Prey availability for a declining sub-population of Bonelli's Eagles (*Aquila fasciata*)

Technical University of Braunschweig

Institute for Geoecology

Department for Landscape Ecology and Environmental Systems Analysis

Max Martin Hoppe

Student number: 4162554

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First Supervisor: Prof. Dr. Frank Suhling

Second Supervisor: Dr. Pedro J. Leitão

INSTITUT FÜR GEOÖKOLOGIE
Landschaftsökologie und
Umweltsystemanalyse

Statutory Declaration

I declare that I have authored this master's thesis "Prey availability for a declining sub-population of Bonelli's Eagles (*Aquila fasciata*)" independently, that I have not used any other than the declared sources, and that the thesis has not been previously presented.

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Ich erkläre hiermit an Eides statt, dass ich die vorliegende Masterarbeit

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Abstract

The Bonelli's Eagle (*Aquila fasciata*) is a rare raptor, whose population is decreasing in most parts of Europe. The negative trend has been particularly dramatic in the Portuguese-Spanish international natural parks "Douro Internacional" and "Arribes del Duero". One of the main reasons for this is the decline of their two main prey species, European Rabbits (*Oryctolagus cuniculus*) and Red-legged Partridges (*Alectoris rufa).* I used Boosted Regression Trees (BRT) to predict the spatial distribution of their probability of occurrence (PO) based on latrine counts of rabbits and driven transect census of partridges. The predictions were used to evaluate differences in the prey availability between occupied and unoccupied areas in general, as well as between individual occupied and abandoned territories. The results indicate significantly higher PO of partridges in occupied areas than in unoccupied areas. Similar, but insignificant results were found for rabbits. Some of the abandoned territories could have been left due to the lack of optimal prey. Other currently occupied territories with critically low prey availability have been identified. Important land-use variables predicting the occurrences of prey species are discussed.

Zusammenfassung

Habichtsadler (*Aquila fasciata*) sind seltene Greifvögel, deren Bestand in vielen Teilen Europas abnimmt. Einer der Hauptgründe für diese Abnahme ist der Bestandseinbruch der beiden Haupt-Beutetiere, Wildkaninchen (*Oryctolagus cuniculus*) und Rothuhn (*Alectoris rufa*). Der negative Trend war besonders dramatisch in den internationalen Naturparks „Douro Internacional" und „Arribes del Duero" in der portugiesisch-spanischen Grenzregion. Basierend auf Latrinen-Zählungen von Kaninchen und gefahrenen Transekten-Zählungen von Rothühnern habe ich mittels Boosted Regression Trees (BRT) die räumliche Vorkommenswahrscheinlichkeit dieser beiden Arten vorhergesagt. Diese Vorhersagekarten wurden benutzt, um Unterschiede zwischen besetzten Adler-Territorien und unbesetzten Gebieten, sowie zwischen besetzten und kürzlich verlassenen Territorien zu erkennen. Die Ergebnisse zeigen, dass die Vorkommenswahrscheinlichkeit von Rothühnern in besetzten Territorien signifikant höher war als in unbesetzten Gebieten. Für Kaninchen gab es ähnliche, jedoch nicht signifikante Tendenzen. Einige Territorien könnten mangels optimaler Beutetiere verlassen worden sein. Andere zurzeit besetzte Territorien haben sehr geringe Beutetiere-Bestände. Wichtige Landnutzungsvariablen, die das Vorkommen der beiden Haupt-Beutearten vorhersagten, werden diskutiert.

Resumo

A Águia de Bonelli (*Aquila fasciata*) é uma ave de rapina rara, cujas populações estão em declínio em várias partes da Europa. Esta tendência negativa tem sido particularmente dramática nos parques naturais do "Douro Internacional" e "Arribes del Duero". Uma das maiores razões para esse decréscimo é a redução das duas espécies-presa mais importantes, o Coelho-Bravo (*Oryctolagus cuniculus*) e a Perdiz-Vermelha (*Alectoris rufa*). Usei Boosted Regression Trees (BRT) para prever a distribuição espacial da sua probabilidade de ocorrência, com base em censos de latrinas para os coelhos, e censos em transectos de carro para as perdizes. As previsões foram usadas para avaliar diferenças na presença das presas, entre áreas ocupadas e não-ocupadas em geral, assim como entre territórios

ocupados e abandonados. Os resultados indicam probabilidades de ocorrência significantemente superior de perdizes em áreas ocupadas do que em áreas não-ocupadas. Para os coelhos as tendências foram semelhantes, mas não significantes. Alguns dos territórios abandonados podem ter sido deixados por falta de presas ótimas. Variáveis de uso do solo, usadas para prever a ocorrência das espécies presa, são discutidas.

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1. Introduction

The Bonelli's Eagle (*Aquila fasciata* – Vieillot 1822) is a top predator in Mediterranean ecosystems and is considered to be an umbrella and flagship species (Real et al., 2016). It is a non-migratory species (Hernández-Matías et al., 2013) with a global population of more than 20,000 pairs.

In Europe, the species exclusively breeds in Mediterranean habitats below 1500 meters above sea level, mainly surrounded by shrubland (Carrete et al., 2002). Their nests are mostly located in cliffs higher than 20 meters (Arroyo et al., 1990), except for a recently growing tree-nesting population in southern Portugal (Dias et al., 2017). The recent IUCN Red List of Threatened Species categorizes its status as *Least Concern (LC)*. However, the European population size is estimated to consist of only 1100 to 1200 pairs, with still declining trends for the metapopulation (BirdLife International, 2016). Spain holds most of the European subpopulation, while approx. 120 pairs breed in Portugal (SPEA, unpublished Data) and approx. 30 pairs in southern France (Burger et al., 2013). Together, the local populations in these three countries are part of one demographically and genetically connected population (Hernández-Matías et al., 2013).

The Bonelli's Eagles' population suffered a significant decrease of approx. 30 % over the last five decades in Europe (BirdLife International, 2016). In Spain, the population declined by 25 % between 1980 und 1990 (Arroyo et al., 1995). In Portugal, the population declined by 15 % within the last decade of the 20th century, with a particularly severe loss in the northeast of the country (Arroyo & Ferreiro, 1999).

The International Douro Natural Park in northeastern Portugal (PNDI) and northwestern Spain (PNAD) is the northwesternmost nucleus of Bonelli's Eagles. Since the year 2000, the number of couples in PNDI & PNAD dropped from 19 to only 14, with most losses on the Portuguese side. The mean productivity of 0.6 fledged chicks per couple is the lowest on the Iberian Peninsula (Hernández & Real, 2014).

Human activities are either directly or indirectly responsible for the decline of populations, mainly persecution through shooting (Ontiveros & Pleguezuelos, 2000; Carrete et al., 2002), but also trapping and poisoning (Real et al., 2001). In some areas, electrocution on power lines is a substantial risk for an increased mortality (Real & Mañosa, 1997).

The apparent causes for population declines in the study area are the high subadult and adult mortalities and an extremely low reproductive success, as demographic results of the threats and pressures mentioned above (Arroyo & Ferreiro, 1999; Hernández-Matías et al., 2013). The higher adult mortality can aggravate the lower reproductive success, as more subadults are involved into breeding (Balbotín et al., 2003). These individuals have lower experience and competitive abilities and tend to occupy lower quality habitats and consequently have less success breeding (Martínez et al., 2008; Penteriani et al., 2003; Carrete et al., 2006).

The scarcity of suitable habitats and breeding locations, as well as decreasing prey densities, intensifies intraguild competition among the multiplicity of raptors in the Iberian Peninsula (Martínez et al., 2008; Carrete et al., 2006; Gil-Sánchez et al., 2004). The most important competitive species for the Bonelli's Eagle is the Golden Eagle (*Aquila chrysaetus*) (Gil-Sánchez et al., 2004). The Golden Eagle has similar

habitat and feeding requirements to the Bonelli's Eagle but is in competitive advantage due to its bigger size and higher weight (Carrete et al., 2006).

The Bonelli's Eagle's productivity is prone to be reduced by the shortage of prey (Arroyo & Ferreiro, 1999; Muñoz et al., 2005). It is a species with facultative siblicide (Hernández-Matías et al., 2016). The death of the younger chicks by enforced starvation is relatively frequent and might be connected to food stress (Hernández-Matías et al., 2016). The two most important species in the Bonelli's Eagles' diet are the European Rabbit (*Oryctolagus cuniculus*) and the Red-legged Partridge (*Alectoris rufa*) (Ontiveros & Pleguezuelos, 2000; Palma et al., 2006; Moleón et al., 2007; Moleón et al., 2009). In case of scarce optimal prey species, the importance of secondary, suboptimal prey grows (Moleón et al., 2012). The consumption of these species provides less energy in relation to the hunting effort. Most secondary prey species are common small to mid-sized birds - mainly Pigeons (*Columbidae*) (Ontiveros & Pleguezuelos, 2000) - and Iberian hares (*Lepus granatensis*) (Ontiveros et al.,2005; Caro et al., 2011). Both main prey species are popular game species and have suffered recent population declines, partially because of intense human persecution (Buenestado et al., 2009; Smith & Boyer, 2008; Millán, 2009; Tapia & Domínguez, 2007).

The rabbits' population diminished in two massive outbreaks of diseases: Myxomatosis in the 1950s and the rabbit haemorrhagic disease (RHD) in the 1980s/1990s (Delibes-Mateos et al., 2009). The obliterating impacts of these diseases on rabbits were especially high in suitable habitats with originally higher densities (Calvete et al., 2006). Because of these outbreaks and consequently lower densities of rabbits, the hunting pressure on partridges increased. The hypothesis of hyper-predation by raptors has been disproven (Blanco-Aguiar et al., 2012).

The loss of habitat due to agricultural intensification negatively influences both species (Ales et al., 1992; Delibes-Mateos et al., 2009; Blanco-Aguiar et al., 2012). Rabbits and partridges have similar habitat requirements, preferring diverse, patchy mosaics of Mediterranean shrubland with low human populations (Ferreira & Delibes-Mateos, 2010; Monzón et al., 2004; Martins et al., 2002; Jiménez-García et al., 2006; Herranz et al., 2000). For partridges, the highest densities are found in pseudo-steppe landscapes in central and southern Spain (Casas et al., 2009; Vargas et al., 2006), while the densities are lower in the northern Iberian Peninsula (Gortázar et al., 2002; Tapia & Domínguez, 2007).

For rabbits, habitat management is suggested to be the most effective approach to reverse the negative population trends, along with changes in hunting practices (Delibes-Mateos et al., 2009).

Soutullo et al. (2008) found that even a slight decrease of the pre-adult mortality of Bonelli's Eagles could stabilize the population. The action plan for the Bonelli's Eagle points out the big negative influence of food shortage on this population (Arroyo & Ferreiro, 1999). Preliminary reports, realized within the LIFE Rupis project, support the hypothesis of low prey availability for most couples of Bonelli's Eagles (LIFE Rupis, 2016). The population in the study area was found to have an exceptionally high consumption of suboptimal species such as passerines and reptiles, while rabbits and partridges constituted less than half of their food during the breeding period (Hernández et al., 2012).

Although Ontiveros & Pleguezuelos (2000) found that trophic resources were not relevant for choosing nesting sites in Granada (SE Spain), this could differ in low density areas like the study area (see Chapter **2.1**). The food availability for the Bonelli's Eagles in the study area and its ecological causes need to be understood in order to improve their current demographic situation.

Due to the severity of the population declines, conservation measures are currently focused on the LIFE-Rupis project.

The aim of this study is to predict the spatial distribution of the main prey species partridges and rabbits via the probability of occurrence in the joined nature parks. I aim to understand the realized habitat preferences for these species in this area. I will evaluate if the prey availability influences the occupancy or abandonment of territories. In order to do so, I will analyse differences regarding the predicted prey occurrence between 9 occupied, 4 unoccupied territories of Bonelli's Eagles and 24 randomly selected pseudo-absence areas. For modelling, I will use census data collected for LIFE-Rupis in 2017, high resolution land-use maps, topographic and climatic data, and process them on home range level in Boosted Regression Tree Models (BRT). I will identify territories with low prey availabilities. This will help targeting supplementary feedings and habitat management actions for increasing the population of prey species in those areas.

2. Methods

2.1. Study area

The Parque Natural do Douro Internacional (PNDI) in the Northeast of Portugal and the Parque Natural de Arribes del Duero (PNAD) in the Northwest of Spain, are located along the river Douro (Spanish: Duero) and its tributary Águeda. High breeding densities and species diversity make this area one of the most important regions for the conservation of rupicolous birds (Monteiro, 2011). Breeding raptors and scavengers include Griffon Vultures *Gyps fulvus*, Golden Eagles, Eagle Owls *Bubo bubo* and Peregrine Falcons *Falco peregrinus* (Monteiro, 2011). European Rabbits and Red-legged Partridges exist in the area, though probably in low abundance (Monteiro, 2011). Between 2001 and 2017, the number of breeding pairs of Bonelli's Eagles in PNDI declined from 14 to 8 (ICNF, 2017). Established in 1998, PNDI protects an area of 85,146 ha. A Special Protection Area (SPA) of 50,744 ha is part of the Natura 2000 network. The PNAD covers another 106,105 ha (*Fig. 1*).

The local climate is Mediterranean with subcontinental influence (Ozenda & Borel, 2000). It is marked by a long, intense summer dryness and annual mean temperatures of more than 15°C. There are orographically induced microclimatic differences between the plateaus (max. 900 m a.s.l.) and the valley (min. 125 m a.s.l). The climate in the plateaus is comparatively milder, while the temperature amplitude is more pronounced in the valley. The average annual precipitation locally falls below 400 mm in the southern parts of PNDI and reaches up to 1000 mm in the northern-central PNDI. This corresponds with the Atlantic influence in the so-called Terra Fria ("Cold Land") and the more continental Terra Quente ("Hot Land") (Monteiro, 2011).

The human population density in the region is very low, with about 14 inhabitants per km² (INE, 2012) and still suffers declines and aging, caused by high unemployment rates and very low average incomes (IGP, 2005). Agriculture is the main economic sector in the region (Rodrigues, 2008). The most important agricultural products are wine, olives, almonds, and animal farming products, mainly from sheep and goats. As in many areas of the Mediterranean, agricultural intensification took place mainly in lowlands with rich soils, whereas mountainous or highland regions, like the study area, tend to be abandoned, leading to the conversion of small areas of pasture and fields into shrubs (Ales et al., 1992).

Despite the low population density and land abandonment, human disturbance impacts wildlife. Hunting is not prohibited in the park, which is known to be one of the most severe sources of disturbance (Hill et al., 1997).

2.2. Field work

2.2.1. Bonelli's Eagles' territories

The locations of Bonelli's Eagles' nests, their occupancy, and breeding success in the study area are systematically surveyed by different local organizations, and thus can be considered accurate and complete. A dataset of occupied and abandoned territories on the Portuguese side was provided by the project coordinator SPEA. In 2017, 9 territories were occupied and 4 were abandoned. Territories are

defined as circles of 4 km radius around the nests. This corresponds with their home range size during the breeding season (Pérez-García et al., 2013).

2.2.2. Prey Species' census

Given the large size of the study area, the census of rabbits and partridges was executed by different teams - Palombar in the northern and ATN in the southern half on the Portuguese side, and Junta de Castilla y León-Fundación Patrimonio Natural de Castilla y León on the Spanish side. All surveyed transects in the study area and the position of the study area within the Iberian Peninsula are shown in *Fig. 1*.

Red-legged Partridges were surveyed only on the Portuguese side of the study area. They were mapped on 13 driven transects of about 12.5 km length by teams of two (driver and observer). Driven transects are an accurate and efficient method for estimating partridge densities (Borralho et al., 1996). Each transect was surveyed three times between beginning of March and end of April 2017 to increase the chance of detecting occupied areas. In addition to visual observations, acoustic observations of calling males were made on 9 listening points per transect. A total of 65 encounters were recorded during the census.

For the European Rabbit census, latrines consisting of at least 20 droppings in discrete clusters of 0.04 m², similar to the definition by Delibes-Mateos et al. (2009), were mapped along walked transects of 2.5 hours each. In total, 54 transects with a length of 282 km were completed between June and November 2017 - 33 in the Spanish part and 21 in the Portuguese part of the international park. A total of 829 latrines was recorded during this census.

Fig. 1*: Left: Location of the study area. Right: Location of the rabbit census transects in light grey and partridge census transects in black within the "Parque Natural do Douro Internacional" (PNDI) in Portugal and the "Arribes del Duero Natural Park" (PNAD) in Spain.*

2.3. Data analysis

2.3.1. Extracting predictors

I used a large set of variables, consisting of landscape metrics, climatologic and topographic maps, to model the probability of occurrence of rabbits and partridges. Two high-resolution land-use maps were combined. For Portugal, I used COS2010 (DGT, 2016) with a resolution of 0.5 m. For Spain, I used a map derived from the Copernicus Land-monitoring Service with a resolution of 2.5 m (EEA, 2015), that covers the NATURA 2000 area in PNAD. These two maps were combined by condensing the categories to a total number of 13 land-use categories: urban, crops, crops with permanent cultures, agroforestry, vineyards, groves, pastures, woodland, forests, shrubs, rocks, water and rest (see supplementary materials *App.1* for recategorization table).

For extracting landscape metrics information, I used FRAGSTATS (McGarigal et al., 2012). On Class-level, I calculated 22 metrics and on Landscape-level, 16 metrics (*Table 1*). For calculating the core metrics, I used a fixed Edge Depth of 25 m as done by Narce et al. (2012), and for the Distribution Statistics, a search radius of 500 m. A list of all used landscape metrics and how to interpret them, is compiled in the supplementary materials (*App. 2*)

Table 1: FRAGSTATS landscape metrics used in the initial models.

Acronym	Variable	Unit	applied on Class level	applied on Landscape level
PLAND	Percentage of Landscape	%	yes	no
ED	Edge Density	m ha^{-1}	yes	yes
AREA AM/MN	Patch area	ha	no	yes
PARA AM/MN	Perimeter-Area ratio	-	yes	yes
SHAPE AM/MN	Shape Index	-	yes	yes
FRAC AM/MN	Fractal Dimension Index	-	yes	yes
CONTIG AM/MN	Contiguity Index	-	yes	yes
TCA	Total Core Area	ha	yes	no
CPLAND	Core Percentage of Landscape	%	yes	no
NDCA	Number of disjunct core area	-	yes	no
DCAD	Disjunct Core Area Density	no. km^{-2}	yes	no
CORE MN	Core area	ha	yes	no
DCORE MN	Disjunct Core area distribution	ha	yes	no
CAI MN	Core Area Index	%	yes	no
ENN MN	Euclidean Nearest Neighbor	m	yes	no
PROX MN	Proximity Index	-	yes	no
NP	Number of patches	-	no	yes
PD	Patch density	no. km^{-2}	yes	yes
AI	Aggregation index	%	yes	yes
COHESION	Patch Cohesion Index	-	yes	no
PR	Patch richness	-	no	yes
SHDI	Shannon Diversity Index	-	no	yes

For bioclimatic information, CHELSA Bioclim variables, with a resolution of ca. 1 km, were obtained (Karger et al., 2017). Furthermore, the average of 16-daily maximum value composite NDVI data from CGLOPS (2017), was calculated for September 2016 until August 2017. This period represents the time between the end of the previous year's breeding season and the end of the considered breeding season of 2017 of the Bonelli's Eagles (Real et al., 1998). A digital elevation model of the Copernicus Land Monitoring Service (EU-DEM v1.1) was used for the altitude and for calculating the slope in ArcMap (EEA, 2017).

An OpenStreetMap layer on primary, secondary and tertiary roads, including links, was used as a base for the most important roads in the study area (OpenStreetMap, 2018). As some roads were missing in this layer, asphalted roads connecting villages were detected using aerial photos and manually added. I calculated the Euclidean Distance in ArcMap to roads and to the land-use class 'Urban', as possible indicators for human accessibility and disturbance.

2.3.2. Generating pseudo-absence and presence areas

The point data from the observations were transformed to area data by buffering them. Partridges have a home range of ca. 50 ha (Buenestado et al., 2009), consequently the observations were buffered by 400 meters. Rabbits' home ranges vary depending on the quality of the habitat (Devillard et al., 2008). Therefore, a buffer of 90 m was used, corresponding with an assumed average of 2.5 ha home range (Villafuerte, 1994). In case of overlapping presence-buffers, all except for one were eliminated. This guaranteed the independence of the observations. As a result, the number of presences declined to 42 for partridges and to 188 for rabbits. Pseudo-absences were generated along the surveyed transects, with the respective buffer distance to the next observed presences and absences. This led to 89 and 920 pseudo-absences for partridges and rabbits, respectively. The resulting prevalence was 0.17 for rabbits and 0.32 for partridges.

For each presence and pseudo-absence, I extracted the information about the predictors within the buffer areas. Regarding the altitude, slope, bioclimate, NDVI and distances to roads and the class 'Urban', I extracted the mean, the minimum and the maximum, to account for differences of these variables within each buffer.

2.3.3. BRT modelling

BRTs combine the advantages of decision trees and boosting (Elith et al., 2008). Decision trees are robust against missing data and irrelevant input variables. Boosting increases the performance of classifiers and makes the models robust against overfitting, leading to high predictive accuracy and good interpretability (Friedman, 2001). The modelling was performed in R (version 3.3.1) using the 'gbm' package (Ridgeway, 2007) and following the working guide instructions by Elith et al. (2008).

In the first step, I built initial models with all predictors included, using all combinations of tree complexities (maximal number of splits for fitting each regression tree) ranging from one to seven, according with the suggestions of Hastie et al. (2009). I used learning rates of 0.01, 0.005, 0.001, 0.0005 and 0.0001 for partridges and 0.05, 0.01, 0.005 and 0.001 for rabbits. Learning rates are the shrinking parameter that determine the contribution of each decision tree to the full model. The higher the learning rate, the higher is the contribution of each used decision tree and the faster is the model learning (Elith

et al., 2008). The functioning learning rates were determined in preliminary tests – models using higher learning rates were void by the program, models with lower learning rates did not converge within the limiting 10,000 steps. All models were executed with a bag fraction of 0.5. In that process, randomly selected subsets of training data were used for building the regression trees, which reduces biases and overfitting of the model (Hastie et al., 2009; De'ath, 2007). The best models using all variables were identified by their cross validated Area Under the Curve (AUC). The AUC classifies the quality of the models by their predictive accuracy. The values range between 0 and 1, representing a completely incorrect and completely accurate prediction, respectively. The best models of this first step were selected for proceeding with the next step.

In the second step, I removed all highly correlated variables (correlation coefficient |r| > 0.7), except for the ones with the highest explanatory influence in the best model selected previously, to prevent model distortion by collinearity (Dormann et al., 2013). Next, I repeated the modelling process with the reduced number of variables, to find the best model without highly correlated variables. Then, I assessed the order and number of variables that can be discarded without changing the predictive deviance in comparison to the full model and removed them, using the 'simplify' function. In the final step, I repeated the modelling process with the reduced number of variables to determine the final models with the highest AUC, which were then used for producing the prediction maps.

The predictors were added as ascii-grids, sized according to the home range of the modelled species - 160 m x 160 m for rabbits and 710 m x 710 m for partridges.

I repeated the whole modelling process to a total of ten models per species to achieve more robust results by averaging them. Furthermore, I calculated averages of the prediction maps and model parameters - number of variables used in the final model, tree complexity and learning rate - for all repetitions. A final AUC-value was calculated using the averaged prediction maps and the observed presence-absence data. Accounting for the combination of partridges' and rabbits' probability of occurrence (PO), I calculated the average of their PO in the ArcMap Raster calculator. The coarser resolution of the partridges' prediction map was chosen as a basis for the interspecific averaging.

2.3.4. Statistics

The number of samples for executing statistical tests needs to exceed 30. In order to find significant differences in the PO of the prey species between occupied and unoccupied territories, I added 24 randomly distributed pseudo-absences. A minimum distance of 7 km was chosen, corresponding with the minimum distance between two occupied nests in the study area. Their locations and names are shown in *Fig. 2*.

Next, I extracted the predicted probabilities of rabbits and partridges - individually and combined - within the 37 Bonelli's Eagles presence and (pseudo-)absence areas. I performed the Mann-Whitney U test to compare the mean deciles (10th to 90th percentile and maxima) of PO between occupied and abandoned/pseudo-absence territories. For assessing the predicted prey availability in each abandoned and occupied territory, I created boxplots of the distribution of PO of rabbits, partridges and their combined PO.
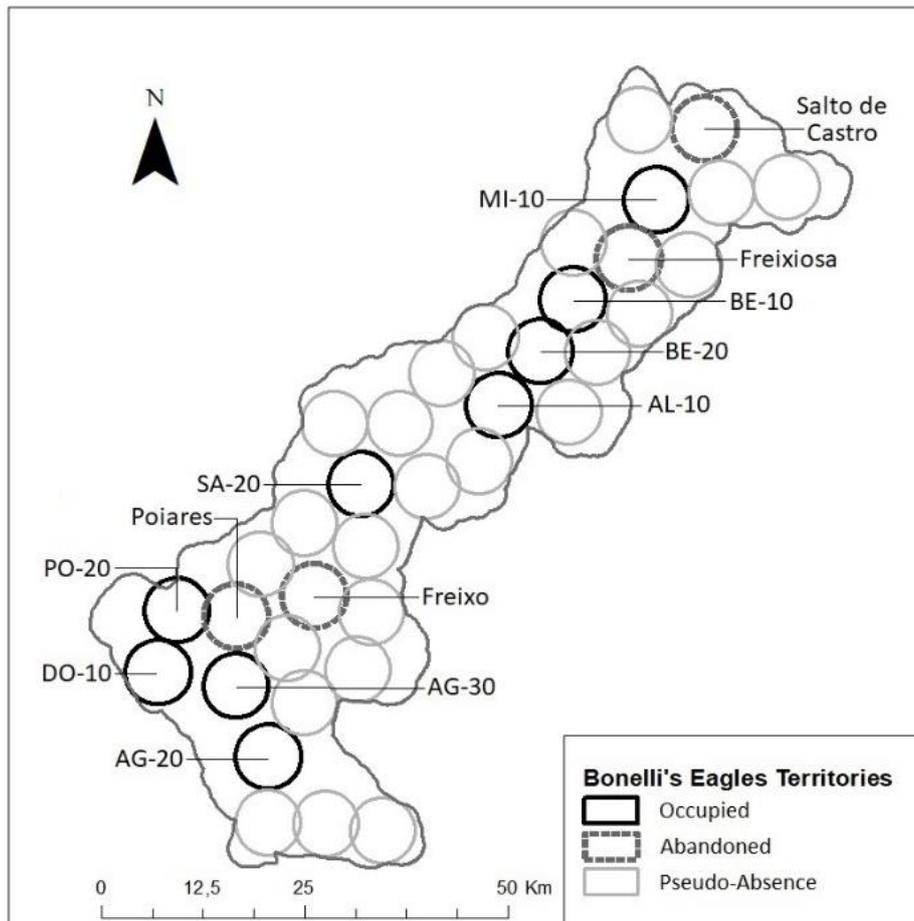
Fig. 2: *Location of occupied, abandoned and pseudo-absence territories of Bonelli's Eagles in PNDI/PNAD, with names of occupied and abandoned territories.*

2.3.5. Selection of important variables

For visual interpretation of predictor variables and responses, I consulted partial dependence plots (PDP) with smoothed response curves and rug plots of the response variables' distribution along the predictors' data range. Because of the high complexity of the models, I chose to only interpret the ecological meaning of important variables. They were defined as variables that were included in at least 9 of the final models with a high explanatory contribution to the model (Friedman & Meulman, 2003). Hence, I chose a threshold value that was higher than due to chance (see e.g. Müller et al., 2013). As the average number of predictors were 32.5 and 31.5 for rabbits and partridges, respectively, this resulted in threshold values of 3.1 and 3.2 % for their relative variable importance (VI).

3.   **Results**

3.1.   Model parameters

For rabbits, between 26 and 43 variables were used for the final models. All variables used in the final models are shown in the supplementary materials (***App. 3***). The tree complexity ranged between 4 and 7 splits in the decision trees. The learning rate ranged between 0.05 and 0.005; mostly 0.01 was used. The AUCs ranged between 0.834 and 0.852 with an average of 0.842, which indicates good and stable models (***Table 2***). The AUC derived from the average of all predictions was higher, with 0.89±0.01.

Table 2*: Number of variables, Learning rate, Tree complexity and AUCs of the ten final models, used for generating the prediction maps for European Rabbits in PNDI & PNAD. The mean AUC was calculated separately from the averaged prediction map and the observed data.*

Repetition	Number of variables	Learning rate	Tree complexity	AUC
1	27	0.005	6	0.843
2	36	0.005	5	0.834
3	26	0.005	6	0.839
4	29	0.01	6	0.846
5	43	0.01	6	0.84
6	28	0.01	5	0.84
7	29	0.01	4	0.839
8	41	0.01	5	0.839
9	26	0.01	7	0.843
10	40	0.05	4	0.852
Min	**26**	**0.005**	**4**	**0.834**
Max	**43**	**0.05**	**7**	**0.852**
Mean/Median	**32.5**	**0.01**	**5.5**	**0.89±0.01**

For partridges, the models were similarly complex, with a mean number of variables of 31.5 (range: 24 to 37). All variables used in the final models are shown in the supplementary materials (***App. 4***). The used tree complexities were ranging from 1 to 6. The learning rate varied between 0.01 and 0.0005, with a median of 0.005. The quality of the models varied considerably more than for the rabbits' models, with AUCs reaching values between 0.734 and 0.829 (average: 0.78). A value of 0.78 labels the predictive accuracy of models as reasonable, but because of the larger variation of the AUCs, as well as tree complexity and learning rate, the models showed larger variations (***Table 3***). The AUC of the average maps, however, was lower, with 0.70±0.05.

Table 3: Number of variables, Learning rate, Tree complexity and AUCs of the ten final models, of the ten final models used for generating the prediction maps for Red-legged Partridges in PNDI & PNAD. The mean AUC was calculated separately from the averaged prediction maps and the observed data.

Repetition	Number of Variables	Learning rate	Tree complexity	AUC
1	37	0.0005	5	0.734
2	34	0.005	1	0.75
3	32	0.001	3	0.771
4	24	0.01	3	0.829
5	33	0.005	4	0.779
6	27	0.005	6	0.813
7	29	0.005	1	0.806
8	33	0.001	1	0.787
9	32	0.005	2	0.777
10	34	0.001	3	0.751
Min	**24**	**0.0005**	**1**	**0.734**
Max	**37**	**0.01**	**6**	**0.829**
Mean/Median	<u>**31.5**</u>	**0.005**	**3**	<u>**0.70±0.05**</u>

3.2. Important Variables

For rabbits, eleven variables were found to have a high importance for explaining the rabbits' distribution (**Table 4**). These variables occurred in at least 9 of the repetitions and had a mean contribution to the model of more than 3.1 %.

The Aggregation Index of the class "shrubs" was the most important variable explaining the rabbits' presence. It occurred in all ten models with a mean importance of 10.7 %. The second most important variable was the NDVI (VI: 8.3 %), followed by temperature seasonality (VI: 7.2 %).

Table 4: Mean Variable Importance (VI) of the most influential variables, exceeding a VI of 3.1 % in at least 9 of 10 models predicting the European Rabbits' PO.

Variable Name	Mean Variable Importance (VI)
Aggregation Index 'Shrubs'	10.7 %
Normalized Difference Vegetation Index (NDVI)	8.3 %
Temperature Seasonality	7.2 %
Mean Distance to Major Roads	6.5 %
Precipitation Seasonality	5.4 %
Minimal Slope	5.4 %
Perimeter-Area Ratio	4.3 %
Minimal Altitude	4.3 %
Maximal Slope	4.2 %
Annual Precipitation	3.9 %
Mean Distance to Class 'Urban'	3.5 %

The Partial Dependence Plots (PDPs) of selected important variables were used for interpreting the prey species' responses to predictors (**F*ig. 3*)**.

The Aggregation Index of Shrubs (AIS) was the most important variable for the rabbits' models. With an increasing AIS, the modelled probability of occurrence of rabbits increased, peaking at 100 %, which represents a single, compact patch of shrubs. For the NDVI, maximum probability was predicted at low values of around 0.38, plateauing at low values between 0.4 and 0.5, before rapidly declining to the minimum for values higher than 0.55. The temperature seasonality, as well as precipitation seasonality, were present in all models, with an average influence of 7.2 % and 5.4 %, respectively. In both cases, lower seasonalities propose a tendency of higher rabbit probability of occurrence (PO). Rabbits showed a negative response to small distances to roads. The response was negative between 0 and 1500 meters, neutral between 1500 and 2500 meters distance, and strongly positive for distances above 2500 meters. A strongly positive response for areas with a very low minimal slope of less than ca. 5 % was detected, and a weaker response to low maximal slope values of less than 10 %. For the mean Perimeter-Area ratio on landscape-level, slightly positive responses occurred at very low and at higher values, while the response was negative in low- to midrange values. For the minimal altitude a positive response for values above 700 m was found. The annual rainfall had a slightly positive influence between 450 and 500 mm, and around 600 mm. Slightly negative influences were found at around 550 mm. There was an increased probability of rabbits' occurrence with increasing distance to the class 'Urban' for the first kilometer. The maximal positive response was found at ca. one kilometer distance. A slight negative effect occurred between ca. 1.5 and 3 km, followed by an increase between 3 and 4 km.

Fig. 3*: Partial Dependence Plots (PDP) with smoothed response curves of important variables for the prediction of European Rabbits' probability occurrence (PO) along their data range. The depicted variables occurred in at least 9 of 10 repetitions of the final models with a relative influence of over 3.1 %. The rug plots show the distribution of the response variables – presences on top of the x-axis and absences on the bottom of the x-axis.*

For partridges, four variables had a high influence on the final (***Table 5***). The Shannon's Diversity Index (SHDI), accounting for the number of patch types, was the most important variable explaining the partridges' distribution, occurring in all models with a mean importance of 8.2 %. The second most important variable was the Minimal Distance to the class 'Urban' (VI: 6.5 %), followed by the Fractal Dimension Index of the class 'Groves' (VI: 6.3 %) and the minimal distance to major roads (VI:5.75 %).

Table 5*: Mean Variable Importance (VI) of the most influential variables, exceeding a VI of 3.1 % in at least 9 of 10 models predicting the Red-legged Partridges' PO.*

Variable Name	Mean Variable Importance (VI)
Shannon's Diversity Index of landscape	8.2 %
Minimal Distance to Class 'Urban'	6.5 %
Fractal Dimension Index 'Groves'	6.3 %
Minimal Distance to Major Roads	5.75 %

The PDPs for partridges, that the analysis of the response to predictor variables was based on, is shown in ***Fig. 4***. A strong response was detected for SHDI-values of more than 1.5. High distances to the class 'Urban' positively influenced the partridges' occurrence. The fractal dimension index of groves had a positive influence for values over 1.1. Bigger minimal distances to roads resulted in a positive response.
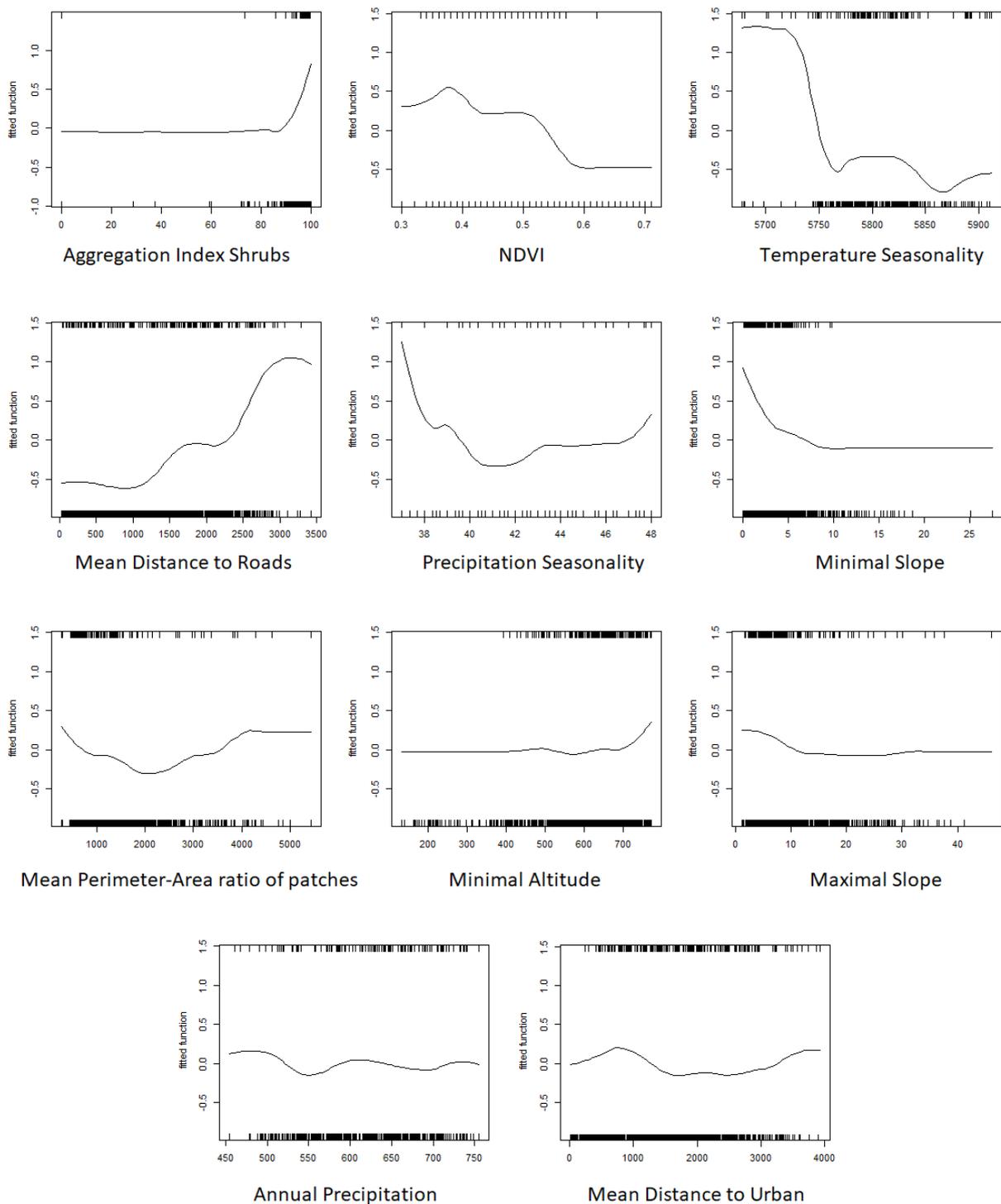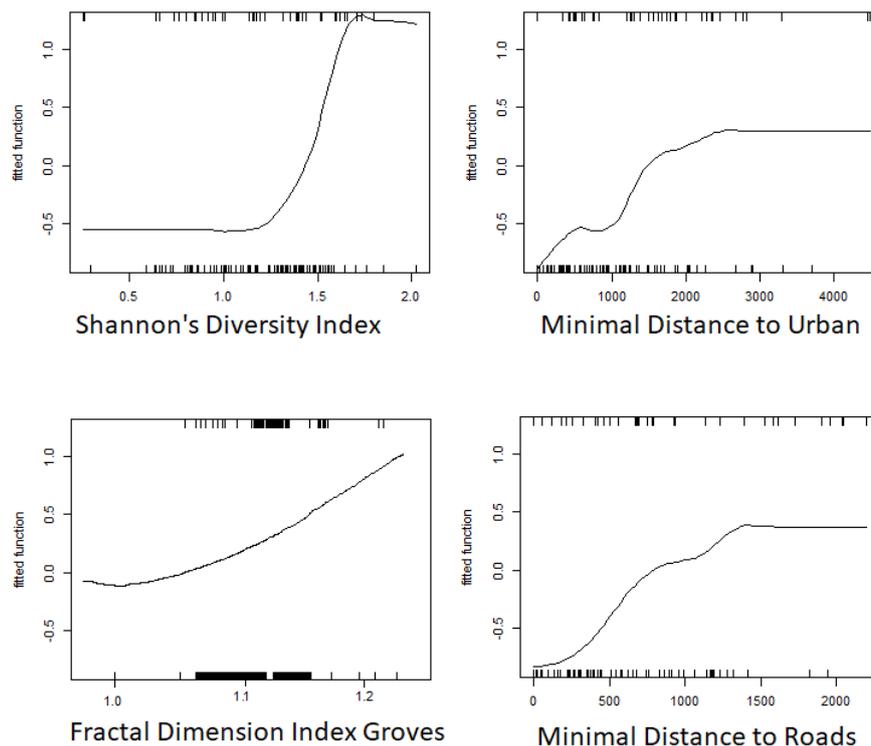

Fig. 4*: Partial Dependence Plots (PDP) with smoothed response curves of important variables for the prediction of Red-legged Partridges' probability of occurrence (PO) along their data range. The depicted variables occurred in at least 9 of 10 repetitions of the final models with a relative influence of over 3.1 %. The rug plots show the distribution of the response variables – presences on top of the x-axis and absences on the bottom of the x-axis.*

3.3. Prediction maps

The averaged prediction maps for rabbits' and partridges' PO are shown in ***Fig. 5***. The different resolutions are caused by the different home range sizes of the two species, which the calculation of the parameters used for generating the prediction maps was based on. The predicted probability of occurrence for rabbits was very low for most of the study area, mainly in the northern half and along the central canyons. Several areas of high to very high PO were found, for example, in the west of the southern half and in the far northeast.

For partridges, the predicted probability of occurrence was marked by more moderate values. Higher values tended to occur in the southern half and close to the canyons, while lower values occurred in the west of the northern half of the study area.
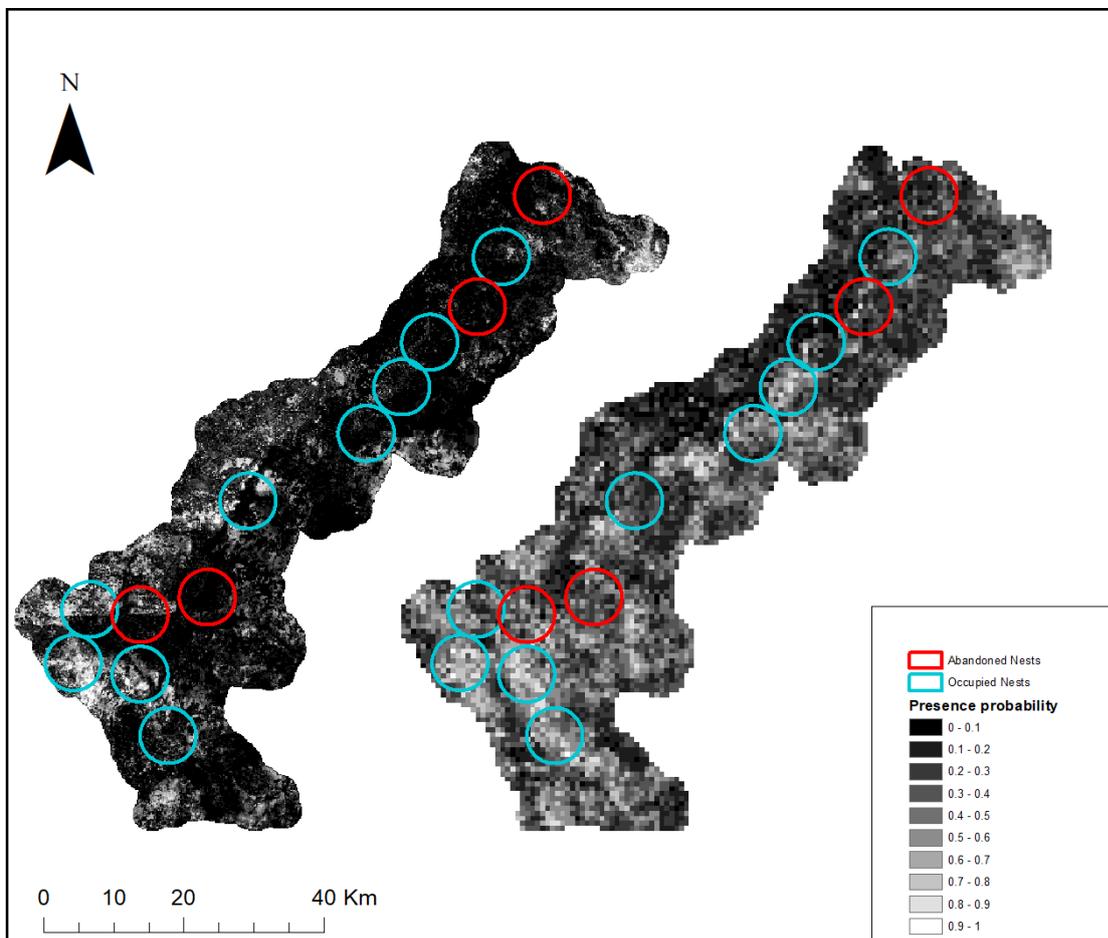
Fig. 5: *Predicted probabilities of occurrence of rabbits (left) and partridges (right) in the PNDI & PNAD. The blue circles represent the occupied territories of Bonelli's Eagles, the red circles represent abandoned territories in 2017.*

3.4. Statistical differences of prey probability of occurrence (PO) between occupied, abandoned and pseudo-absence areas

The comparison of mean values of the prey species' PO for all deciles, between occupied, abandoned and pseudo-absence areas, is shown in ***Fig. 6***.

For both rabbits and partridges, the modelled PO was higher in the occupied territories than in the abandoned and pseudo-absence areas at all deciles. The mean probability of rabbits' occurrence was the lowest for the abandoned territories and the highest for occupied territories. The probability of rabbits' occurrence in pseudo-absence areas was closer to the ones in occupied rather than in abandoned territories. For partridges, the PO was slightly higher in abandoned than in pseudo-absence areas.
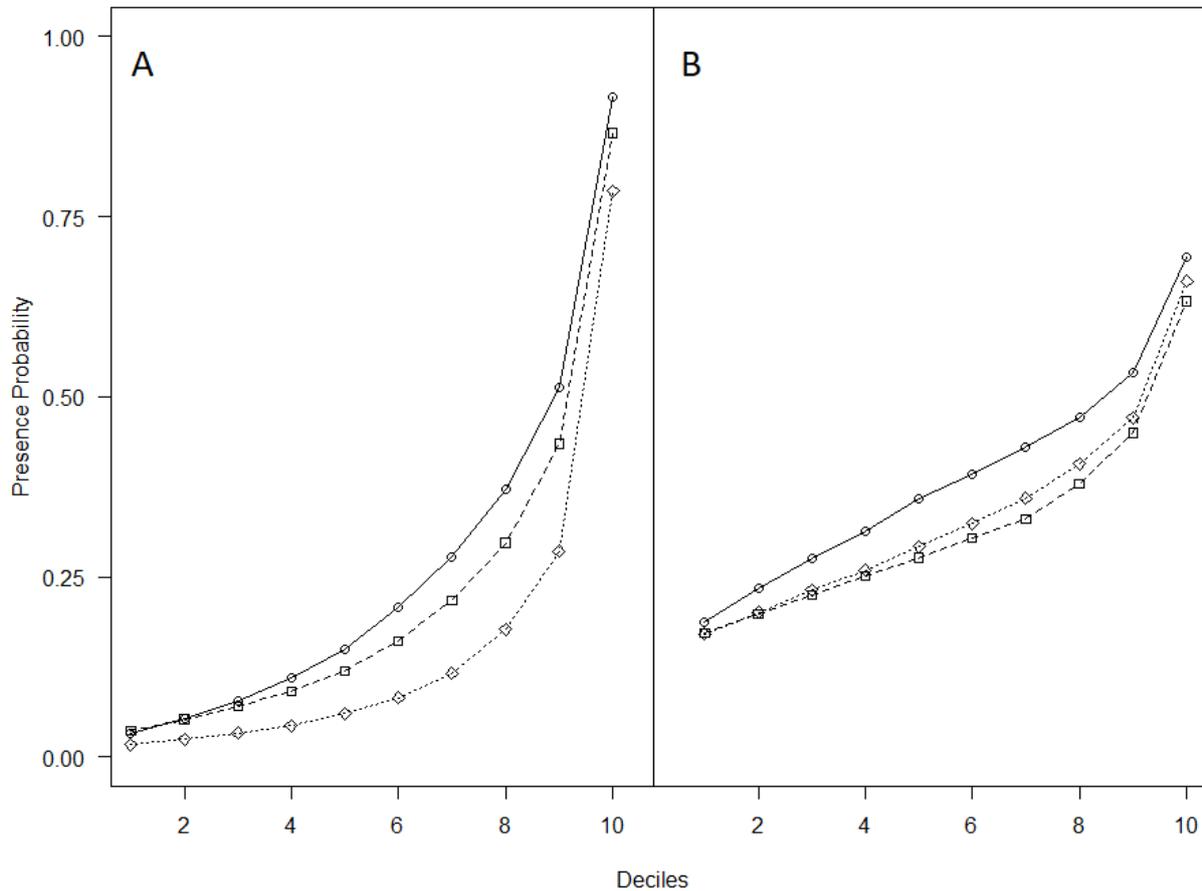
Fig. 6: *A: Rabbits; B: Partridges. Differences of the prey species' probability of occurrence (PO) between occupied* —⊖—, *pseudo-absence* –⊟– *and abandoned* ⋯◇⋯ *territories of Bonelli's Eagles in PNDI & PNAD. Values shown are the mean Po of each decile (10th to 100th percentile)*

The significance of the difference between presence and absence areas was tested with the Mann-Whitney U test. Absences were defined as the combination of abandoned territories and pseudo-absence areas. For rabbits, the p-value of this test decreased with higher deciles, reaching the minimum of 0.154 at the 10th decile (*Table 6*). The p-value showed a decreasing trend for higher deciles for partridges, but on lower levels. Between the 6th and 8th decile and at the 10th decile, the p-value was below 0.05, with a minimum of 0.007 for the 10th decile.

Table 6: *Significance of the differences in prey availability between occupied and abandoned/pseudo-absence territories of Bonelli's Eagles in PNDI & PNAD. For each decile, p-values of the Mann-Whitney U test are shown for differences in the modelled probability of rabbits' and partridges' occurrence.*

Deciles	1	2	3	4	5	6	7	8	9	10
Rabbits	0.79	0.57	0.66	0.50	0.43	0.47	0.41	0.34	0.30	0.15
Partridges	0.35	0.20	0.12	0.08	0.06	0.04	0.04	0.04	0.06	0.01

3.5. Prey availability in individual territories

Analyzing the prey availability in the territories individually (*Fig. 7*), the occupied territories *DO_10*, *PO_20* and *AG_30* had the highest PO for rabbits, with medians above 20 %. All these territories were situated in the southwest of PNDI. The lowest Po for rabbits were found in the occupied territory *BE_10* and the abandoned territories *Poiares* and *Castro*, with medians of around 5 %. In the abandoned territories *Freixo* and *Freixiosa*, the rabbits' PO was comparable to the PO of some occupied territories, like *AL_10*, with medians below 10 %.

Regarding the PO of partridges, the occupied territories *AG_30* and *DO_10*, as well as *AG_20*, had the highest values (medians: >50 %). They were located in the southwest of PNDI. The lowest values were found in the occupied territory *BE_10*, and the abandoned territories *Freixiosa* and *Castro*, with medians of around 20 %. The other abandoned territories *Freixo* and *Poiares* mean PO were comparable to occupied territories *AL_10* and *AG_20*.

When accounting for the combined PO of rabbits and partridges, the territories *DO_10*, *AG_30*, *PO_20* and *AG_20* had the highest value, with medians above 30 %. Among the abandoned territories, *Freixo* had the highest combined PO of rabbits and partridges, positioned at the 6th rank of all 13 analyzed territories. The abandoned territories *Poiares* and *Freixiosa* ranged at the lower half, still having a higher combined probability than the occupied territories *MI_10* and *BE_10* and the abandoned territory *Castro*. These three areas with the lowest values were located in the northern half of the study area. It became apparent that there were similar tendencies of rabbits' and partridges' PO within the same territories. Most territories with the highest PO of rabbits had high PO for partridges and vice versa (e.g. *DO_10* and *AG_30*), while many territories with very low rabbits' PO also had low PO for partridges (e.g. *BE_10* and *Castro*).
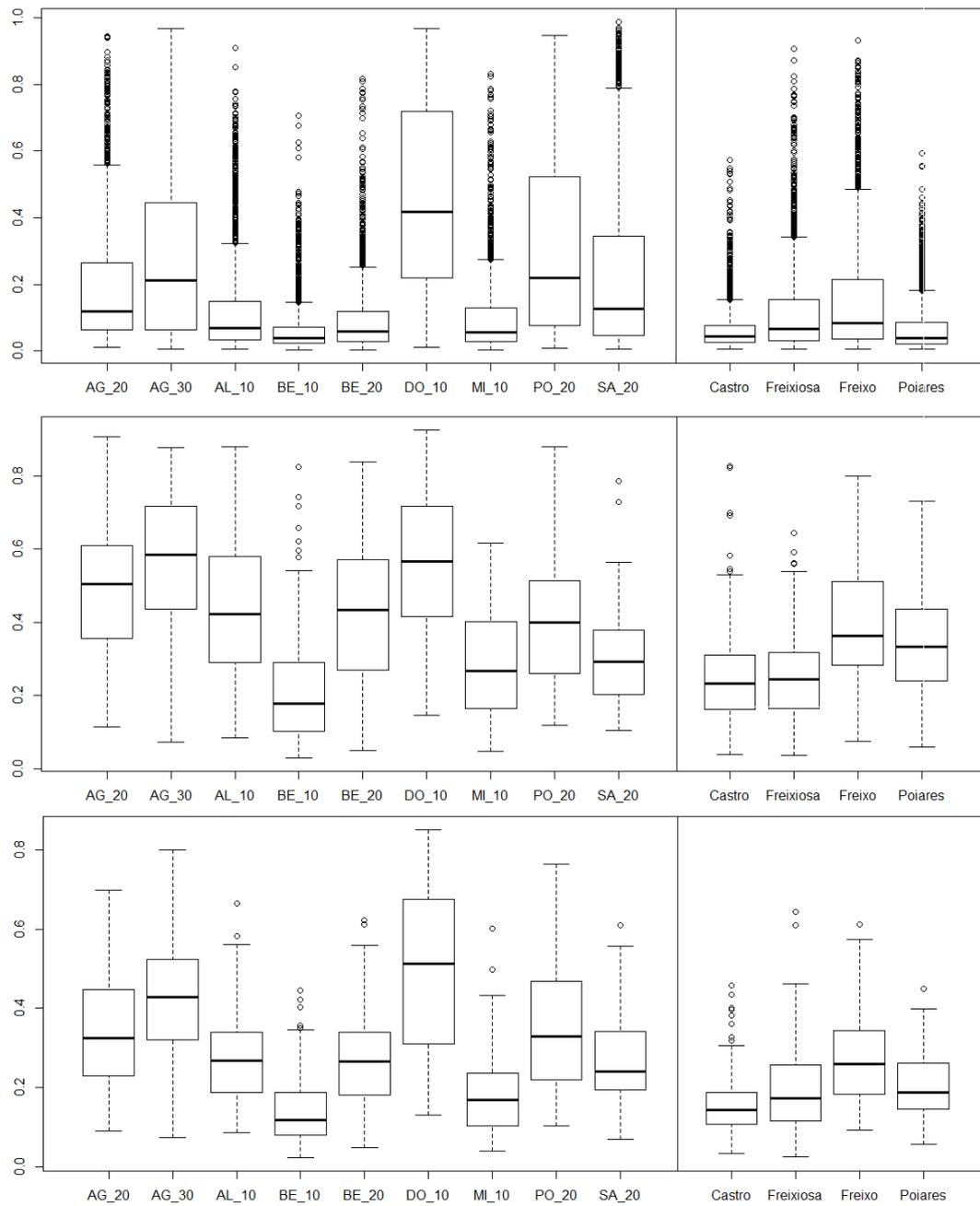
Fig. 7: *Boxplots of the modelled probability of occurrence (PO) of rabbits (top), partridges (center) and rabbits and partridges averaged (bottom), in occupied (left) and abandoned (right) territories of Bonelli's Eagles in PNDI. Thick lines indicate the median. The upper and lower boundaries of the boxes show the 75 % and 25 % quantiles, respectively. The bars at the end of the dotted lines are the extrema or the 1.5-fold of the interquartile range; the hollow circles are outliers.*

4. Discussion

4.1. Model quality

Both models provide adequate results that can be applied in conservational planning. This is indicated by their cross validated AUCs. The final averaged model for rabbits had a good predicting performance with an AUC of 0.89±0.01. The data used for modelling were latrine-counts. Hence, the predicted PO is that of permanent territories and not that of exploring individuals. Although this method has limitations, it is widely applied and useful to map the distribution of patchy populations (Putman, 1984; Iborra & Lumaret, 1997) and reliable even in low-density areas (Ferreira et al., 2010). Because data from Spain and Portugal were available, the models accounted for differences in the used land-use maps for both sides of the study area. The total number of presences and pseudo-absences used for modeling was high, with 1108 observations.

The model for partridges, however, needs to be interpreted with more caution for several reasons. First, the predictive accuracy of the average model was comparatively low with an AUC of 0.7±0.05. As the AUCs of the individual repetitions were higher, the existence of increased differences between the repetitions of the models is a source of this deterioration. One reason for the poor predictive accuracy could be the lack of data on water availability, which consequently could not be included as a predictor variable in the models. Water availability is known to be one of the most important variables for predicting the abundance and distribution of partridges (Borralho et al., 1998; Reino et al., 2016; Díaz-Fernández et al., 2013), especially during spring and summer. Furthermore, census data were available only from the Portuguese side of the study area. Therefore, I could neither account for differences between the land-use maps, nor for actual differences in habitat use or abundance of partridges between the two countries. In total, the number of presences and pseudo-absences the models were based on, was comparatively low, with only 131 observations. Consequently, the results, especially for the Spanish side, need to be interpreted cautiously.

4.2. Important Variables

4.2.1. Rabbits

The presence of shrubs, especially their high aggregation index, was the most important variable explaining the occurrence of rabbits. Shrubs are an important component of rabbits' habitats, as they provide shelter in their otherwise open foraging habitats like grassland, crops and pastures (Monzón et al., 2004; Martins et al., 2002; Carvalho & Gomes, 2003). The rabbits might prefer and be able to develop healthy populations where this important shelter is abundant, as it lowers the predative pressure.

The positive response for lower NDVI values indicated an avoidance of areas with higher primary productivity like forests, which is also supported by Planillo & Malo (2017). However, NDVI values cannot directly be used for classifying vegetation types (Cord et al., 2013).

Rabbits' PO responded positively to a lower seasonality of temperature and precipitation. The climatic seasonality is more pronounced in valleys (Monteiro, 2011). This is additionally supported by the positive

influence of very low values of minimal slope, maximal slope, and of higher minimal altitude. This suggests a tendency of higher rabbit PO towards the plateaus in contrast to the valleys, which was also found by Carvalho & Gomes (2004).

The minimal distance to main roads was the fourth most influential predictor and had a negative impact on the rabbits' PO for distances below 1500 m. Roads are associated with many negative effects on biotic ecosystems (Trombulak & Frissell, 2000), including increased human accessibility, e.g. for hunters. Sauvajot et al. (1998) discovered an increased landscape alteration associated with road proximity that negatively affected populations of mammals, especially within ca. 500 m radius.
The rabbits' response towards the Perimeter-Area ratio indicates that the habitats occupied by rabbits, consist of either big or small patches and less so of midsized patches (in relation to the size of the assumed home range of rabbits – ca. 2.5 ha).

The responses of rabbits' PO to the annual precipitation were hardly interpretable. Delibes-Mateos et al. (2009) found positive effects on rabbits' population trends in areas with annual rainfall between ca. 360 and 620 mm, which largely overlaps with the range found in the study area.

The positive response within 1 km distance to the class 'Urban' could be caused by the fact, that most villages in the study area are situated close to the rivers' valleys. Here, a transitioning zone between agriculture on the plateau and shrubs close to the canyons exists, which presumably offers best habitats for rabbits.

In conclusion, the PDPs of important variables suggest that in this area, rabbits are preferably found in plain highlands, covered by low-NDVI vegetation types, with highly aggregated shrub patches. A combination of big and small patches seems to be preferred. Their PO is increased in areas that are more than 2.5 km away from major roads. Other variables' tendencies are difficult to interpret.

4.2.2. Partridges

The SHDI indicated the importance of a high landscape diversity for partridges in the study area. Landscapes with diverse vegetation and diverse habitats, including a high edge index, are known to be important for high survival rates of this species (Buenestado et al., 2009; Herranz et al., 2000). In a diverse landscape they can use a variety of food sources and additionally profit from shelter availability given by high edge indices. A negative response to close distances to 'Urban' and to major roads was found, in accordance with findings by Tapia & Domínguez (2007) who described a negative influence of human presence on partridges' occurrence. This could be a direct consequence of the partridges' higher mortality or result indirectly by avoidance of areas close to humans as a response to hunting and mortality on roads. The positive response to a higher fragmentation index of groves suggests, that partridges were more likely to be found in complexly shaped patches of groves. This could be a positive response to highly diverse and complex landscape. Groves themselves can offer food and shelter on a small range and therefore support the species to obtain higher productivities and lower mortalities by reduced predation.

4.3. Prey availability in individual territories

The PO of partridges was significantly higher in occupied territories of Bonelli's Eagles than in abandoned territories and pseudo-absence areas. For rabbits, a similar tendency was found, but not on a significant level (p-value > 0.1). One reason for the differences not being significant, was that the modelled PO in occupied territories was only slightly higher than in pseudo-absence areas. The pseudo-absence areas might include occupied territories on the Spanish side, as I did not have access to data on their location. This implies that the pseudo-absence areas could contain high-quality areas for the species of prey and shift their PO to higher values. The difference between occupied and abandoned territories, however, was more pronounced. Similar tendencies of rabbits' and partridges' PO within the same territories were found. Therefore, the eagles might not be able to compensate the lack of one of the main prey species with an increased consumption of the other. These individuals would be dependent on sub-optimal prey species.

In conclusion, there was a tendency of higher modelled prey species' PO in occupied territories, and lower probabilities in abandoned territories. The most apparent exceptions were the occupied territories *MI_10* and *BE_10*, that ranged among the lowest values for both prey species' PO. Bonelli's Eagles in these territories might face limited food availability and could abandon these in the near future. The abandoned territory *Freixo* on the other hand, apparently offers sufficient prey and could be reoccupied if other disturbing factors, that will be discussed below, become irrelevant. A case study surveyed the composition of the diet Bonelli's eagles in four territories in the study area during the breeding season of 2014 (Hernández & Real, 2014). In the territory *MI_10*, only 20 % of all prey were European Rabbits and Red-legged Partridges. The rest consisted of secondary prey, mainly *Passeriformes.*

However, there were exceptions to this pattern. Some territories were abandoned, despite relatively good modelled prey availability. This could be caused by factors that were not considered in this study. One factor could be the acute death and/or general increased mortalities of Bonelli's Eagles in those specific areas. Apart from natural reasons, anthropogenic causes like persecution (Ontiveros & Pleguezuelos, 2000; Carrete et al., 2002; Real et al., 2001) or electrocution on power lines, which is a known problem in the study area (Real & Mañosa, 1997; Hernández & Real, 2014), could be responsible. Another factor could be the competition with other raptors, primarily Golden Eagles, who are competitively stronger than Bonelli's Eagles (Carrete et al., 2006) and have a population of ca. 20 couples in the study area (Monteiro, 2011).

The exceptional nature of occupied territories, despite very low modelled prey availability, could be caused by several reasons. First, only the PO was modelled, which does not necessarily reflect the species' abundance (Thuiller et al., 2014; Weber et al., 2017), although cases of correlations between occurrence and density exist (see e.g. Carrascal et al., 2015). Consequently, there is a chance that, despite generally low modelled PO, prey exists in sufficient abundance to be a food source for the Bonelli's Eagles within those territories. Additionally, it is acknowledged, that the population of Bonelli's Eagles in the study area consumes considerable amounts of secondary prey species besides their ideal prey - rabbits and partridges (Hernández et al., 2012). One potentially important secondary prey species is the Iberian Hare. During the rabbit census on the Portuguese side, also latrine data of hares were

collected, but were not included in this study. These data indicate that hares might occur more commonly in the north of the study area. Here, rabbits are predicted to be scarcer and hares could act as a supplementary prey species. This is also where the occupied territories *MI_10* and *BE_10*, with low modelled primary prey PO, are located. Lastly, supplementary feeding is a conservation measure that has been applied in many territories and could therefore compensate for low natural food resources (Hernández & Real, 2014).

5. Conclusion

Low prey availability is one of the main reasons for the decline of Bonelli's Eagles in the international Natural Parks PNDI and PNAD. Since 2001, the number of breeding couples dropped by 26 % in this most northwesterly nucleus of the species' distribution. This could be by an increased mortality due to persecution and electrocution on power lines, as well as a low breeding success and the abandonment of territories, which is directly related to the prey availability in the territories. Their two most important prey species, European Rabbits and Red-legged Partridges have suffered population declines for many decades due to diseases, habitat loss and persecution.

I used BRTs to predict the PO of the rabbits and partridges, based on census data, collected in 2017. I detected differences in prey availability between occupied, abandoned and pseudo-absence areas of Bonelli's Eagles and analyzed the predicting factors for the distribution of these species. Rabbits were predicted to be preferably found in the plain highlands with single patches of shrub and distance from major roads. Partridges preferred complex landscapes with groves and shrubs with low human disturbance. Both species, therefore, indicate sensitivity towards human disturbance. Although the actual reasons cannot be determined, it seems likely that hunting plays a role, as these are the two most important hunted species in the region. The predictive accuracy for the rabbits' model was very high. For partridges, however, the model quality was only sufficient, likely due to lower sample size, scale effects and the potential lack of water availability as one important variable. I found that occupied territories had significantly higher PO of partridges and - though not on significant levels - of rabbits, than abandoned and pseudo-absence areas. Despite a general tendency of higher prey availability in occupied territories, some show a very low predicted prey availability. On the other hand, some abandoned territories have a moderate prey availability. Thus, it can be concluded, that the availability of the two primary prey species is not a definite determinant for abandonment or occupancy of territories. Other factors like increased adult mortality, persecution, the availability of secondary prey and supplementary feeding, or interspecific competition with, for example, Golden Eagles could also influence it. My results highlight the potential positive influence of a higher preys' occurrence on occupancy of Bonelli's Eagles' territories, but even more the influence of very low prey availability on abandonment of the territories. This could be caused by the generally low prey densities of the study area, in contrast to findings in high density areas in SE Spain.

Rabbits and partridges seem to have similar large-scale habitat requirements in the study area, as suggested by the similar tendencies of both species in the individual territories. Therefore, territories with very low prey availability face the risk of future abandonment, as a compensatory effect of higher abundance of one of the prey species in case of absence of the other, is unlikely.

These results can be used, individually for each territory of the study area, to plan habitat management or other conservational measures. Continuing the efforts for establishing a better hunting practice in the region could possibly improve the prey availability for Bonelli's Eagles.

Acknowledgements

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Supplementary Material

App. 1: *Reclassification table of land-use classes used for combining the EEA and COS2010 land-use maps.*

EEA Code	Description EEA	CODE	Description	COS2010 Code	Description COS2010
1111 1113 1411	URBAN FABRIC Industrial, commercial and military units Green urban areas and leisure facilities	1	Urban	111	Continuous urban fabric
				112	Discontinuous urban fabric
				122	Road and rail network and associated spaces
				132	Waste dumps
				133	Construction Zone
				141	Urban green spaces
				121	Industry
				141/142	Sports, cultural and leisure grounds and historical zones
2111	Arable irrigated and non-irrigated land	2	Crops	211	Non-irrigated temporal crops
				212	Irrigated temporal crops
2311 2321 2331	Annual crops associated with permanent crops Complex cultivation patterns Land principally occupied by agriculture with significant areas of natural vegetation	3	Crops with permanent cultures and/or seminatural vegetation	241	Temporal crops and/or pastures associated with permanent crops
				242	Crop systems and complex mosaics
				243	Agriculture with natural and semi-natural spaces
2341	Agro-forestry	4	Agroforestry	244	Agroforestry
2211	Vineyards	5	Vineyards	221	Vineyards
2221 2231	Fruit trees and berry plantations Olive groves	6	Cultivated groves (olives or fruits)	222	Fruit orchards
				223	Olive orchards
4211 4212	Semi-natural grassland with trees (T.C.D. >30%) Semi-natural grassland without trees (T.C.D.<30%)	7	Pastures and Grassland	231	Permanent pastures
3231 3141	Other natural and semi-natural coniferous forest Broadleaved evergreen forest	8	Forests	311	Broad-leafed forests
				312	Coniferous forests
				313	Mixed forests
				324.07	Other woody formations
				324.08	Clear cuts of broad-leafed forests
				324.09	Clear cuts of coniferous forests
				324.10	New plantations of broad-leafed forests
				324.11	New plantations of coniferous forests
				33402.5	Burnt Eucalyptus forests
				33403	Burnt coniferous forests

3131 3411	Other natural and semi-natural broadleaved forest Transitional woodland and scrub	9	**Half-open Forests with shrubs**	324.01	Woodland of broad-leafed trees
				324.02	Woodland of broad-leafed and coniferous trees
				324.03	Single-species woodland of coniferous trees
				324.04	Mixed-species woodland of coniferous trees
				324.05	Woodland of broad-leafed with coniferous trees
				324.06	Woodland of coniferous with broad-leafed trees
				334021	Burnt cork oak forests
				334022	Burnt holm oak forests
				334023	Burnt oak forests
				334024	Burnt chestnut forests
				334027	Burnt forests of other broad-leafed trees
5112	Shrub	10	**Shrub and sparse vegetation**	321	Natural herbaceous vegetation
5211	Sclerophyllous vegetation			322	Shrubs
6111	Sparsely vegetated areas			323	Sclerophyll vegetation
5111	Heathlands and Moorlands			333	Sparse Vegetation
6221	Bare rocks and rock debris	11	**Rocks**	332	Bare rocks
9111	Interconnected running water courses	12	**Waterbodies**	5	Waterbodies
9113	Highly modified natural water courses and canals				
9211	Natural water bodies				
9213	Ponds and lakes with completely man-made structure				
9215	Standing water bodies of industrial sites				
1211	Roads	13	**Rest**	131	Mining areas
1311	Mineral extraction, dump and construction sites			334011	Burnt areas (not forests)
1321	Land without current use				
6213	River banks				

App. 2: FRAGSTATS variables used in the initial models and their meaning after McGarigal et al., 2012.

Variable	Interpretation
Percentage of Landscape [%]	How much of the landscape is comprised of a particular patch type
Edge Density [m/ha]	Length of edges of a particular patch type per area
Patch area [ha]	Patch area summarized at class level
Perimeter-Area ratio	Ratio of the patch perimeter (m) to area (m²)
Shape Index	Patch perimeter (m) divided by the square root of patch area (m²)
Fractal Dimension Index	Approaches 1 for shapes with very simple perimeters such as squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters
Contiguity Index	Assesses spatial connectedness of patches of a class
Total Core Area [ha]	Sum of core areas of each patch type (Core area: area within a patch beyond 25 m distance)
Core Percentage of Landscape [%]	Percentage of the landscape comprised of core area of the corresponding patch type
Number of disjunct core area	Number of disjunct core areas contained within each patch of the corresponding patch type
Disjunct Core area Density [number/100 ha]	Number of Disjunct core area per unit area
Core area [ha]	Core area of each class within a 25 m buffer of each patch
Disjunct Core area distribution	Core area index per disjunct core
Core Area Index	Quantifies the core area for the entire class.
Euclidean Nearest Neighbor	Measure of patch isolation
Proximity Index	Comparative index of the size and proximity of patches of the same type within 500 m
Number of patches	Number of patches per class
Patch density [number /100 ha]	Density of patches per landscape/class
Aggregation index [%]	Percentage of adjacencies of the same class
Patch Cohesion Index	Physical connectedness of the corresponding patch type
Patch richness	Number of patch types per landscape, simple measure of landscape composition
Shannon Diversity Index	Measure of diversity of patch types, with sensitivity towards rare patch types

App. 3: Variables used in the final rabbits' models.

Bioclimate	Mean annual precipitation
	Mean precipitation seasonality
	Mean precipitation of the driest quarter
	Mean precipitation of the warmest quarter
	Mean diurnal Temperature range
	Mean temperature seasonality
	Mean annual temperature range
Distance to human infrastructure	Mean distance to major roads
	Mean distance to class *urban*
Topography	Maximal slope
	Minimal altitude
	Minimal slope
NDVI	Mean Normalized Difference Vegetation Index (NDVI)
Landscape metrics	Aggregation index of patches on landscape level
	Aggregation index of the class *forests*
	Aggregation index of the class *groves*
	Aggregation index of the class *shrubs*
	Aggregation index of the class *half-open forests with shrubs*
	Area weighted mean of patch areas on landscape level
	Patch cohesion index of the class *pastures*
	Patch cohesion index of the class *half-open forests with shrubs*
	Mean contiguity index of the class c*rops with permanent cultures*
	Edge density of the class *crops*
	Edge density of the class *groves*
	Edge density of the class *pastures*
	Edge density of the class *shrubs*
	Mean fractal dimension index on landscape level
	Mean perimeter-area ratio of patches on landscape level
	Area-weighted mean of the perimeter-area ratio of the class *crops with permanent cultures*
	Mean perimeter-area ratio of the *class crops with permanent cultures*
	Mean perimeter-area ratio of the class *crops*
	Area-weighted mean perimeter-area ratio of the class *crops*
	Mean perimeter-area ratio of the class *forests*
	Area-weighted mean of the perimeter-area ratio of the class *forests*
	Mean perimeter-area ratio of the class *groves*
	Area-weighted mean of the perimeter-area ratio of the class *groves*
	Mean perimeter-area ratio of the class *pastures*
	Area-weighted mean of the perimeter-area ratio of the class *pastures*
	Mean perimeter-area ratio of the class *shrubs*
	Area weighted mean of the perimeter-area ration of the class *vineyards*
	Mean perimeter-area ratio of the class *half-open forests with shrubs*
	Patch density of patches on landscape level
	Patch density of the class *forests*
	Patch density of the class *vineyards*
	Percentage of landscape of the class *agroforestry*

*Continuation of **App. 3***

Landscape metrics	Percentage of landscape of the class *crops*
	Percentage of landscape of the class *groves*
	Percentage of landscape of the class *pastures*
	Percentage of landscape of the class *vineyards*
	Area-weighted mean of the landscape shape index
	Mean shape index of the class *crops with permanent cultures*
	Mean shape index of the class *pastures*
	Area-weighted mean of the shape index of the class *vineyards*
Landscape core metrics	Mean core area index of the class *crops with permanent cultures*
	Mean core area index of the class *crops*
	Mean core area index of the class *forests*
	Mean core area index of the class *shrubs*
	Mean core area index of the class *half-open forests with shrubs*
	Mean core area of the class *groves*
	Percentage of landscape of core areas of the class *shrubs*
	Mean disjunct core area distribution of the class *groves*
	Mean disjunct core area distribution of the class *shrubs*
	Total core area of the class *crops with permanent cultures*
	Total core area of the class *shrubs*
	Total core area of the class *vineyards*
	Total core area of the class *half-open forests with shrubs*

App. 4: Variables used in the final partridges' models.

Bioclimate	Minimal annual precipitation
	Minimal precipitation of driest quarter
	Mean precipitation of the driest quarter
	Mean isothermality
	Maximal annual temperature range
	Mean annual temperature range
	Mean temperature of the wettest quarter
Distance to human infrastructure	Minimal distance to major roads
	Minimal distance to the class *urban*
Topography	Maximal slope
	Mean Slope
	Mean contiguity index of patches on landscape level
	Mean contiguity index of the class *vineyards*
	Edge density of the class *crops with permanent cultures*
	Edge density of the class *shrubs*
	Mean euclidean neighbor of the class *forests*
	Mean euclidean nearest neighbor of the class *groves*
	Mean euclidean nearest neighbor of the class *shrubs*
	Mean euclidean nearest neighbor of the class *half-open forests with shrubs*
	Mean euclidean nearest neighbor of the class *vineyards*
	Mean fractal dimension index on landscape level
	Mean fractal dimension index of the class *groves*
	Mean fractal dimension index of the class *shrubs*
	Mean perimeter-area ratio of patches on landscape level
	Mean perimeter-area ratio of the class *crops with permanent cultures*
	Area-weighted mean perimeter-area ratio of the class *shrubs*
	Mean perimeter-area ratio of the class *vineyards*
	Patch density of the class *shrubs*
	Percentage of landscape of the class *shrubs*
	Percentage of landscape of the class *half-open forests with shrubs*
	Mean proximity index of the class *groves*
	Area-weighted mean shape index on landscape level
	Mean shape index of the class *forests*
	Mean shape index of the class *shrubs*
	Shannon's diversity index of landscape classes
Landscape core metrics	Mean core area index of the class *forests*
	Mean core area index of the class *shrubs*
	Mean core area index of the class *vineyards*
	Mean disjunct core area distribution of the class *shrubs*