	11.60	0.000	0,0861
Least-square Regression		Model *y*=100.18 -7.53*x*	Std. Error = 3.512	*p*-value = 0.007	R^2 = 0.007

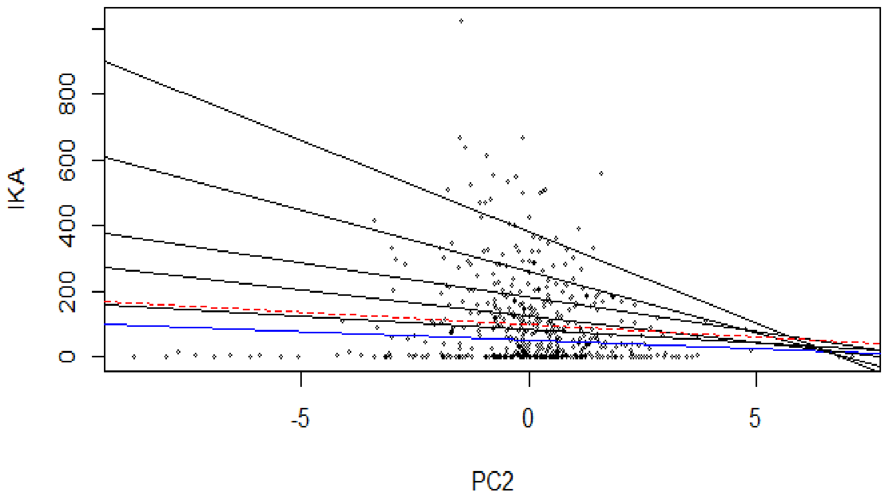

Figure 2 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC2 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 6 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC3).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.29	1.000	0,0000
	30th	7.23-2.03*x*	1.44	0.148	0,0013
	40th	22.14 -5.90*x*	2.95	0.045	0,0051
	50th	48.14 -5.72*x*	4.06	0.159	0,0073
	60th	83.76 -6.60*x*	2.45	0.175	0,0041
PC3	70th	119.83 -8.19*x*	6.41	0.202	0,0041
	75th	150.34 -7.01*x*	7.33	0.339	0,0032
	80th	178.28 -11.87*x*	9.40	0.207	0,0079
	85th	213.62 -23.52*x*	9.47	0.013	0,0124
	90th	268.72 -27.56*x*	12.69	0.030	0,0243
	95th	377.35 -46.63*x*	22.12	0.035	0,0345
	99th	574.63 -80.66*x*	33.74	0.017	0,1108
Least-square Regression		Model *y*=100.18 -10.78*x*	Std. Error = 3.659	*p*-value = 0.003	R^2 = 0.015

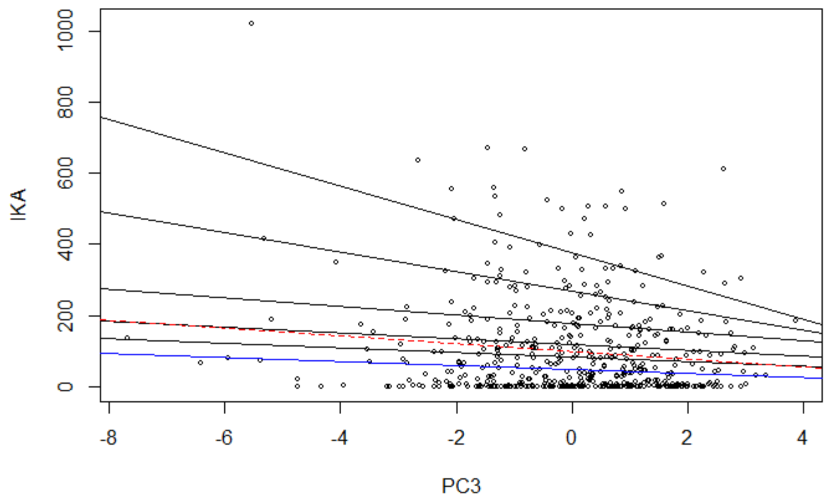

Figure 3 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC3 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 7 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC4).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
	10th	0.00 + 0.00*x*	0.00	1.000	0.0000
	20th	0.00 + 0.00*x*	0.63	1.000	0.0000
	30th	10.11+ 5.26*x*	2.15	0.014	0.0087
	40th	28.49 + 13.88*x*	2.09	0.000	0.0262
	50th	53.46 + 19.85*x*	4.25	0.000	0.0371
	60th	83.50 + 23.22*x*	5.29	0.000	0.0324
PC4	70th	121.27 + 24.64*x*	5.84	0.000	0.0326
	75th	145.73 + 24.97*x*	6.88	0.000	0.0354
	80th	165.71+ 26.09*x*	7.52	0.000	0.0302
	85th	210.48 + 22.20*x*	9.47	0.013	0.0229
	90th	273.53 + 20.95*x*	14.47	0.148	0.0135
	95th	365.63 + 27.93*x*	19.44	0.151	0.0172
	99th	571.34 + (-29.94)*x*	24.17	0.216	0.0162
Least-square Regression		Model *y*=100.18 + 15.95*x*	Std. Error = 3.659	*p*-value = 0.003	R^2 = 0.026

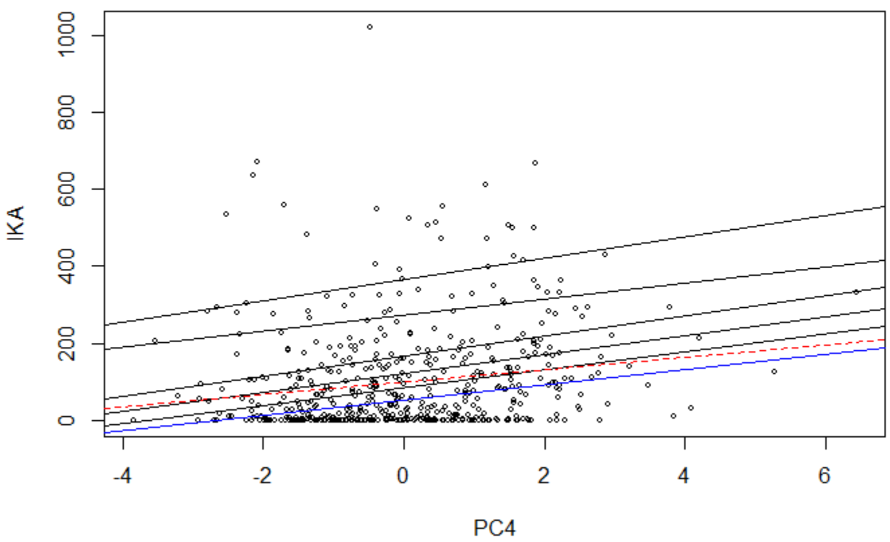

Figure 4 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC4 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 8 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC5).

	Quantile	Model *y*=	Std. Error	*p*-value	R[1]
	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.20	1.000	0,0000
	30th	6.03 + 0.91*x*	0.73	0.216	0,0006
	40th	22.20 + 2.18*x*	4.05	0.589	0,0008
	50th	47.16 -2.85*x*	6.35	0.653	0,0002
	60th	85.56 -7.00*x*	6.15	0.254	0,0008
PC5	70th	128.78 -21.16*x*	7.77	0.006	0,0084
	75th	152.51 -31.66*x*	9.54	0.000	0,0160
	80th	176.42-32.76*x*	10.34	0.001	0,0189
	85th	210.05 -40.07*x*	14.01	0.004	0,0258
	90th	258.44 -54.61*x*	16.28	0.000	0,0229
	95th	377.41 -85.11*x*	11.00	0.000	0,0267
	99th	597.64 -19.70*x*	36.65	0.591	0,0044
Least-square Regression		Model *y*=100.18 -20.11*x*	Std. Error = 5.062	*p*-value = 0.000	R^2 = 0.029

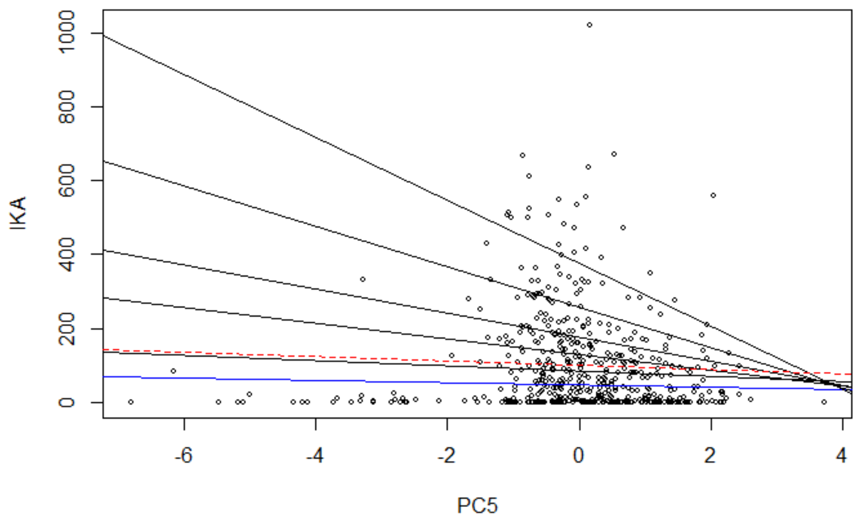

Figure 5 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC5 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 9 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC6).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.33	1.000	0,0000
	30th	7.38 -2.92*x*	1.27	0.021	0,0043
	40th	24.07 -13.10*x*	4.89	0.000	0,0161
	50th	45.67 -2.85)*x*	6.35	0.007	0,0156
	60th	82.63 -18.86*x*	6.96	0.007	0,0135
PC6	70th	122.90 -27.68*x*	5.24	0.000	0,0183
	75th	146.59 -25.33*x*	8.11	0.000	0,0207
	80th	176.55-36.84*x*	10.02	0.001	0,0207
	85th	216.30 -43.94*x*	13.00	0.001	0,0266
	90th	265.79 -33.02*x*	17.25	0.056	0,0282
	95th	384.50 -51.28*x*	18.45	0.005	0,0481
	99th	526.45 -37.71*x*	50.82	0.458	0,0540
Least-square Regression		Model *y*=100.18 -11.29*x*	Std. Error = 5.507	*p*-value = 0.040	R^2 = 0.029

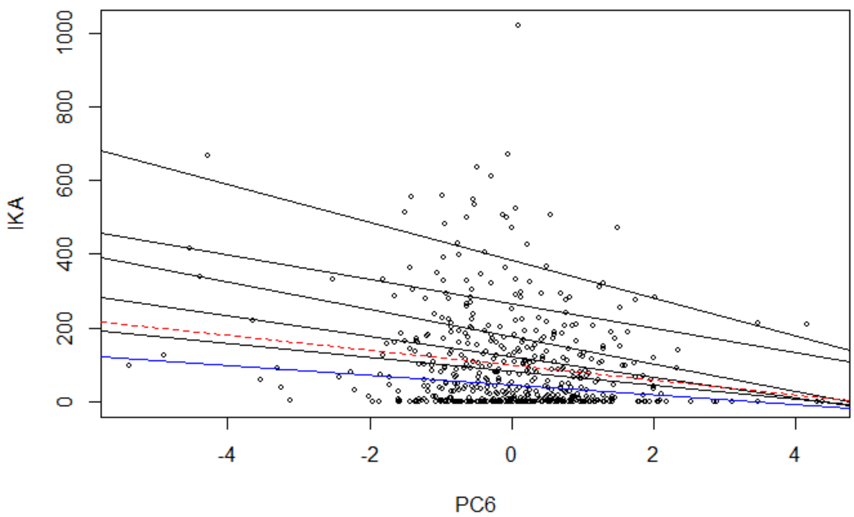

Figure 6 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC6 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 10 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC7).

	Quantile	Model *y*=	Std. Error	*p*-value	R[1]
	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.23	1.000	0,0000
	30th	5.87 -2.06*x*	2.00	0.302	0,0019
	40th	24.07 + (-8.46*x*	2.94	0.004	0,0051
	50th	47.04 + (-8.88*x*	5.61	0.113	0,0039
	60th	85.94 + (-14.10*x*	7.29	0.054	0,0061
PC7	70th	123.33 -20.60*x*	5.24	0.015	0,0079
	75th	149.65 -14.35*x*	8.47	0.090	0,0103
	80th	183.21-9.48*x*	9.48	0.028	0,0060
	85th	206.42 -26.63*x*	15.90	0.095	0,0079
	90th	273.29 -18.61*x*	18.61	0.292	0,0042
	95th	387.84 -22.04*x*	26.29	0.402	0,0073
	99th	572.38 -38.21*x*	85.24	85.24	0,0041
Least-square Regression		Model *y*=100.18 -11.29*x*	Std. Error = 5.507	*p*-value = 0.040	R^2 = 0.029

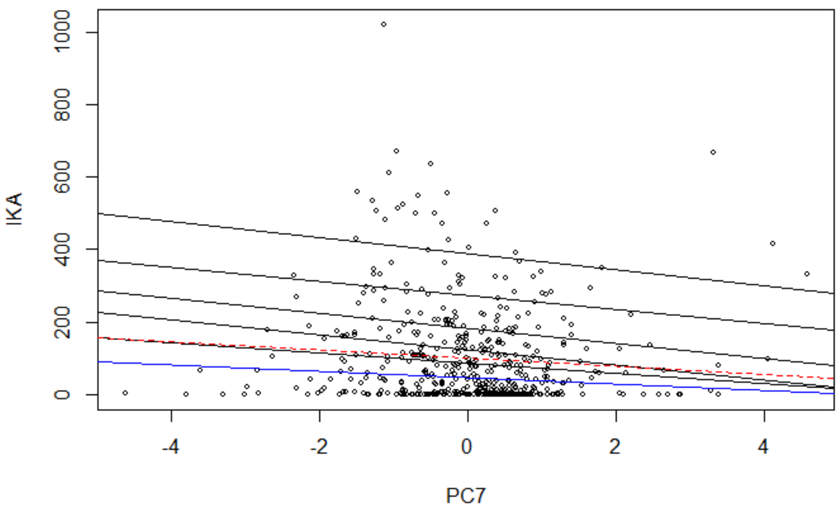

Figure 7 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC7 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.

Table 11 – Estimates of slope, intercept, standard error for the H0: slope=0 for thirteen selected regression quantiles, where *y* is the dependent variable (IKA) and *x* is the independent variable (PC8).

	Quantile	Model *y*=	Std. Error	*p*-value	R^1
	10th	0.00 + 0.00*x*	0.00	1.000	0,0000
	20th	0.00 + 0.00*x*	0.45	1.000	0,0000
	30th	5.85 -0.51*x*	2.17	0.812	0,0000
	40th	21.71 -1.23*x*	1.91	0.517	0,0001
	50th	48.22 -4.27*x*	4.88	0.381	0,0008
	60th	84.89 -7.00*x*	6.17	0.257	0,0010
PC8	70th	120.88 + 9.5*x*	5.24	0.282	0,0011
	75th	151.34 + 12.48*x*	8.82	0.158	0,0020
	80th	171.48+ 2.64*x*	10.91	0.808	0,0006
	85th	207.14 -2.96*x*	11.84	0.802	0,0001
	90th	282.78 + 5.84*x*	19.13	0.760	0,0001
	95th	365.21 + 33.75*x*	7.49	0.000	0,0059
	99th	560.96 + 51.95*x*	10.69	0.000	0,0202
Least-square Regression		Model *y*=100.18 -11.29*x*	Std. Error = 5.507	*p*-value = 0.040	R^2 = 0.029

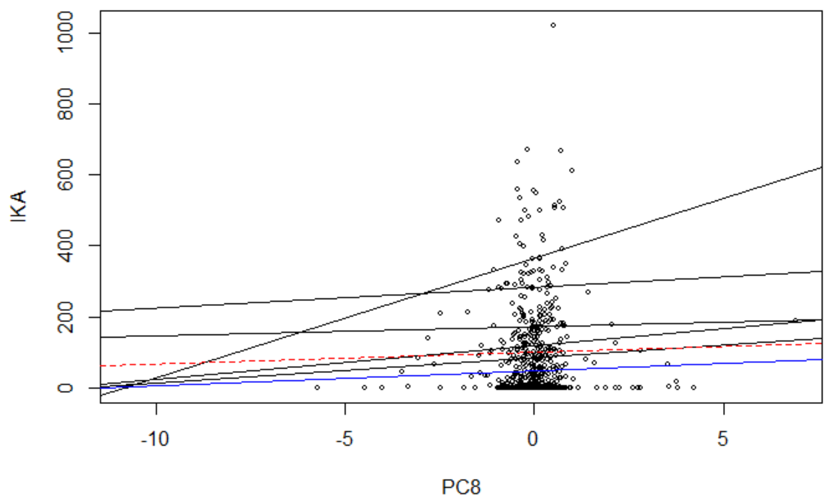

Figure 8 – regression lines for the 0.60, 0.70, 0.80, 0.90 and 0.95 quantiles of PC8 in black, the median fit in blue and the least squares estimates of the conditional mean function as the dashed red line.