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SCOPS OWLS IN VALAIS: DISTRIBUTION MODELING AND HABITAT CHARACTERISTICS

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par

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Résumé

Les paysages d'Europe centrale ont drastiquement changé depuis les années 50, particulièrement en raison de l'intensification des activités humaines. Les prairies extensives sont l'un des milieux les plus affectés par le management agro-pastoral intense qui est pratiqué en Europe. En Suisse, le Petit-duc Scops, *Otus scops*, est une espèce en danger typiquement représentative de ces habitats. Notre but est d'établir la répartition potentielle du Petit-duc Scops en fonction des conditions climatiques et des principales structures végétales du paysage. Pour cela, nous avons construit un modèle de distribution de l'espèce (SDM) à l'aide d'un Ensemble of Small Models (ESM) pour *O. scops* en Suisse. Nous avons trouvé que la répartition potentielle actuelle du Petit-duc Scops est la même que la répartition de l'espèce montrée dans les données historique des années 50. La perte des territoires qu'a subi l'espèce doit être due à des changements à un niveau plus fin. Pour cela, nous nous sommes concentrés sur 48 territoires de Petit-duc Scops dans la zone principale de présence de l'espèce, pour pouvoir détecter plus finement quels milieux ou structures les affectent directement. Nous avons analysé 30 milieux, grâce à une classification multivariée (MuMIn), tout d'abord en tant que prédicteurs de la présence potentielle du Petit-duc Scops sur un site, puis pour la fréquence d'occupation d'un site. Nous avons trouvé que de grandes surfaces de milieux ouverts (entre 75 et 90% du territoire), avec peu de couverture forestière, offrent un environnement favorable pour l'espèce. Environ 1ha de prairie d'*Arrhenatherion* extensif et 5% de la surface du territoire occupée par des ourlets boisés devraient assurer une mosaïque d'habitats idéale et une qualité suffisante pour les sites de reproduction. Nous n'avons pas pu montrer un impact de la densité de *Tettigonia viridissima*, la principale proie du Petit-duc Scops, sur les territoires. Nous avons par contre pu détecter un potentiel effet d'agrégation au sein de l'espèce, qui affecterait leur choix durant la sélection des territoires. La préservation des populations de Petit-duc Scops semble très dépendante de la restauration des paysages agro –pastoral traditionnels ou du moins extensifs. Nos résultats suggèreraient de protéger des surfaces 50 fois plus grandes que celles actuellement concernées par les plans de conservations mis en place pour le Petit-duc Scops.

Abstract

The landscapes of Central Europe have changed drastically since the fifties, essentially due to the intensification of human land use. Extensive grasslands were among the habitats most affected by the intense agro-pastoral management practiced in Europe. In Switzerland, the Scops Owl, *Otus scops*, is a typical conservation-sensitive species representative of these habitats. We aimed to assess the realized environmental range of the Scops Owl according to topo-climatic conditions and main landscape structures. We built a Species Distribution Model (SDM) with an Ensemble of Small Models (ESM) for *O. scops* in Switzerland. We found that the potential range of the species was the same than in the historical data from the 1950s, the loss of territories must be due to changes at a finer level. Therefore, we focused on 48 Scops Owl territories in the core zone of presence of the species to detect more finely which habitats and structures directly affect their presence. We analyzed 30 habitats predictors using multivariate classification (MuMIn), to firstly understand what influence the presence<- of the Scops Owl, and secondly the occupancy frequency of the territories. We found that a large amount of open areas (between 75% and 90% of the surface) with a low forest cover offered a favourable habitat for the Scops Owls. Approximately 1ha of extensive *Arrhenatherion* grasslands and about 5% of the territory area covered by wooded hems should ensure the adapted mosaic of habitats and the quality of breeding sites. We could not show an impact of *Tettigonia viridissima* density on the territories, which is the main prey of the Scops Owls. We were able to detect a potential aggregation effect of the owls, affecting their choices during territory selection. The preservation of Scops Owl populations seemed tightly dependent on the restoration of traditional or at least extensive agro-pastoral landscapes. Our results suggest that 50 times larger areas of extensive grassland should be protected than the areas covered by the actual conservation plans for the species.

Introduction

Mainly due to the intensification of the human land use, the landscapes of Central Europe have changed drastically since the fifties. The increase of the population involved a constant extension of built-up areas. The general economic pressure modified completely the agro-pastoral sector by forcing farmers to constantly increase their productivity. This led to a gradual intensification of the land management, with higher frequency of harvests, more inputs of fertilizers and a progressive removal of all the unproductive structure, such as bushes and hedges (Hofstetter et al., 2015). The economic pressure is also the cause of the disappearance of small farmers who were maintaining a mosaic of various cultivations (Hofstetter et al., 2015) and therefore various habitats for plant and animal species, creating heterogeneous landscapes of high biological diversity. The landscape is now increasingly moving towards large mono-culture fields and artificial intensive grasslands.

Furthermore, the declining profitability of agro-pastoral activities caused widespread land abandonment, leading to woodland expansion into previously open cultivated areas, such as pastured grasslands and meadows (Cernusca et al., 1996). The woodland areas increased through natural regeneration mostly at the expense of extensive grasslands and meadows (Barbaro et al., 2001). In particular, extensive meadows were the first affected by the intensive human use of land, and the remaining ones have become one of the most threatened habitats of Europe (Canals & Sebastià, 2000).

Intensification of grasslands exploitation, standardization of the landscape and woodland expansion could benefit to a few ubiquitous species associated to culture fields or woodlands, it has dramatically affected most native species linked to extensive zones of meadows, groves and orchards (Laiolo et al., 2004). This includes the characteristic plants of these habitats, and the wildlife directly dependent on it, like insects and their bird predators. The latter could also be affected by the loss of heterogeneous landscape and a mosaic of different habitats required to nest, hide or hunt. A typical conservation-sensitive species, which uses and is representative of these habitats, is the Scops Owl, *Otus scops.*

The Scops Owl is a small nocturnal raptor, which breeds mainly from southern Europe to central Asia and migrates to sub-Saharan African for wintering (Malle & Probst, 2015). Switzerland is at the northern limit of its distribution range. It is the most threatened owl in Europe (Arlettaz, 1990; Marchesi & Sergio, 2005) and one of the least studied (Marchesi & Sergio, 2005), which does not help the establishment of conservation plans and assessments for this species. Their population tends to be in decline almost in every parts of Europe (Marchesi & Sergio, 2005; Denac, 2009; Šušmelj, 2011), due to the loss of their suitable habitats; however, in Switzerland it appears to have increased slightly in recent years (Maumary et al., 2007), although the reasons for this remain unclear.

In Switzerland, the Scops Owls show similar habitat uses than the northern Italian, the Austrian or the Slovak populations (Marchesi & Sergio, 2005; Šušmelj, 2011; Sierro & Arlettaz, 2013). They nest in the cavities of large trees (Arlettaz, 1990; Malle & Probst, 2015), and particularly appreciate open areas of extensive grassland, bocages and orchards at low or middle elevation (Arlettaz, 1990; Šušmelj, 2011; Sierro & Arlettaz, 2013). Usually, they never nest within forests or in dense built area (Šotnár et al., 2008; Denac, 2009). Thus, their suitable ecological conditions are often contrary to those favored by current agricultural practices. This species is also a trophic specialist, mainly feeding its chicks with Orthoptera species, mostly Tettigonidae such as *Tettigonia viridissima* (70-95% of the diet) (Marchesi & Sergio, 2005; Latková et al., 2012), but also other large invertebrates, or occasionally small birds or mammals (Arlettaz, 1990; Malle & Probst, 2015).

The Scops Owl was a regular breeder at the beginning of the 20th century in grassland habitats of medium and low elevations in Valais (Martigny to Brig), close to Geneva and more locally in the cantons of Graubünden and Ticino and occasionally in the canton of Vaud (Knaus et al., 2011). As everywhere on in Europe, its populations decreased drastically between the 1970s and the 1990 (Knaus et al., 2011). In Valais in 2001, only one known breeding couple remained on the Sion hillside suggesting an upcoming extinction (Maumary et al., 2007). In recent years, the species now seems to have gradually re-colonized our regions, mostly in the plains but the reasons for this improvement are still unclear. Today, the number of individuals has slightly increased (Sierro & Arlettaz, 2013; Pradervand, 2015), but the population remains fragile and mainly confined to the central Valais and Ticino. There is thus an urgent need to better understand the ecology of this species and the potential threats to its remaining populations.

In this study, we aimed to assess in more details the realized environmental range of the Scops Owl in Switzerland, according to topo-climatic conditions and the main landscape structures, in order to better understand the factors that may cause population declines. We made a state of play of the current population and focused then on the Scops Owl territories of these past fifteen years to detect more finely which habitats and structures affect directly the presence of the birds. This allowed us to highlight more finely which factors have had a major influence on Scops Owls within their territory, and suggest finer management advices.

Material and Methods

The study followed a two steps procedure: 1) an exploratory model made from existing data and made to established the actual potential range of the species; 2) habitats models made from collected field data and used to described the territory needs of the species.

EXPLORATORY MODEL

Precise *Otus scops* observations from 2000-2015 (GPS coordinates) were gathered from the Swiss Ornithological Institute database. All the data have an atlas code describing, with a simple scale, main behaviors or reproduction signs of the observed bird. It indicates if reproduction is possible, probable or certain ("Code international de l'atlas" in Table S1 in Appendix, www.ornitho.ch). Only data with an atlas code of minimum 4 (ensuring at least "a couple during the nesting period in a suitable habitat") were kept for the analysis. The suitability of the sites has been checked using aerial photography to ensure the points were precise enough. Sites were considered as suitable if there was a pair with a male singing, near to a potential nesting site (old trees, orchards, hedges of wooded hems; Martínez, Serrano, and Zuberogoitia 2003). In total, 30 observations were finally kept to build the species distribution model (SDM) (see Figure S1 in Appendix).

In order to build the SDM for *O. scops*, we chose 8 uncorrelated (correlation <0.7 to avoid overfitting of the data, Dormann et al. 2013) predictors considered as important for the Scops Owls during the nesting period described in detail below. In Switzerland, the owls begin to sing in April and nest until mid-August (Galeotti & Sacchi, 2001; Sierro & Arlettaz, 2013; Malle & Probst, 2015). 4 climatic predictors averaged for the closest time period available (1961-1990) were extracted for the sites (at the breeding spot): a continentality index, the sum of precipitations (April - September), the mean solar radiations (April – September), the growing degree-days (GDD; April - September). We also used four vegetation variables: the amount of open vegetation (over a 20 ha circle, upper average Scops Owl territory size ; Denac, 2009; Sierro & Arlettaz, 2013), the distance of the site to the closest forest, the Normalized Difference Vegetation Index (NDVI) at the breeding site point (NDVI BS) and the mean of the NDVI all over the territory (NDVI mean, 20 ha circle).

The continentality index expresses the general seasonality of climate and is thus an important variable to depict particular locations in Switzerland showing more Mediterranean climate due to its intra-alpine situation (Zimmermann & Keinast, 1999). The sum of precipitations and the solar radiations are two variables representing the average climate during the nesting season. GDD is a measurement of heat accumulation used to predict plants development rates (Zimmermann & Keinast, 1999), as well as insects development rate, such as orthopterans which are the most important preys for Scops Owl (Sergio et al., 2009; Sierro & Arlettaz, 2013; Malle & Probst, 2015), which depend on upon both temperature and plant development. The GDD was calculated with a base temperature threshold of 3°C, usual average limit for the plants to grow (Zimmermann & Keinast, 1999).

Scops Owls avoid forests to minimize the risk of predation by long eared owls and tawny owls (Arlettaz, 1990; Sergio et al., 2009). The distance to the closest forest should thus depict this avoidance. It was obtained using the distance analysis tool in ArcGIS 10.2 (ESRI, 2011) with the "Vector25" layer from Swisstopo (2007). Herbage surfaces are hunting ground for the Scops Owl (Sierro & Arlettaz, 2013; Malle & Probst, 2015) , they were calculated from the "Vector25" layer using open areas. The open area surface was summed over a 20ha circle moving window. The NDVI is an indicator of the productivity of live green vegetation (Pettorelli et al., 2011).

All the predictor layers had a 25m resolution and were calculated for the whole of Switzerland below 1300 m, the altitudinal limit of Scops Owls' observations in Switzerland (Arlettaz, 1990). We simulated 1000 absences, but removed the absences over 1300 m and within the 250m radius circular window of the presence territories, resulting in 760 pseudo-absences. We generated these pseudo-absences as a neutral contrast allowing to use discriminant methods requiring presences (1) and absences (0).

We used an Ensemble of Small Models (ESM) approach to deal with the small number of available observations and to limit the risk of overfitting if using more than 1 variable per 10 occurrences, in agreement with Harrell's rule-of-thumb (Guisan and Zimmermann 2000; Harrell and Lee 1996). This technique creates small models with all possible combinations (here pairs) of *n* variables among the predictors, using different modeling techniques. We chose to use combinations of two predictors for the small models and to run ESM with two modeling techniques for the ensemble (maximum 4 degrees of freedom with models allowed up to the 2nd order): Generalized Linear Model (GLM) (McCullagh & Nelder, 1989) and Generalized Additive Model (GAM), as these were known to produce satisfactory results in SDMs (Guisan et al., 2002). We used the 'biomod2 library (Thuiller et al., 2013) in the R software (3.03, R Foundation for Statistical Computing, Vienna Austria). These models were then averaged to an ensemble model using small models weighted by AUC (Area under the curve) scores (Fielding & Bell, 1997; Breiner et al., 2015). The quality of the final model was assessed by Boyce and TSS (True skill statistics) scores (Hanley & McNeil, 1982; Hirzel et al., 2006;

Breiner et al., 2015). This ESM was then projected on the whole area in order to obtain a predictive map showing probabilities of presence of the species to target fieldwork on potentially occupied areas.

DATA COLLECTION

Prospecting phase

From April 28th to June the 28th, acoustic surveys were conducted between 8:45 PM and 2:00 AM, during the period where the owls should be the most active (Galeotti et al., 1997; Denac, 2009; Panzeri et al., 2014). The surveys were only made under favorable weather conditions, with low wind and no rain. The prospection areas were based on previous years' data and on potential areas highlighted by the SDM.

Territory maps

In order to analyze and quantify the habitats present on the Scops Owl territories, 48 sites were selected among the 71 known nesting sites from previous years monitoring (Swiss Ornithological Institute : database and internal reports; Sierro 2000:2016) and surveys of this year. To best cover the possible occupancy frequencies, we chose to picked randomly the same number of sites (12) in 4 categories of presence frequency since 2000: none (historical sites), 1 year, 2-4 year, 5 year and more (Figure S2 in Appendix). We had in total: 36 sites, where the species have been present between 2000-2016 and 12 historical sites, where the species was known to breed between 1984 and 1989 but have not been recorded after 1990, were considered as absences (Raphael Arlettaz personnal comments; Swiss Ornitological Institute database).

In the literature, the estimates for *O. scops* territory range from less than 1ha (Panzeri et al., 2014) to 30ha (Martínez et al., 2007), depending on the type of habitat. We categorized the vegetation on circa 20 ha around the breeding site, an upper average territory size (a 250m radius circular window) (Denac, 2009; Sierro & Arlettaz, 2013), on the selected sites. The open vegetation were classified according to vegetation classes following Delarze et al. (2015) and reflecting the quality of the habitat and forested areas according to their structure (bush, hem, forest). We differentiated the parts of the open vegetation mowed after the 1st of July for mountain areas which were considered more extensive (Mountain zone II according to the “Office Federal de l’agriculture”, 2015). For the analyses, we kept 29 uncorrelated variables (correlation <0.7, Dormann et al. 2013) describing the territories: 24 mapped habitat categories, 2 groups of variables (calculated by addition of others habitats; *Arrhenatherion* and Herbage) and 3 variables calculated based on mapped data (Richness, Edges and Open areas) (For the full list of variables, see Table 1). The excluded variables were listed in Appendix (Table S2).

Table 1. List of the uncorrelated Scops Owl habitat predictors (cor<0.7), used in the GLMs

Habitat	Abbreviation	
Mesobromion	*Meso.*	Percentage of Mesobromion grassland
Mesobromion Late mowing	*Meso. LM*	Part of the Mesobromion mowed after the July the 1st
Extensive Arrhenatherion	*Ext. Arr.*	Percentage of extensive Arrhenatherion grassland
Extensive Arrhenatherion Late mowing	*Ext. Arr. LM*	Part of the extensive Arrhenatherion mowed after the July the 1st
Intensive Arrhenatherion	*Int. Arr.*	Percentage of intensive Arrhenatherion grassland
Intensive Arrhenatherion Late mowing	*Int. Arr. LM*	Part of the intensive Arrhenatherion mowed after the July the 1st
Arrhenatherion[1]	*Arr.*	= "Ext. Arr." + "Int. Arr."
Intensive medow	*Intensive.*	Percentage of meadow with an intense management
Intensive pasture medow	*Patsure*	Percentage of meadow with an intense pasture
Steppes	*Steppes*	Percentage of steppe
Fallows	*Fallows*	Percentage of fallows
Herbage[1]	*Herbage*	= "Meso." + "Arr." + "Intensive" + "Pasture" + "Steppes" + "Fallows"+ "Grassy RS"
Forest	*Forest*	Percentage of forest
Bushes	*Bushes*	Percentage of bushes
Wooded hems	*W. hems*	Percentage of gathered arbustive structures, higher than 2m, dissociated from the forested areas
Gardens	*Gardens*	Percentage of domestic vegetal area
Crops	*Crops*	Percentage of crops, mainly aromatic herbs and cereal
Fruit crops	*Fruit c.*	Percentage of intensive fruit tree culture
Ochards	*Orchards*	Percentage of orchards
Vineyard	*Vineyard*	Percentage of vineyard
Soccer field	*Soccer F.*	Percentage of soccer field
Grassy roadside	*Grassy RS*	Percentage of Grass bands or slopes on the roadside
Construction	*Const.*	Percenatge of unnatural structures (Buildings, concrete roads…)
Water	*Water*	Percentage of water, like lake, river and pond
Dirt track	*D. track*	Percentage of non-concrete roads
Edges[2]	*Edges*	Calculated as the "Forest" and "W. hems" polygons perimeters
Richness[2]	*Richness*	= (number of different habitats in a territory) / (total of different habitats used for the mapping)
Open areas[2]	*Open a.*	Surfaces lower than 2m, calculate with DEM-DSM
Distance to the Coteau	*Coteau*	Distance between the territory and the only remaining nesting site on the Coteau in 2001. Not a predictor, variable used to estimate if there was spatial autocorrelation.

[1] Gathered habitat variable, [2] Calculated variables

The area of each habitat category was calculated in QGIS 2.18.0 (2016), and converted in percentages at each of the sites. These proportions were used subsequently as predictors for the analyses. The different groupings of habitats were created with R (v 3.3.2, R Core Team 2016) and used to define the level of accuracy required to describe the *O. scops* habitat.

The habitat richness was calculated using the number of different habitats in each territory divided by 24, the total of the different categories of habitat used for the mapping. It represented an estimation of the environmental complexity. The length of the forest edges was calculated as the perimeter of the forest and the wooded hems by using QGIS 2.18.0 (QGIS Development Team, Open source Geospatial Foundation, 2009). For the open areas, we subtracted the Digital Surface Model (DSM) to the Digital Elevation model (DEM) obtained from the LIDAR measurements of Swisstopo (Alti-3D, 2005) in ArcGIS 10.2 to obtain a layer reflecting vegetation heights. We categorized it over our study area, to identify all areas for 3 categories, according to the vegetation strata: lower than 2 m, between 2m and 5m, and higher than 5m. Structures lower than 2m represented the open areas of the landscape. The trees higher than 5m could have cavity large enough to allow nesting. Areas of each strata were summed per territory and then converted as the percentage of the sites to be used as a predictor. Only the structures lowest than 2m was kept for the analyses (Open areas), due to the correlation with the two others variables (cor>0.7).

As Scops Owls are recolonizing ancient nesting grounds and sometimes show gregarious behaviour, there may be some spatial autocorrelations in the data. To test this, we calculated a distance layer from the only remaining nesting site in 2001 (variable “*Coteau*”, Table 1). As spatial autocorrelation is part of the distribution of the species, we chose to use it in the models (as a variable) as an indicator of the strength of the autocorrelation signal. A significance of this variable in the model would then indicate that some spatial autocorrelations could affect the response variable, and the importance of this variable according to the others will indicate the strength of the autocorrelation.

Tettigonidae counting

Tettigonia viridissima is the most important prey for Scops Owls (Sergio et al., 2009; Sierro & Arlettaz, 2013; Malle & Probst, 2015a; Pradervand, 2015). To account for the *Tettigonidae* abundance, we selected randomly 10 listening points in 32 territories and counted the number of singing individuals. The number of singing *Tettigonidae* was then summed per territory. The counting was done between 29th August and 12th September, between 8 PM and 1 AM. The first part of the night is one of the most active periods for this grasshopper species (Deb & Balakrishnan, 2014).

HABITATS MODELS

The habitats models were produced in a two steps method. Firstly, we fitted models to a binomial variable, presence (1; minimum 1 breeder between 2000 and 2016) or absence (0; no breeder between 2000 and 2016), to analyze what can affect the presence or the absence of *O. scops* in a territory. Secondly, we fitted Poisson models to site occupancy, i.e. the number of bird presences in each site (from 0 to 15 presences between 2000 and 2016), to understand what differentiates a high or low quality habitat for *O. scops*. We assumed that the sites used nearly every year had a higher quality than the sites visited only once during the previous 16 years. This second approach keeps more available information, but is also more sensitive to sampling limitations.

Presence/absence model

Generalized Linear Models (GLM) (Elith et al. 2006; Guisan, Edwards, and Hastie 2002) were constructed to test at first the relative importance of the variables. Models were made with all possible combinations of two predictors, among the 30 available, each time using both linear and quadratic terms (i.e. allowing maximum 4 degrees of freedom with models allowed up to the 2nd order), in agreement with Harrell's rule-of-thumb (Guisan and Zimmermann 2000; Harrell and Lee 1996). The quadratic terms were always considered together with their respective linear terms in order to allow the quantification of a proper quadratic curve response by the model. The importance of each predictor in explaining the presence of the birds was assessed using Multi-Model Inference (Burnham, Anderson, and Huyvaert 2011). Using the MuMIn R package (Barton, 2015), the models were then ranked by AICc score, and an Akaike weight was computed for each model (Burnham and Anderson 2002). These Akaike weights were used to estimate the relative importance (RI) of each predictor. We used a combination of two predictors for the models (maximum 4 degrees of freedom with models allowed up to the 2^{nd} order). To quantify the effect of the most important predictors calculated with the MuMIn, a final GLM was constructed with the three variables with the higher RI. The linear or linear + quadratic terms were used, depending on which one had the larger RI. This final model quality was assessed by Kappa, TSS scores (Fielding & Bell, 1997; Allouche et al., 2006) and the model deviance (d2) (Guisan & Zimmermann, 2000). A randomization test was made to see if the final model was significantly different from a random model, see Figure S3 in Appendix.

Territory occupancy model

To analyze what could affect the frequency of territory occupancy by *O. scops*, we fitted models to the number of bird presences on each site since 2000. The Poisson distribution of this response variable was verified using a Kolmogorov-Smirnov test (Justel et al., 1997). The same framework used for the binomial model was applied. The three most important variables were selected based on RI ranking in order to construct a final GLM. We checked the deviance (d2) and, we calculated the mean error (me) and the standard deviation (sd) between the data predicted by the model and the observed data (real site occupancy) to test the quality of the final model. The randomization test was made the same as for the binomial model (Figure S3 in Appendix).

Decreasing territory area

In order to detect if territory size could influence the models, the same Poisson and Binomial analyses were run for different territory size in order to determine the most likely territory size of *O. scops*. A set of 5 different radiuses was used: 250m, 200m, 150m, 100m and 50m.

Results

Large scale exploratory model

The final species distribution model had a Boyce Index of 0.99 and a TSS of 0.93 which indicted a very good model (Swets, 1988). It was constructed with ESMs with a Boyce Index ranging from 0.42 to 0.89 and TSS from 0.849 to 0.965. The topoclimatic variables all contributed to the final model, but GDD (14,28%), the distance to the nearest forest (13,34%) and the NDVI at the nesting spot (13,05%) are the most important ones to describe the presence of *O. scops* (Table 2).

Table 2. Importance of the topoclimatic and global vegetation structures predictors (%) used in the ESM to construct the species distribution model of the Scops Owl in Switzerland.

Predictors	%
GDD	14.28
Dist. to Forest	13.34
NDVI BS	13.05
NDVI mean	12.48
Solar Radiations	12.31
Precipitations	12.12
Continental Ind.	11.64
Herbage	10.77

The projection map highlighted areas from lowland to medium elevation (around 1200m), mainly in the Rhone valley in central Valais and the valleys in the Southern and Eastern Alps as favorable for the Scops Owl. Several sites from Geneva to the Seeland including the Northern shore of the Lake Neuchâtel are also highlighted but with much lower presence probabilities. Globally, the potential distribution of the species was the same as in the 1950s, thus historical areas were still highlighted based on topoclimatic criterion (Figure 1) (Knaus et al., 2011).

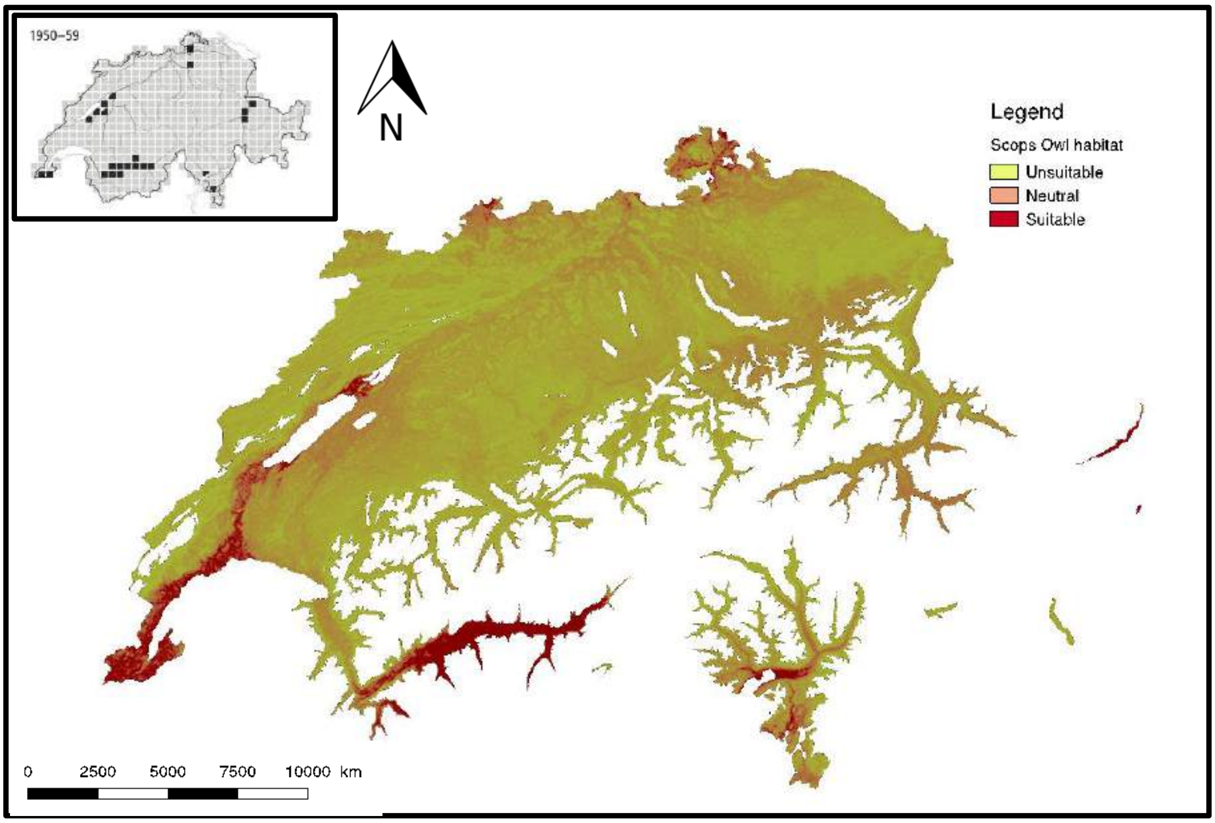

Figure 1. Species Distribution Model, showing the portential range of *Otus scops* in Switzerland, for the areas below 1300m. Areas categorized in suitable (red), neutral (orange) and unsuitable habitats, according to topoclimatic and global vegetation structures predictors. In index, the historical distribution of the species in Switzerland from 1950 to 1959 (Knaus et al., 2011): the black squares represent the regions where Scops Owls were observed during this period.

Presence/absence analysis with a 250m radius circular window

In the binomial model, the most important predictors assessed using the MuMIn were structural variables on their quadratic form: the percentage of open areas (RI=0.67) and percentage of forest (RI=0.51) in the territories (Table 3). The distance between the territories and the Coteau (RI=0.27) was the third variable highlighted. The last substantial predictor (RI=0.25) was the extensive *Arrhenatherion* area in a territory.

Table 3. Most important predictors and their relative importance (RI) in the MuMIn analyses with the binomial distribution of Scops Owl data for the 5 different territory sizes (50m to 250m radius circular window around the breeding site). The most important predictors were expressed in quadratic term, except when specified.

250m		**200m**		**150m**		**100m**		**50m**	
Pred.	**RI**	**Pred.**	**RI**	**Pred.**	**RI**	**Pred.**	**RI**	**Pred.**	**RI**
Open a.	0.67	**Coteau**	0.80	**Coteau**	0.50	**Coteau**	0.96	**Coteau**	0.83
Forest	0.51	Richness	0.65	Ext. Arr.	0.30	Arr.	0.74	Arr.	0.61
Coteau	0.27	Open a.	0.15	Grassy RS [a]	0.26	Int. Arr.	0.15	Open a.	0.19
Ext. Arr.	0.25	Ext. Arr.	0.15	Open a. [a]	0.24	Steppe	0.03	Int. Arr.	0.13
Edges	0.05	Forest	0.09	Int. Arr.	0.12	Ext. Arr.	0.02	Steppe	0.03

[a] Variable expressed in the linear term

The final GLM built with the three most important predictors explained 67% of the deviance (d2) and had a TSS of 0.92 and a Kappa of 0.85 (Table 4). The deviance explained by this model was higher than the 95% confidence interval of the randomization test (see Figure S3 in Appendix). It appeared to be valuable to have more than 75% of open areas in the territories. Most of the presence territories had between 75% and 90% of open areas (Figure 2). The percentage of forest was less obvious, the low sampling disrupting the reading of results. However, it seemed that too large forest areas were not an advantage for the species.

Table 4. Evaluations metrics values (TSS and Kappa) and deviance of the GLMs constructed with the 3 most important predictors with a binomial distribution of the Scops Owl data for the 5 different territory sizes (50m to 250m radius circular window around the breeding site).

GLM		TSS	Kappa	d2
250 m	***Open areas*** ***Forest*** ***Coteau***	0.92	0.85	0,673
200 m	***Coteau*** ***Richness*** ***Open areas***	0.86	0.84	0.558
150 m	***Coteau*** ***Ext. Arr.*** ***Grassy RS*** [a]	0.86	0.76	0.586
100 m	***Coteau*** ***Arr.*** ***Int. Arr.***	0.749	0.72	0.536
50 m	***Coteau*** ***Arr.*** ***Open areas***	0.8	0.67	0.527

[a] Variable with the linear term used in the GLM

With decreasing territory sizes, the distance between the territories and the last remaining breeding site in 2001 (*Coteau*) was systematically the most important variable (0.50<RI<0.96) in the models. The spatial autocorrelation and thus potentially the recolonization by the species may have had an impact. The results must therefore be interpreted with caution.

The predictive quality of the final models was overall decreasing with decreasing territory size, but the explained deviance stayed between 0.67 and 0.52. The best model to predict the presence or absence of *O. scops* was with a 20ha territory (250m radius circular window). The different *Arrhenatherion* predictors (extensive, intensive or global) appeared regularly with a high RI in the different territory sizes models. The details of important predictors are presented in the Table 3.

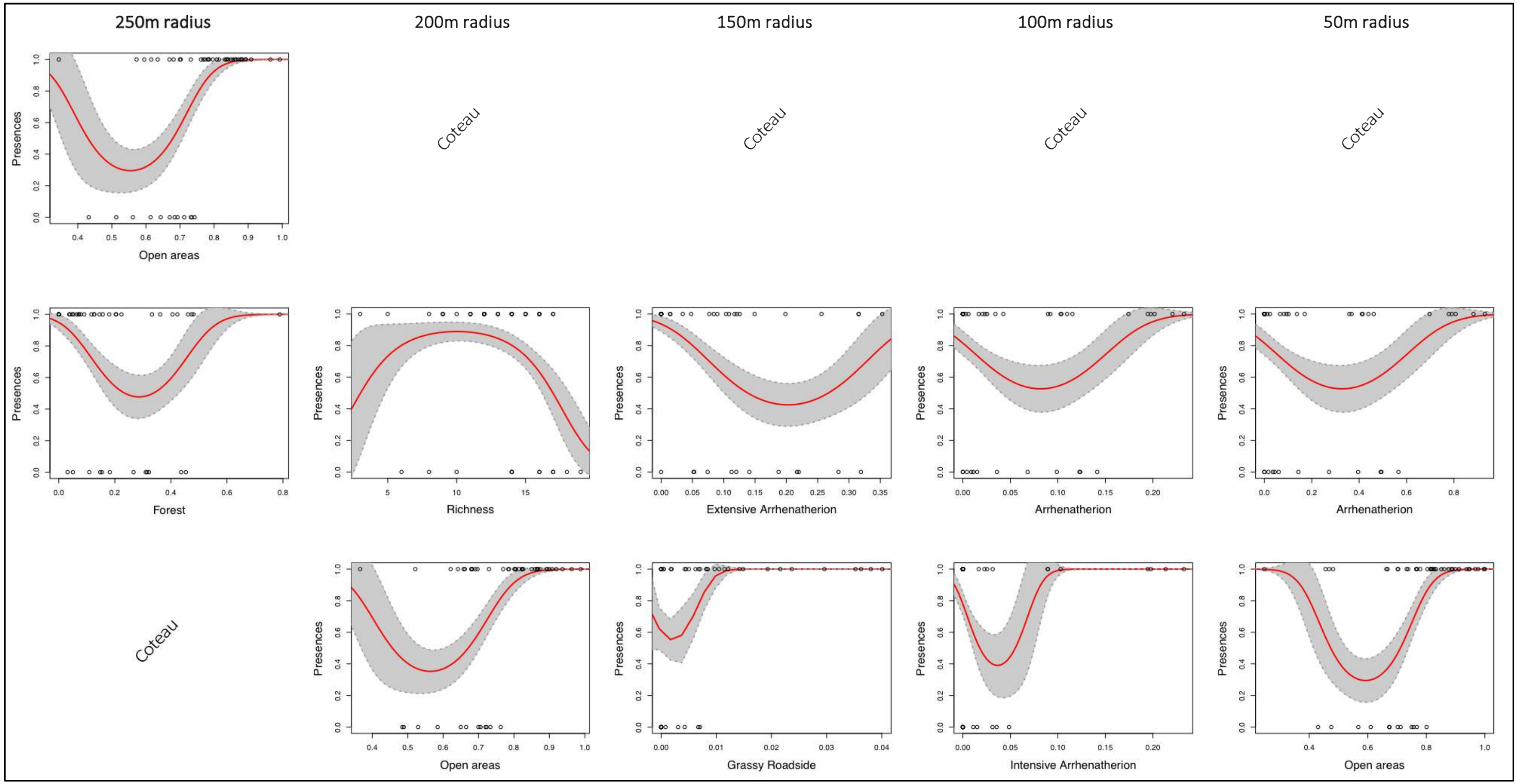

Figure 2. Plot of the data of the presence (1; minimum 1 breeder between 2000 and 2016), absence (0; no breeder between 2000 and 2016) Scops owl according to the 3 most important predictors obtained with the MuMIn analyses and used together in a final GLM, for each of the 5 different territory sizes (250 to 50m radius circular window around the breeding site). Downward, from the highest RI to the lowest RI. Red lines show the predictions made in final GLMs according to each predictor; Grey shades show the 95% confident limits of these predictions.

Frequency of occupancy

Our presence frequency data had a Poisson distribution according to the Kolmogorov-Smirnov test ($p<0.001$). The most important variables to predict the frequency of occupancy, assessed by the MuMIn with the frequency of occupancy models, were the percentage of areas covered by extensive *Arrhenatherion* (RI=67), orchards (RI=0.51), wooded hems (RI=0.27) and *Mesobromion* with a late mowing (RI=0.25), generally in their quadratic form (Table 5). The distance to the Coteau variable had not a significant importance (RI<0.01). The final GLM built with the three main predictors explained 37,8% of the deviance (d2), and its predictions had a mean error of 2.11 and a standard deviation of 2.79 with the observed data (Table 6).

Table 5. Most important predictors and their relative importance (RI) in the MuMIn analyses with the Poisson distribution of Scops Owl data for the 5 different territory sizes (50m to 250m radius circular window around the breeding site). The most important predictors were expressed in quadratic term, except where noted.

250 m		200 m		150 m		100 m		50 m	
Pred.	**RI**	**Pred.**	**RI**	**Pred.**	**RI**	**Pred.**	**RI**	**Pred.**	**RI**
Ext. Arr.	0.67	Ext. Arr.	0.83	W. hems	0.99	Edges	0.99	Edges	0.99
Orchards	0.51	Orchards	0.52	Ext. Arr.	0.99	Steppe	0.98	Steppe	0.98
W. hems	0.27	W. hems	0.25	Steppe	<0.01	Richness	0.01	Richness	0.01
Meso. LR	0.25	Edges	0.1	Ext. Arr. [a]	<0.01	Soccer F.	<0.01	Soccer F.	<0.01
Ext. Arr. [a]	0.05	Vineyard	<0.01	Orchards	<0.01	Fallows	<0.01	Fallows	<0.01

[a] Variable expressed in the linear term

Table 6. Deviance of the GLMs constructed with the 3 most important predictors with a binomial distribution of the Scops Owl data for the 5 different territory sizes (50m to 250m radius circular window around the breeding site).

	GLM	d2
250 m	***Ext. Arr.*** ***Orchards ****** ***W. hems *****	0,378
200 m	***Ext. Arr.*** ***Orchards ****** ***W. hems *****	0.407
150 m	***W. hems****** ***Ext. Arr.*** ***Steppe***	0.341
100 m	***Edges****** ***Steppe*** ***Richness***	0.336
50 m	***Edges****** ***Steppe*** ***Richness***	0.336

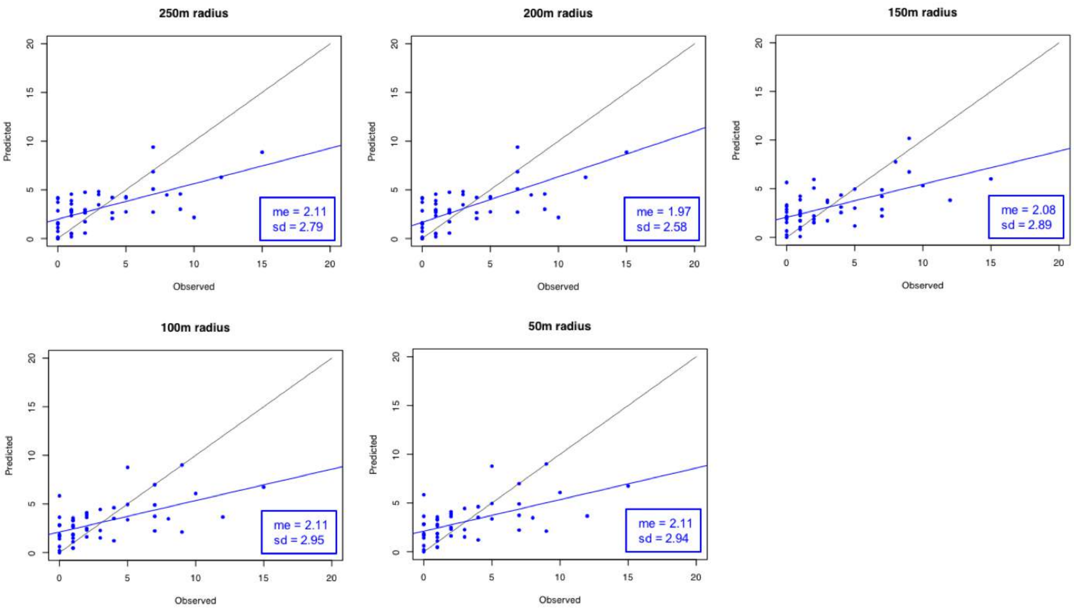

Figure 3. Predicted frequency of occupancy by the GLM constructed with 3 most important predictors according to the MuMin analyses for the 5 different territory sizes (50m to 250m radius circular window around the breeding sites) compared to the observed frequency of occupancy. In index, the mean error (me) and the standard deviation (sd) of the predictions.

When reduced, the territories area showed quite similar results for the 200m radius with the same 3 most important habitat variables highlighted, but the final GLM constructed with these 3 predictors had a higher explained deviance (d2=0,407) and its predictions had lowest mean error (me=1.97) and standard deviation (sd=2.56) with observed data (Table 6, Figure 3). The most important predictors according to the MuMIn analysis was the extensive *Arrhenatherion* areas. The quality of a territory seemed to be enhance, if it was covering 6% of its area (about to 1ha) (Figure 4). The wooded hems appeared to increase the quality of the habitat, with an optimum near to 5% of the territory (Figure 4). The orchards areas seemed to improve the territory quality, but it could be due to a sampling limitation: we only found 11 sites with this habitat. These two last predictors were both significant in the final GLM. The two smallest territories areas models (100 m and 50 m radius) do not share variables with larger territory sizes. Only two predictors had a relative importance higher than 0.01: the length of the edges (RI=0.99) and the steppe area (RI=0.98, Table 5). The steppe area was highlighted only due to sampling limitations, with these small territory sizes only two sites have steppe areas (Figure 3). Their final GLMs explained deviances were also the same with a d2=0.336. The length of the edges was the only significant predictor in the final model; the edges seems to be valuable close to the nest although not with a density that is too large (Figure 3)

At a scale of 150m radius, there could have transition between the larger (250m, 200m radius) and the smaller (100m and 50m radius) territories, with a mixed of important predictors from both side. The most important variables were more similar to the larger territories, such as the wooded hems (RI=0.99) and the extensive *Arrhenatherion* (RI=0.99), but was still followed by the steppes, which was a good predictor in the small radius models. The deviance of all models constructed with the 3 best predictors for each territory size was the highest for the model with 200m radius (d2=0.407), but had globally a tendency to decrease with the territory size. The predictions made with the same models always under estimated the frequency of occupancy, however the smallest mean error and standard deviation were also both obtained for the model with 200m radius (me=1.97, sd=2.79) (Figure 3).

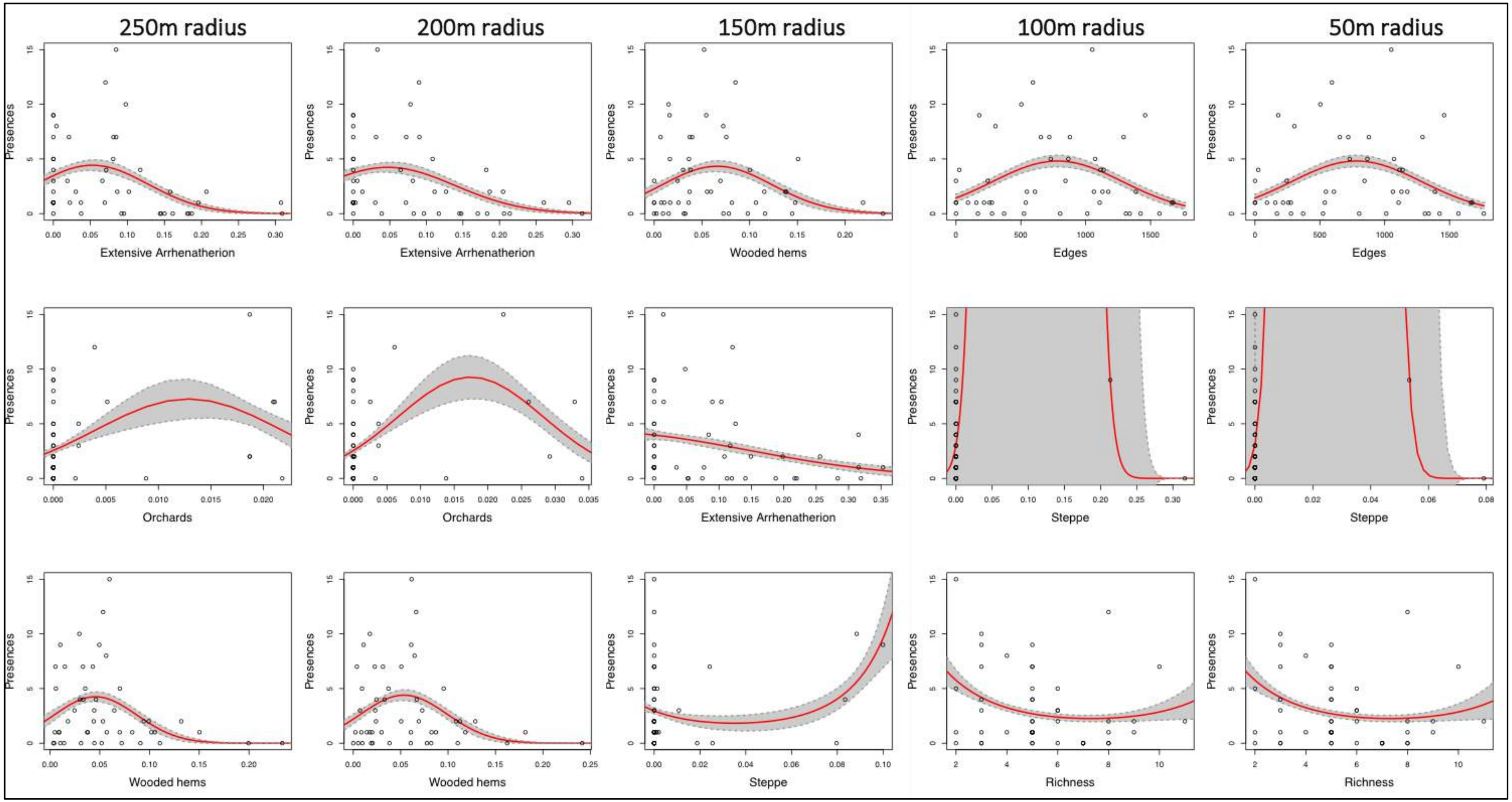

Figure 4. Plot of the number of Scops owl presence records during the past 16 years, according to the 3 most important predictors obtained with the MuMIn analyses, for each of the 5 different territory sizes (250 to 50m radius circular window around the breeding site). Downward, from the highest RI to the lowest RI. Red lines show the predictions made in final GLMs according to each predictor; Grey shades show the 95% confident limits of these predictions.

Tettigonia viridissima

The presence/absence and frequency models never highlighted *Tettigonidae* data as a variable explaining the presence/absence or frequency of Scops Owls (Table 3, Table 5).

Discussion

The final species distribution model obtained with the ESM can be considered as being informative of the Scops Owl's potential range in Switzerland. The species have favorable habitats in medium to low altitudes, with adapted topoclimatic conditions and general vegetation structures, mainly the Rhone valley, and the valleys in the Alps south of the Rhone and in Ticino. These favourable zones for the species intersect with historical ones, suggesting that the topoclimatic requirements have remained the same over time. Their potential range did not change since the 1950s. The loss of territories together with the possible recent re-colonisations must be due to other territory changes at a finer level: the fine scale quality of the vegetation or the structure may play an important role. We found that a large amount of open areas (between 75% and 90% of the surface) with a low forest cover offered a favourable habitat for Scops Owls. Approximately 1ha of extensive Arrhenatherion grasslands and about 5% of the territory area covered by wooded hems should ensure the quality of breeding sites. We could not show an impact of Tet*tigonia viridissima* density on the territories.

What explains the presence of Scops owls?

Habitat global structure

The requirements in the Scops Owls territories for open areas was already known from previous studies, as shown by Sergio et al. (2009) and observed in Switzerland by Arrletaz (1990), but there was no estimate of the optimal quantity required by the species. Scops Owls used these zones mainly to hunt (Sierro & Arlettaz, 2013). In our study, we confirmed the requirement of open areas around the nesting site and it appeared to be valuable to have more than 75% of open areas in the territories, since most of our presence sites had between 75% and 90% of open areas. According to many studies, Scops Owl were also known to avoid dense forests (Šotnár et al., 2008; Sergio et al., 2009). This is mainly to avoid direct presence of predators that nest in forests, such as the Tawny Owl, *Strix aluco* (Galeotti & Gariboldi, 1994; Marchesi & Sergio, 2005). We did not found any nesting sites in forest and we rather observed a negative impact of large surfaces of forests. However, many territories had small forest areas. This negative effect is mainly due to the species associated to them (Scops Owl predators) and the closure of the habitat, that does not offer open areas to hunt. Overall, it seemed that it is the global structure of the habitat that defines favorable sites, and mostly influences the possibility of nesting for the Scops Owl.

Habitat quality

We found that about 1 ha of extensive Arrhenatherion meadows in a territory and 5% of wooded hems around the breeding site were the most significant signs of a high-quality habitat for *O. scops*. Many studies conducted in similar topo-climatic conditions areas also suggested the benefit of extensive grasslands in Europe (Marchesi & Sergio, 2005; Denac, 2009; Sergio et al., 2009), and Switzerland (Arlettaz, 1990; Sierro & Arlettaz, 2013). The valuable quality of the orchards was also established (Arlettaz, 1990; Denac, 2009; Šušmelj, 2011). In our analyses, this predictor was also highlighted and seemed to indicate that they were valuable for the species. However, this habitat was only present in 11 sampled territories, which was not enough to ensure that this conclusion was not only due to a sampling limitations. Orchards could be an interesting habitat for the species, but seems not essential to it. This particular habitat is composed of old fruit trees in extensive grasslands. It is a favorable combination for the Scops Owl, but unfortunately tends to disappear for the benefit of dense fruit crops with small amount of intensive grasslands. Whereas these two habitats were important for the species, it was also likely that the habitat that surrounded them was also valuable for the Scops Owl. Extensive *Arrhenatherion* meadows were often accompanied by other extensive grasslands, such as *Mesobromion* or other dry habitats such as steppic vegetation. We estimate that about 1 ha of extensive *Arrhenatherion* could ensure a favorable global habitat for Scops Owl on its territory. Regarding wooded hems, these structures were almost always surrounded by open areas, and most of the time by various types of grasslands. This often implied a mosaic landscape with various surfaces available to hunt, but also enough available structures to hide or roost. The importance of a heterogeneous landscape for *O. scops* was already assumed, among others, by Šušmelj et al. (2011) in a study conducted in Slovenia. Here, we assumed that around 5% of the wooded hems in a territory was an optimum quantity to have an adapted habitat for the Scops Owl. This should bring enough tree structures with the necessary shelter, without closing the landscape too much, as we already showed that open areas were essential for the species.

Food abundance

The grasslands were essential for the Scops Owl, since they mostly harboured their prey. The principal conservation plans implemented for *O. scops* in Switzerland aim for the protection of the Orthoptera and their habitats (Sierro & Arlettaz, 2006). We tested the quantity of *T. viridissima*, the main Scops Owl prey, but no importance of this predictor emerged from our models. There are three possible explanations: either our small amount of data did not allow to highlight an influence of *T. viridissima* abundance, or, as we chose only historical sites as absences, all sampled sites had a fairly high density. The last possibility was that the density of *T. viridissima* did not have an impact on territory choice for the Scops Owl. Since this grasshopper species is generally absent during the settlement period of *O. scops* (April-May) (Malle & Probst, 2015), it could be possible that other Orthoptera, such as the field cricket (Gr*yllus campestris*), served as an indicator of the amount of available food. It will still be important to set-up conservation measures to protect Orthopthera, such as *T. viridissima* in Valais, but the choice of favorable territories for Scops Owls could emanate from the other habitats or landscape structures, for example the ones which facilitate hunting through the accessibility of preys.

In Valais, in addition to monitoring the species for years and the installation of nest boxes (Pradervand, 2015), the main action for Scops Owl conservation was a “Grass bands” project (Sierro & Arlettaz, 2003, 2004, 2006), whose main goal was to protect Orthoptera, such as Tettionidae. It consisted in keeping extensive grass bands, with a particular mowed planning among the years, on the margin of low intensive or extensive grasslands. This action was conducted since 2003 in collaboration with local farmers, who obtained financial contributions. This action was a success and increased the biomass of Orthoptera in the related grasslands (Sierro & Arlettaz, 2006). The grass bands were from 36 m^2 to 429 m^2 (mean=195.8m^2) in size. Our results suggest that it would be better to protect much larger areas to keep suitable habitats for the Scops Owl, approximately 1ha of extensive Arrhenatherion (10’000m^2). However, this corresponds to an area that is 50 times larger and the actual economic pressure makes this hardly feasible. It would be a too large constraint for the farmers and a large loss compared to their current land management. The “Grass bands” project was a good compromise, as it allowed to keep and increase density of Orthoptera in grasslands, as long as the concerned field does not intensify too much.

Spatial autocorrelation

We tested a possible spatial autocorrelation among the breeding sites by inserting a variable representing the distance between the sampled territories and the last known nesting site in 2001, on the Sion hillside. This variable was highlighted as the most important one in almost every presence-absence model. It indicated a probable spatial impact of the re-colonization from the hillside and not only a choice due to the habitat. As suggested by Marchesi et al. in 2005, although the species is territorial, there could be a coloniality effect leading to the aggregation of individuals in the high-quality areas. This could explain some unoccupied or never used territories despite their apparent good quality habitats.

Size of Scops Owl territory

The studies conducted on *O. scops* proposed various sizes to estimate its territory, from less than 1 ha for Panzeri et al. (2014) to 30 h for Martinez et al. (2007). The real territory size undeniably varies for each individual, but certainly also depends on the quality of the available habitats and the arrangement of the structures surrounding the breeding site. In this study, we chose to test the influence of a circular neighboring window of about 20 ha (250 m radius) around the breeding site and then to decrease this size to evaluate the influence of the window size, from 20 ha to less 0.78 ha (250 m to 50 m radius). The largest size seemed the most useful to define breeding success for the Scops Owl, and it seemed less influenced by spatial autocorrelation. Unfortunately, working on larger territory sizes would be complex and incorporate habitats totally decoupled from owl potential territory, such as most nesting sites are in small and diversified habitats.

On the other hand, to predict the occupancy frequency, predictors calculated within a territory of only ca. 12 ha (200 m radius circular window) explained the largest part of the related model deviance. There were two ways to explained this difference. Even if the average Scops Owl territory area was between 12 ha and 20 ha, or there are two different scales to define a territory. Such it is two different predictions, possibility of breeding and occupancy frequency, it is possible that favorable breeding sites were estimated on a large area around the breeding site, such as 20ha, and the quality of territory habitat (estimated by the occupancy frequency) is only predict on a smaller are, like 12ha. This could be due to predation pressure effective over large areas, but smaller areas used for hunting.

Modeling limitations

O. scops is an endangered species in Switzerland (www.vogelwarte.ch), is one of the 50 species with priority conservation status. Unlike studies conducted in southern Europe, where the density of individuals is higher, the quantity of data available for our analyses is small. We mostly predicted a higher frequency of occupancy for the lowest quality sites (0 to 3 presences since 2000), and a lowest frequency for the others (3 and more presences since 2000). This is mainly due to our sampling limitations (only a few sites with a high frequency). The sampled Scops Owl territories were representative of their habitat in Switzerland, but the small amount of data could also create a bias for the rarest habitats. Moreover, the territory maps were made with various categorization of the habitats. Some variables that emerged from it appeared only in a reduced number of territories, mostly when the analyses were made for the smallest territory sizes. We chose to keep all predictors for each MuMIn analysis in order to be consistent among the models. This could lead to some predictors being highlighted only due to sampling limitations. Therefore, since we already knew broadly where the Scops Owls bred, we chose historically abandoned sites as absences. These sites seemed quite good, because individuals nested there several years ago, and only specifics must have changed since. This gave us the possibility to attempt identifying which details made differences for the species. On the other hand, it did not allow us to highlight the main known preference of the species.

Perspectives

This study allowed us to make a thorough inventory of *O. scops* present in Valais in 2016. By means of quantitative analyses of their territories in Switzerland, we confirmed conclusions of previous studies on the Scops Owl habitats preferences. We highlighted among them which habitats seemed to have the highest influence for the species and proposed some quantitative optimum areas for these substantial habitats. For further studies, additional testing could be conducted to refine the optimal territory size for Scops Owl. It could be estimated by using adapted GPS on foraging adult, and analyzing their movements around the breeding site. This type of GPS now very light and thus available for small species, as the total weight of the GPS should not be over 5% of the body weight of the bird. It has been successfully used on larger owls such as the Barn Owl (*Tyto alba*) (Schalcher, 2017). This type of experiment could also allow us to notice if there is a difference in territory size according to the quality of the available habitats on the nesting site. It would moreover indicate on which habitats the owls forage. It would also be interesting to test the aggregation impact of the coloniality effect on the bird's territory choice. It could be tested by simulating the presence of Scops Owl in suitable unused territories, chosen according to the important breeding conditions established this year. If there are some aggregation effects of the species, territories near to the simulated presences could become more attractive.

As others studies already highlighted, the preservation and recovery of Scops Owl populations seem tightly dependent on the restoration of traditional agro-pastoral landscapes. Extensive approaches to manage grassland ecosystems could probably only be achieved nowadays at a large scale through subsided schemes. Similarly to the "Grass bands" project, it will be important to establish which low cost measures will be the most valuable for the conservation of biological diversity in Switzerland. Continue to preserve species like the Scops Owl could be a good way to achieve that, such as we assumed that the preservation of the apex predators support biodiversity conservation (Sergio et al., 2006).

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Appendix

Nidification possible (30)	
1	Observation de l’espèce pendant la période de nidification.
2	Observation de l’espèce pendant la période de nidification dans un biotope adéquat.
3	Mâle chanteur présent en période de nidification, cris nuptiaux / tambourinage entendus ou mâle vu en parade.
Nidification probable (40)	
4	Couple pendant la période de nidification dans un biotope adéquat.
5	Comportement territorial d’un couple (chant, querelles avec des voisins, etc.), au moins 2 jours dans le même territoire.
6	Comportement nuptial (mâle et femelle observés).
7	Visite d’un site de nidification probable.
8	Cris d’alarme ou de crainte des adultes ou autre comportement agité suggérant la présence d’un nid ou de jeunes aux alentours.
9	Plaque incubatrice d’une femelle capturée.
10	Transport de matériel, construction de nid ou forage d’une cavité.
Nidification (50)	
11	Oiseau simulant une blessure ou détournant l’attention
12	Découverte d’un nid ayant été utilisé pendant la saison en cours
13	Jeunes venant de s’envoler (nidicoles) ou poussins en duvet (nidifuges).
14	Adultes gagnant ou quittant un site de nid, comportement révélateur d’un nid occupé dont le contenu ne peut être vérifié (trop haut ou dans une cavité).
15	Adulte transportant des fientes.
16	Adulte transportant de la nourriture pour les jeunes.
17	Coquilles d’œufs éclos.
18	Nid avec adulte vu couvant.
19	Nid avec œufs ou jeunes.
Données négatives	
99	Espèce non trouvée malgré une recherche ici

Table S1. List of the atlas codes, used to describe the main behaviors or signs of reproduction for observed birds (www.ornitho.ch)

Environment	Abbreviation	
Mesobromion early mowing	*Meso. EM*	“Meso.” – “Meso. LM”
Extensive Arrhenatherion early mowing	*Ext. Arr. EM*	“Ext. Arr.” – “Ext. Arr. LM”
Intensive Arrhenatherion early mowing	*Int. Arr. EM*	“Int. Arr.” – “Int. Arr. LM”
Arrhenatherion early mowing	*Arr. EM*	“Ext. Arr. EM” + “Int. Arr. EM”
Arrhenatherion late mowing	*Arr. LM*	“Ext. Arr. LM” + “Int. Arr. LM”
Trees	*Trees*	“Forest” + “Wooded hems”
Extensive grassland	*Ext. grassland*	“Meso.” + “Ext. Arr.”
Extensive grassland late mowing	*Ext. grassland LM*	“Meso. LM” + “Ext. Arr. LM”
Extensive grassland early mowing	*Ext. grassland EM*	“Meso. EM” + “Ext. Arr. LM”
Low intensity grassland	*LI grassland*	“Meso.” + “Ext. Arr.” + “Int. Arr.”
Low intensity grassland late mowing	*LI grassland LM*	“Meso. LM” + “Ext. Arr. LM” + “Int. Arr. LM”
Low intensity grassland early mowing	*LI grassland EM*	“Meso. EM” + “Ext. Arr. EM” + “Int. Arr. EM”
Closed areas	*Closed a.*	Surfaces between 2m and 5m high, caluclate with DEM-DSM
Raised structures	*R.structure*	Surfaces higher than 5m, caluclate with DEM-DSM

Table S2. List of the correlated Scops Owl habitat predictors (cor>0.7), thus not used in the GLMs

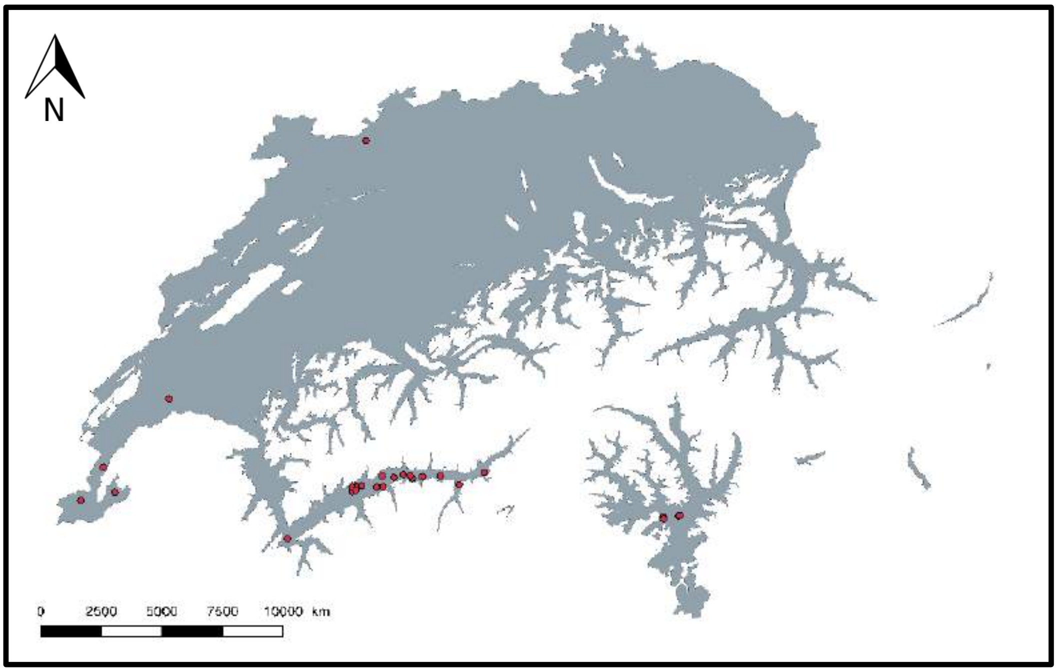

Figure S1. Map of Switzerland, below 1300m with the 30 Scops Owls observation data (red dots) used to construct their SDM.

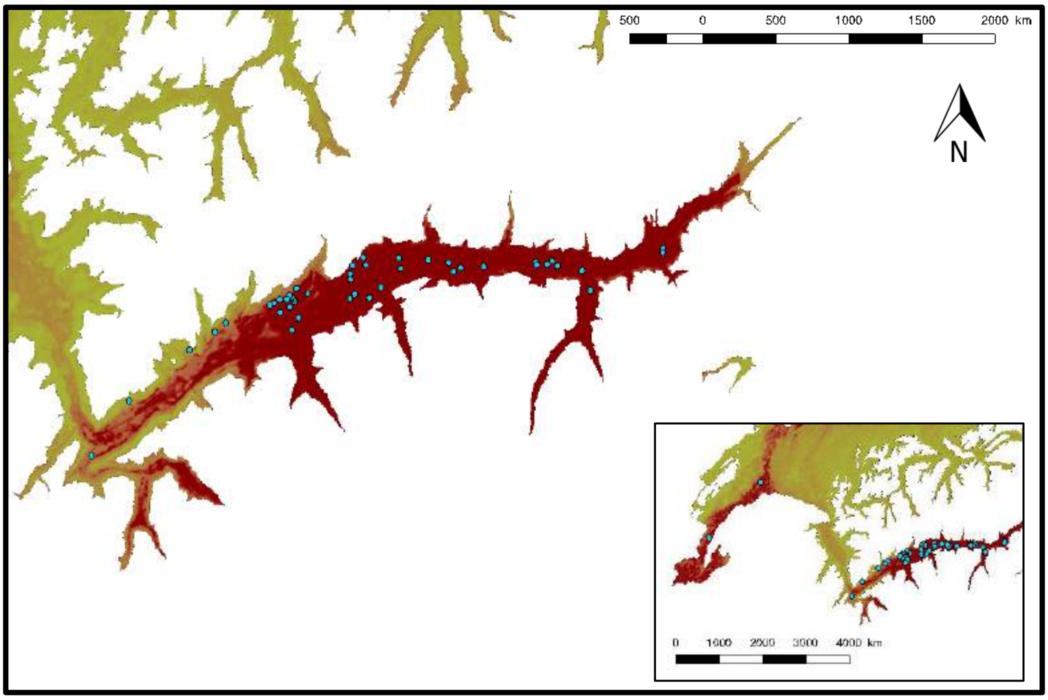

Figure S2. Zoom on the Valais on the SDM map of the Scops Owl, with the sampled sites (blue dots) used for the habitat analyses (GLMs). In index, a larger zoom to show the two sites in the cantons of Vaud and Geneva.

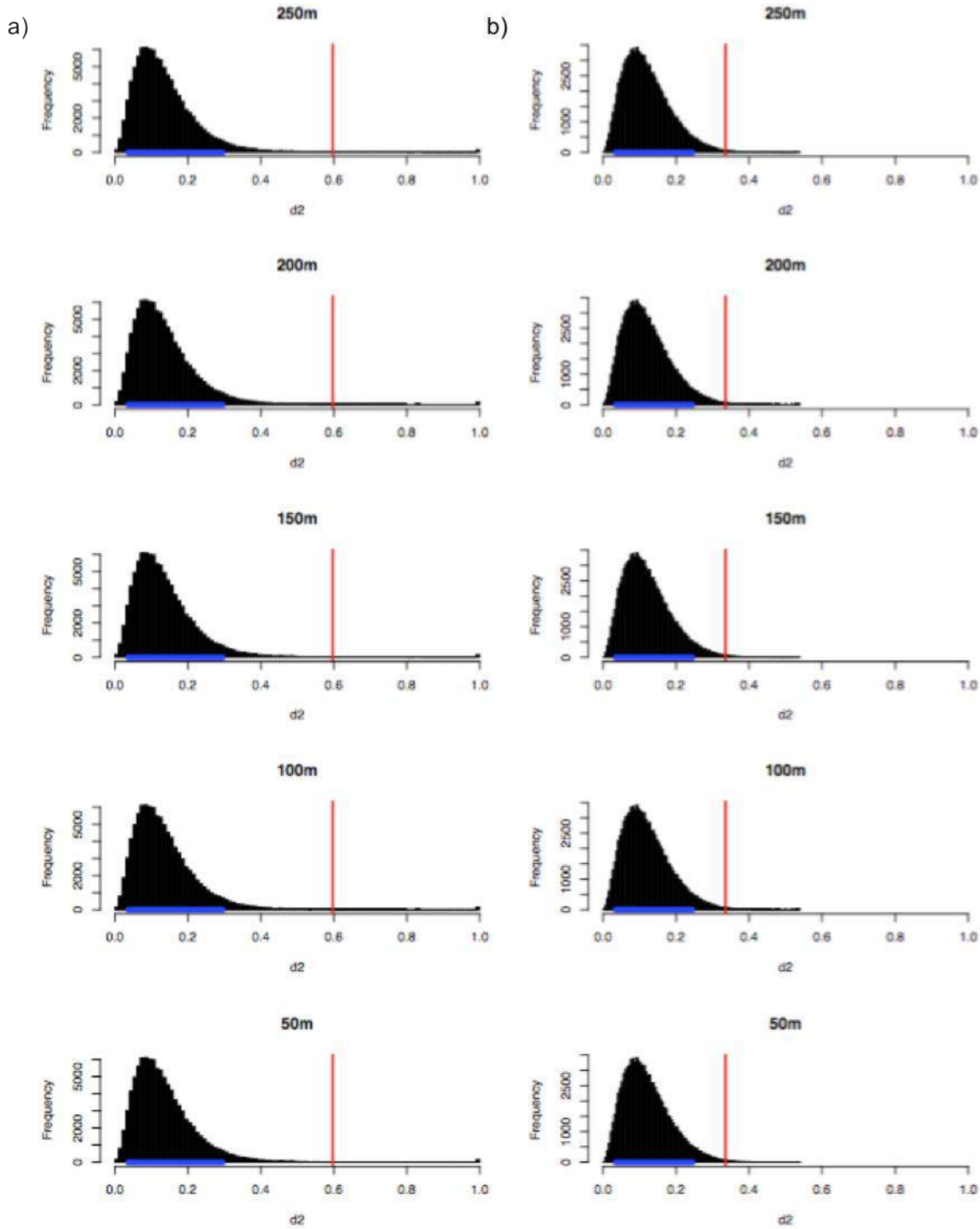

Figure S3. Distribution of the random GLM deviances made with 3 most important predictors according to the MuMin analyses (black), with the 95% confident interval (in blue) and the deviance of the true GLMs (red), for the 5 different territory sizes (50m to 250m radius circular window around the breeding site). a) with a binomial distribution of the response variable with a probability of presence, p=0.7, b) with a Poisson distribution of the response variable with a mean presence, λ=3.125.

We ran 100’000 times a model with a random binomial distribution response variable with the same probability of presence as our data ($p=0.7$). We then tested if our final model deviance was out of the 95% confidence interval of the random models’ deviance distribution. The randomization test was made as for the binomial model, with a Poisson distribution with a $\lambda=3.125$ (mean of the bird’s presence). The final binomial models deviances are all higher than the confident interval of the random model deviance distribution.