



UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Ecole de biologie

**A MULTISCALE MODELLING APPROACH TO UNDERSTAND THE
REQUIREMENTS OF A RARE AND ENDANGERED OWL IN
SWITZERLAND**

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation, spécialisation « Ecologie et Evolution Computationnelles»
*Master Thesis of Science in Behaviour, Evolution and Conservation,
specialisation « Computational Ecology and Evolution»***

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Janvier 2019

Abstract

In Europe, agricultural practices have progressively evolved towards high productivity. This has led to the degradation of semi-natural habitats such as grasslands, threatening extensive agriculture followers, like the Scops owl (*Otus scops*). Although it is amongst the rarest breeding birds in Switzerland, the ecology of this species remains poorly known. In this work, we aimed to assess its habitat preferences using a multi-scale approach, combining vegetation and food abundance surveys. We generated a large set of multi-scale predictors and classified each of them at their best scales through multi-model inferences (MuMIn). We used the most important predictors at their best spatial scale to build Ensembles of Small Models (ESMs), which allowed us to build very high-resolution habitat suitability maps. We also showed that at least 60% of open meadows within a 50 m radius from the nest was essential for the Scops owl. Structures like wooded hems also showed a high importance, covering roughly 13% of the territory. However, we could not show food limitations between sites as the main prey of this owl was very abundant over the whole area. Given these major findings, this study provides valuable tools for conservation planning like precise requirements for the habitat and habitat suitability maps.

Key-words : Intensification, NDVI, AUC, Scops owl (*Otus scops*), rare species, habitat suitability models, *Tettigonia viridissima*, conservation

Résumé

En Europe, l'exploitation agricole a progressivement évolué vers une hausse de la productivité. Ce changement a entraîné la dégradation des prairies semi-naturelles, menaçant par conséquent toutes les espèces inféodées aux milieux d'agriculture extensive telles que le Petit-duc Scops (*Otus scops*). Parmi les oiseaux nicheurs les plus rares de Suisse, ses préférences en termes d'habitat et de régime alimentaire restent très peu connues. Dans cette étude, notre objectif était de comprendre ses besoins écologiques en menant des relevés de végétation sur des sites de présences actuelles et historiques puis, en prenant en compte l'abondance de nourriture, en quantifiant sa proie principale. Nous avons produit un large panel de différents prédicteurs à plusieurs échelles spatiales, puis sélectionné la meilleure échelle par prédicteur. Nous avons ensuite utilisé une technique d'inférence multimodèle (MuMIn) pour classer les prédicteurs selon leur importance. En sélectionnant seulement les plus importants, nous avons créé des Ensembles de Petits Modèles (ESMs) dans le but de modéliser la distribution des Petits-duc Scops. Nous avons montré qu'au moins 60% de prairies ouvertes sont essentielles à proximité de son nid. Les structures telles que les ourlets boisés ont également une grande importance, puisqu'elles représentent environ 13% de la surface dans un rayon de 100 m autour du nid. Nous n'avons pas pu montrer de limitation dans son régime alimentaire car sa principale proie était abondante dans toute la région analysée. Notre étude a permis de construire des modèles de distribution de l'espèce à très haute résolution qui pourront aider dans la planification de mesures afin de préserver cette espèce.

Mots-clés : Intensification, NDVI, AUC, Petit-duc Scops (*Otus scops*), espèce rare, modèles de distribution d'habitat, *Tettigonia viridissima*, conservation

Introduction

Over the last few decades, the landscape of Central Europe has evolved rapidly. On the one hand, mechanisation of agricultural practices on productive lands led to intensification and loss of natural structures. On the other hand, low productivity areas were abandoned, leading to forest expansion (Hofstetter *et al.* 2015). These combined processes have led to a homogenisation of agricultural landscapes, an increase of fertilisation and the loss of structures like bushes, or wooded hems. An example of the most alarming effect of these land-use changes is the degradation of semi-natural grasslands. They are one of the most threatened habitats in Europe (Canals & Sebastià 2000) because of the pastoral abandonment and the transition towards mechanisation, intensification or forest expansion (Laiolo *et al.* 2004). All these gradual changes have a negative effect on many “agriculture follower” species (Donald *et al.* 2001), like several birds species that are dependent on extensively managed areas as reported in the recent French (Nidal & Muller 2015) and Swiss (Knaus *et al.* 2018) bird atlases. Their decline stresses the need to quantify and understand their preferences in terms of habitat for conservation decisions.

It is therefore crucial to assess variation in species habitat preferences and how these preferences might differ spatially and temporarily. Habitat suitability models (HSM) (Guisan *et al.* 2017) are an increasingly used tool in this context, to quantify the effect of potentially important factors affecting species distributions and are therefore essential to set conservation measures (Guisan *et al.* 2013; Meller *et al.* 2014). However, the use of HSM on rare species is often hampered by low sample sizes, which frequently limit the use of such models for the rare and endangered species. Recently a new modelling technique using an Ensemble of Small Models (ESM), enables HSM’s use on poorly documented or rare species, which are most in need of being preserved (Elith *et al.* 2006; Lomba *et al.* 2010; Breiner *et al.* 2015, 2018). The use of HSM has another shortcoming: they do not give any information about the scale at which a predictor matters the most. To improve this, a multi-scale approach needs to be used. It improves models because it permits to understand the scale at which a predictor is the most important for the species (Schindler *et al.* 2013; Bellamy & Altringham 2015; Scherrer *et al.* In press). However, combination of ESM and multi-scale approach is still little used even if it provides satisfying HSM (Progin 2018; Scherrer *et al.* In press). The mix of both techniques can be important, especially for rare bird species. Up to

now, models on mobile species with potentially large territories used coarse resolution (e.g. 1km²), thus ignoring the different spatial requirements of the species (Barbosa *et al.* 2010). Indeed, bird species could have specific and independent needs for the nesting location, the hunting area or territory area (Jaberg & Guisan 2001; Martinez *et al.* 2003; Xie *et al.* 2016). Using a multi-scale approach allows to understand which requirements are needed in which range of the birds' territories and provides a powerful set of information to assess conservation measures (Seavey *et al.* 2009; Xie *et al.* 2016).

The Scops owl (*Otus scops*) is an example of a rare nocturnal bird species linked to semi-natural grasslands from southern Europe to central Asia. Switzerland is thus located at the northern limit of its distribution range. This long-distance migratory raptor is an endangered species on the Swiss red list (Ayé & Spaar 2015) and among the rarest breeding birds in Switzerland (Knaus *et al.* 2018). Its population has encountered a huge decline all over Europe from 1970 to 1990 (Denac 2009; Sergio *et al.* 2009; Šušmelj 2011) and a particularly steep one in the Valais (our study area in the south-western part of Switzerland) till 2000, when only two pairs remained (Sierro & Arlettaz 2013). Then, for unclear reasons, this population started to recover slightly (Pradervand 2018). As this species represents one of the least studied owls in Europe (Marchesi & Sergio 2005), the current focus is to understand its habitat preferences in relation to land-use changes comparing occupied and abandoned territories.

As a trophic specialist, the Scops owl mainly eats and feeds its chicks with orthopterans and moths, and secondly with other invertebrates or small vertebrates like small birds or mammals (Marchesi & Sergio 2005; Muraoka 2009; Latkova *et al.* 2012; Panzeri *et al.* 2014). All these studies showed a strong preference for *Tettigonia viridissima* (Orthoptera species) that could represent up to 87.6 % of the preys brought to the chicks (Latkova *et al.* 2012). Regarding the Valais population of Scops owls, Arlettaz *et al.* (1991) and Pradervand (2018) also described *T. viridissima* as their main prey. The literature mainly focuses on the diet of the owls, but rarely on the food availability. However, agricultural intensification is already shown to have a negative effect on orthopteran density and subsequently on the birds that feed on them (Benton *et al.* 2002; Buri *et al.* 2013).

In this study, we aimed to understand the habitat and main prey requirements of the Scops owl in the Valais, where the species is slightly reexpanding its distribution range despite the

mixed effects of intensification of agricultural practices and land abandonment. This should provide important knowledge and help for conservation purposes to preserve suitable habitat and to enhance food availability. To reach this goal, three combined approaches were used and included both explicative and predictive models. First, we quantified the main habitat units in Scops owl territories to understand this bird's habitat preferences. For this, we classified different types of habitats within presence and absence territories of Scops owl. To assess a possible aggregation behaviour or recolonization phenomenon (e.g. following the hidden lek hypothesis (Wagner 1997)), we checked for presence patterns according to the distance to the area where the two remaining pairs nested in 2000. Then, we focussed on grassland by conducting vegetation surveys. Because most of the studies on the Scops owl habitat selection used the amount of open vegetation as a predictor, without discrimination between grassland types (Denac 2009; Sergio *et al.* 2009), our aim here was to develop a tool to categorise meadows based on the Swiss classification (Delarze *et al.* 2015) to better assess the requirements of this bird in a context of land-use changes and intensification of grassland. Finally, we quantified the abundance of the most important prey, *T. viridissima*, in abandoned and currently occupied territories to see if the main prey could be a limiting factor.

Materials and methods

Study area

The population of Scops owl that was the focus of this study is found in the Valais (46° 4' N, 7° 36' E), located in the south-western part of Switzerland. The elevation of this Swiss canton stretches from 372 m to 4634 m. In this area, the Scops owl breeds between 470 m and 1400 m, where the climate is continental, characterised by cold winters and by hot and dry summers (Andrey *et al.* 2014). The study area therefore takes into account the lowland until the beginning of the mountain belt around 1400 m (Pradervand 2018). The lowland is covered by intensive meadows, intensive fruit cultures (mainly pears and apples) or crop farming. South exposed slopes are used for vineyards, which represent the predominant agricultural land-use type (Bosco *et al.* In press), whereas north exposed slopes are covered by fruit cultures, like apricots. The last extensive agricultural areas and hence, natural meadows, are located between 800 m, which is the upper limit for vineyards, and 1300 m, where coniferous forests start (Arlettaz 1990; Arlettaz *et al.* 1991).

Scops owl survey and historical data

The Valais hosts the biggest Scops owl's population in Switzerland with an average of 25 singing males per year and at least 15 pairs. A hybrid monitoring (data gathered by volunteers and official monitoring on regular presence sites) of the Scops owl is conducted every year. To assess the absence or presence of Scops owls in the studied territories acoustic surveys are conducted every year on all the territories from the 20th of April to the 20th of June, between 9:00 PM and 2:00 AM, when the Scops owls are the most active (Galeotti *et al.* 1997; Panzeri *et al.* 2014). The monitoring only took place under favourable conditions, on warm, calm nights with no rain and low winds. Using this data (Swiss Ornithological Institute database), we selected 34 territories amongst the 71 known presence sites in the Valais between 2000 and 2018 (from these, 26 were used by known pairs). To avoid bias due to differences in occupancy frequencies, we randomly selected the same number of presence sites (17) in 2 categories of presence frequencies since 2000: occasionally used territories, which showed less than one in four years occupancy, and frequently used territories, which showed at least one in four years occupancy. As absence territories, we used 33 territories where the species was present historically (between 1940 and 1999) and 30 random territories (with a minimal distance of 700 m with any other centre of territory, generated in qGIS (Quantum GIS Development Team, 2018)), totalizing 97 studied territories with presence and absence data (**Figure 1**). The central position of each territory corresponds to the nesting site (i.e. nest box or location of the male and female duetting, which means that the female is answering the male song) or to the random point in the case of the 30 random territories. In addition to the previous monitoring (which already considers most of the historical sites), we monitored all absence sites to confirm the absence of the owls from random or historical territories.

As the Scops owl is known to have solitary males that sing actively but do not breed, the location of territories with the presence of pairs ensures a higher probability of nesting. The two territory categories (presence of all Scops owls and presence of only pairs) should limit the bias of working with unfavourable territories due to solitary males singing actively over large areas.

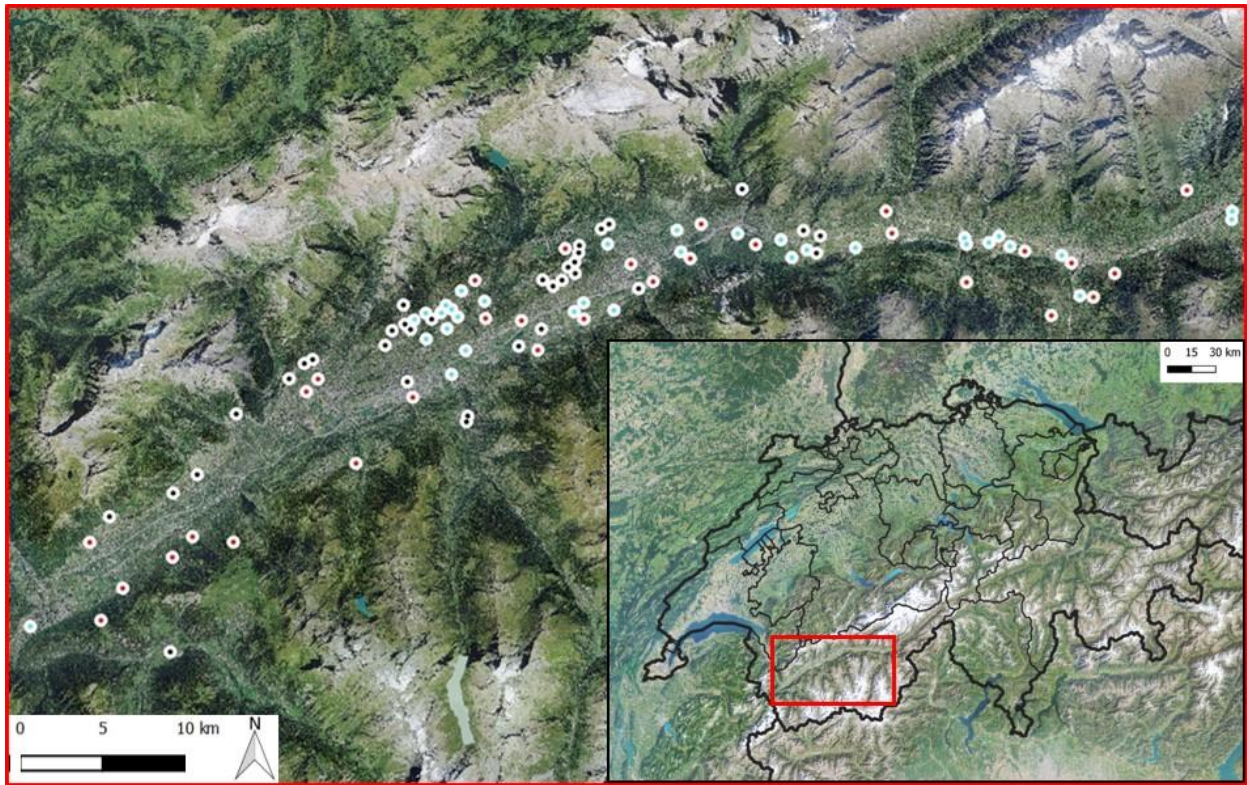


Figure 1. Valais map with all mapped territories. Blue dots represent territories with presence of all Scops owls, at least once between 2000 and 2018. Black and red dots represent absence territories (historical and random, respectively).

Territory maps

In the Valais, Scops owls followed by radio tracking showed a variation of territory size between 1.1 and 9.8 ha (Sierro & Arlettaz 2013). In Europe, territories are known to range from 1.1 to 30 ha, with an average territory size usually below 15 ha. (Galeotti *et al.* 1997; Denac 2009; Panzeri *et al.* 2014; Ramella 2017). We therefore mapped territories based on a 250 m radius (approx. 20 ha, 196141 m² exactly), which represents the upper average of territory size. To quantify and analyse the habitats available in each territory, we mapped all structures in the field. Meadows were classified according to vegetation classes following Delarze *et al.* (2015) and forested areas were classified according to their structure. **Table 1** gives the full list of categories and criteria used for the mapping of the territories. This part of fieldwork has been completed before the first mowing to avoid bias due to vegetation regrowth.

Vegetation survey and model

We aimed to assess automatically the intensification gradient on meadows led by different agricultural practices. To reach this goal, we related different types of meadows

representing intensification gradient over the whole study area to a productivity index using ecological indicator values (EIVs).

We first selected open habitat on the whole study area using canopy cover, to avoid trees, structures or constructions. In ArcGIS (version 10.6, ESRI Inc.), we calculated canopy as the difference between the digital surface model (DSM) and the digital terrain model (DTM) using a 5 m x 5 m pixel resolution (canopy = DSM-DTM). Then we resampled the layer at 10 m using bilinear interpolation to fit the productivity grid layer. DTM and DSM were both obtained from the LIDAR measurement of Swisstopo (Alti-3D, 2005). Open habitat was defined as having a canopy between 0 m and 0.3 m and used for the next steps of the analysis.

Data collection

Within mapped territories, we selected 57 meadows using a balanced sampling (except for steppe, the rarest meadow) for four types of vegetations that represent an agricultural intensification gradient on meadows: *Stipo-Poion* (steppe, very extensive, dry, partly grazed, not watered, not fertilised), *Mesobromion* (meadows with extensive agro-pastoral management: mostly grazed, poorly watered and fertilized), *Arrhenatherion* (more intensively managed, mainly used for hay harvesting, watered and fertilized) and intensive meadows (artificial meadows, close to monoculture) (Delarze *et al.* 2015). On each of them, three sampling plots were selected randomly with a minimum distance of 10 m between them. Each of these plots fitted inside a Sentinel-2 pixel (10 m x 10 m resolution, provided by the Copernicus program led by the European Commission, processed at level 2A/3A by the CNES for the data centre THEIA). We estimated the primary production by using normalized difference vegetation index (NDVI) calculated using the infrared and near infrared bands from Sentinel-2 (Pettorelli *et al.* 2011). To ensure that the NDVI value of the sampling points would reflect the vegetation survey, we avoided edge effects and used uniform pixels without trees, bushes or other structures that could influence NDVI values.

To classify the 57 meadows according to a gradient of intensification (to refine the previously defined categories), we selected 59 indicators plants species specific to the four different vegetation types (**Table S1**) using a mix of two classification guides: Delarze *et al.* (2015) and the determination key of natural open agricultural land for Switzerland (Buholzer

et al. 2015) and complements from two expert botanists (pers. com. Dr. A. Litsios-Dubuis and Dr. P. Vittoz).

Vegetation surveys were conducted before the first mowing for each sampling point(except for 3 plots surveyed 2 to 3 weeks after mowing), assessing the presence and abundance of the 59 indicator plant species (**Table S1**) within a 2 m x 2 m quadrat, that is the best trade-off size between time and species recorded (Pradervand *et al.* 2014).

Vegetation analysis

The selected indicator plant species (**Table S1**) were all related to specific Landolt values, which are EIVs for Swiss plants (Landolt *et al.* 2010). They represent ecological requirements like light, nitrogen, pH, temperature, continentality, dispersity and life form. Means of these Landolt values were computed for each vegetation plot by averaging the respective Landolt values of all species present on a plot taking in account their relative abundance following the method of Dubuis et al (2013).

A Detrended Correspondence Analysis (DCA), using the “decorana” function of the VEGAN package (Oksanen *et al.* 2018) in R (Core Team 2018) was conducted on the plant community dataset, to test whether the computed average Landolt values per plot could be used as a proxy for intensification on each meadow. A DCA spatializes data according to related variables and a given number of axis. In the present case, the DCA spatialized the vegetation surveys according to the Landolt values on two axes. The first axis of this DCA reflected the intensification gradient and was kept for the next analysis as a proxy for the intensification gradient.

Modelling the intensification gradient

The correlation between the value from the first axis of the DCA for each of the 171 vegetation survey plots (3 plots x 57 meadows) and NDVI values was the highest using the NDVI images from April 2018 (**Figure S1**). This can be explained by the fact that the vegetation had already started to grow in April in this area, and none of the meadows had already been harvested (which would introduce a lot of variation in the data). Seven points out of the 171 were dropped for the following analysis because three were on a highly intensive meadows, which were ploughed in April and hence gave a false NDVI response, two were on a new layer of backfill and thus the vegetation was pioneer and therefore not

representative of one of the four used vegetation types, and two other points were on a narrow meadow, where the edge effect of roads could influence the NDVI values (Knop *et al.* 2006). The final correlation between value from DCA axis 1 and April 2018 NDVI for the 164 remaining points was -0.84 (Pearson's product-moment correlation: $t = -19.62$, $df = 162$, p -value $< 2.2e-16$, **Figure S1**), which is defined as strong to very strong (Akoglu 2018).

Within the range of observed NDVI values in our surveys, we built a linear model (lm) to predict and project the intensification gradient (the first axis of the DCA) using the NDVI of April 2018 at the scale of the study area using a 10 m x 10 m resolution (lm: Adjusted R-squared: 0.70, F-stat: 384.8 on 1 and 162 DF, p -value: $< 2.2e-16$, **Figure S1**). The use of DCA's first axis instead of the NDVI directly was preferred, as it allowed to better discriminate between meadow types; it also permitted to encompass the limitation of NDVI to predict fine-scale variation as shown by Löfgren *et al.* (2018) .

We then reclassified the vegetation over the whole study area based on the values of the quantiles of the DCA axis 1 for each vegetation type. To assess the accuracy of the vegetation model, we compared the areas of the different vegetation types given by field territories mapping and modelled data (sum of all 10 m x 10 m pixels per vegetation type per territory) using Student's t-tests (**Table S2**).

Environmental predictors

Based on the territories mapping, we computed coverage percentage of each habitat variable (named as "Mapping categories" in **Table 1**) and coverage percentage of groups of similar habitat types (named as "Merged variables" in **Table 1**). We also assessed habitat heterogeneity as the number of different habitat categories per territory (named as "Richness" in **Table 1**). We calculated the length of edges as polygonal perimeters in qGIS to assess for length of the edge of different structures such as forest, wooded hems and bushes (named as "Edges" in **Table 1**).

We summed the number of pixels of the vegetation intensification model per meadow type per territory to calculate the coverage percentage for spatialized intensive meadows, *Arrhenatherion* and *Mesobromion* (named as "Spatialized vegetation" in **Table 1**). We excluded spatialized *Stipo-Poion* as it was shown to neither converge toward the field mapping nor to correlate to the area given by the field mapping (**Table S2**).

272 Additionally, three different canopy surfaces (named as “Canopies” in **Table 1**) were
273 included: the bushy vegetation from 1 m to 3 m, between 3 m to 6 m for young trees and
274 between 6 m to 15 m for old stands. The total canopy for each territory was calculated as
275 the difference between DSM and DTM (canopy = DSM-DTM) with a 2 m x 2 m resolution in
276 ArcGIS, to which we removed mapped constructions. The mapped constructions raster came
277 from the rasterization of the territory maps shapefile with a resolution of 1 m x 1 m, we
278 resampled it to 2 m x 2 m resolution with the bilinear method.

279 Four bioclimatic variables were also extracted at each territory central point (named as
280 “Bioclimatic variables” in **Table 1**): temperature and precipitation for the closest period
281 available (1981-2010), the mean of growing degree days (GDD) above 3°C from 2000 to 2015
282 and the mean of solar radiation from April to September, which represents the vegetation
283 growth period. Temperature and precipitation are well-known drivers of plant growth
284 (Moles *et al.* 2014) and orthopteran distributions (Eo *et al.* 2017). The GDD allows to assess
285 heat accumulation. It is used to predict development of plants and can be very indicative for
286 insects, reflecting heat accumulation necessary for larval stages (Hodkinson & Bird 1998).
287 This was computed with a 3°C base temperature threshold, as this is the usual average limit
288 for plant growth. Solar radiation reflects slopes and reliefs and can thus also be a good
289 predictor of Scops owl presence (Zimmermann & Kienast 1999; Leempoel *et al.* 2015).

290 To deal with spatial autocorrelation and identify a potential recolonization pattern, we
291 calculated the distance of each territory centre to the last remaining area used by two pairs
292 in the Valais in 2000 (named as “Distance to Grimsuat” in **Table 1**), when the population of
293 Scops owls was at its smallest size (Sierro *et al.* 2003). This also corresponds to the current
294 area with the highest territory density (Pradervand 2017, 2018). This variable could show a
295 potential bias due to recolonization.

296 All environmental data, except the “Distance to Grimsuat” and the bioclimatic ones, were
297 computed for 5 different radii: 50 m, 100 m, 150 m, 200 m, 250 m (from the central point of
298 each territory) conserving the resolution of 10 m x 10 m and thus ranging from 81 pixels to
299 1961 pixels per radii. This allowed a comparison between single scale and multi-scale
300 approaches.

301

	<i>Criteria</i>	<i>In MuMIn all</i>	<i>In MuMIn pairs</i>	<i>T. viri. GLMs</i>
Mapping categories				
<i>Arrhenatherion</i>	Based on Delarze et al. (2015) and Table S1			
<i>Polygono-Trisetion</i>	Based on Delarze et al. (2015)			
<i>Mesobromion</i>	Based on Delarze et al. (2015) and Table S1			Yes
<i>Intensively pastured area</i>	Permanent fences and “path of cattle”	Yes	Yes	
<i>Steppe</i>	Based on Delarze et al. (2015) and Table S1	Yes	Yes	
<i>Intensive meadows</i>	Based on Delarze et al. (2015) and Table S1			
<i>Single-crop farming</i>		Yes	Yes	Yes
<i>Intensive fruit culture</i>	Rows of fruit trees			
<i>Orchard</i>	Sparse fruit trees in meadows			
<i>Vineyard</i>		Yes	Yes	
<i>Garden</i>	Private vegetal area in front of house or building	Yes	Yes	Yes
<i>Soccer field</i>				
<i>Bushes</i>	< 4 m trees	Yes	Yes	
<i>Wooded hems</i>	> 4 m trees	Yes	Yes	Yes
<i>Forest</i>				
<i>Grassy roadside</i>	Vegetation growing close to the road			
<i>Reed</i>				
<i>Fallow</i>				
<i>Water</i>				
<i>Construction</i>	Building, paved road			
<i>Dirt track</i>		Yes	Yes	
<i>Unclassified</i>				
Merged variables				
<i>Grassland</i>	<i>Arrhenatherion</i> , <i>Polygono-Trisetion</i> , <i>Mesobromion</i> , intensive pastured area, steppe, intensive meadows, steppe and grassy road side.	Yes	Yes	Yes
<i>Trees</i>	Wooded hem and forest		Yes	Yes
<i>Vegetation</i>	Bushes, fallow, garden, single crop farming, intensive fruit culture, soccer field, reed and orchard	Yes	Yes	Yes
<i>Unsuitable</i>	Constructions, water, dirt track and unclassified	Yes	Yes	Yes
<i>Fruit culture</i>	Intensive fruit culture and orchard	Yes	Yes	
Richness	Number of mapping categories	Yes	Yes	Yes
Edges				
<i>Bushes</i>	Calculated in QGIS as the perimeter of bushes polygons			
<i>Wooded hems and forest</i>	Calculated in QGIS as the perimeter of wooded hems and forest polygons			Yes
<i>Bushed, wooded hems and forest</i>	Calculated in QGIS as the perimeter of bushes, wooded hems and forest polygons	Yes	Yes	
Spatialized vegetation				
<i>Arrhenatherion</i>	Count of 10 m x 10 m cells per territory * 100 / radius of considered territory size	Yes	Yes	Yes
<i>Mesobromion</i>	Count of 10 m x 10 m cells per territory * 100 / radius of considered territory size	Yes	Yes	Yes
<i>Intensive meadows</i>	Count of 10 m x 10 m cells per territory * 100 / radius of considered territory size	Yes	Yes	
Canopies				
<i>Bushes</i>	Between 1 m and 3m high	Yes	Yes	
<i>Young trees</i>	Between 3 m and 6m high	Yes		
<i>Old Strands</i>	Between 6 m and 15m high		Yes	

Bioclimatic variables				
Temperature	Mean of temperature from 1981 to 2010 ¹			
Precipitation	Mean of precipitation from 1981 to 2010 ¹	Yes	Yes	Yes
Growing degree days	Mean of GDD above 3°C from 2000 to 2015 ²	Yes	Yes	Yes
Solar radiation	Mean of solar radiation from April to September, vegetation growth period ³	Yes	Yes	
Distance to Grimsuat		Yes	Yes	

¹Daily MeteoSwiss Grid-Data Products at 1 km resolution for 1981-2010, means computed by Olivier Broennimann to a resolution of 25 m x 25 m (Broennimann 2018). We resampled in ArcGIS to a 10 m x 10 m resolution, using bilinear interpolation.

²Computed by year by Olivier Broennimann (Broennimann 2018). In R, we did the average of the 15 last available years.

³Computed by month by Niklaus Zimmermann (WSL) (Broennimann 2018). In R, we averaged the solar radiation for the months of April to September.

Scops owl distribution models

Variable selection

To select the best scale for each variable to model Scops owl distribution, we ran univariate general linear models (GLMs) for each variable with the Scops owl as response variable following a binomial distribution. We selected the best scale for each variable according to their area under the receiver operating characteristic curve (AUC) (Bellamy & Altringham 2015; Progin 2018; Scherrer *et al.* In press; Bosco *et al.* In press). Then, only uncorrelated variables (correlation < 0.7) were kept to avoid overfitting of the data (Dormann *et al.* 2013; Lomba *et al.* 2010). For pairs of correlated variables, the one with the highest AUC was kept (Bellamy & Altringham 2015; Hofstetter *et al.* 2015). The columns “in MuMIn all” and “in MuMIn pairs” of **Table 1** indicated selected predictors for the following step.

Variable importance

To select then the best variables to model the Scops owl distribution, we quantified the relative importance of each variable using GLMs with all possible combinations of two variables, expressed as linear and quadratic terms. We used bivariate models each time to avoid overfitting the models (Harrell *et al.* 1996; Guisan & Zimmermann 2000; Guisan *et al.* 2017). To compare the models and to rank the predictors, the multi-model inference (MuMIn) package (Barton 2018) in R was used to compute the Akaike information criterion corrected for small-sample-size (AICc) for each model. These AICc scores permitted then to calculate the relative importance (RI) of each variable (Burnham *et al.* 2011).

Models and projections

We used Ensemble of Small Models (ESM) approach to model the distribution of the Scops owl in the Valais. This strategy was developed to deal with small sample sizes, by creating many small models with different modelling methods and for all possible combinations of predictors, then assembles and weights all of them according to the chosen metric (Lomba *et al.* 2010; Breiner *et al.* 2015). To limit the number of variables and avoid overfitting, we built bivariate models each time in respect to Harrell's rule of thumb (Harrell *et al.* 1996), with three different techniques commonly used to build SDMs: general linear model (GLM), general additive model (GAM), and random forest model (RF) (Breiman 2001; Guisan *et al.* 2002; Elith *et al.* 2006; Lomba *et al.* 2010) in R with BIOMOD2 package (Thuiller *et al.* 2016). For each model, 80% of the data was used to train the model and 20% to evaluate it. The AUC was used both to evaluate the accuracy of each bivariate model (Fielding & Bell 1997) and as weight in the final ESMs. Bivariate models with an AUC smaller than 0.8 were not used to build the ensemble prediction. All ESMs were built in the ECOSPAT package in R (Di Cola *et al.* 2017).

This process was repeated three times. **(1)** We built one ESM per scale (50 m, 100 m, 150 m, 200 m, 250 m) with all uncorrelated variables (except "Distance to Grimsuat" and "Bioclimatic variables", **Table 1**) and one ESM with these variables at their respective best scale to assess how the selection of scale could improve the ESMs. We evaluated each ESM with AUC, specificity and sensitivity. **(2)** We used the ten most important variables given by the MuMIn analysis to obtain an explicative model of the species' ecology and evaluated it by the AUC. **(3)** We used the four most important predictors covering the whole study area at a 10 m x 10 m resolution: "Spatialized vegetation" or "Bioclimatic variables" (**Table 1**) in order to get a predictive model for the Scops owls and obtain fine scale spatial predictions over the area. This predictive model was also evaluated with the AUC in order to compare its accuracy with the previous explicative model. For "Spatialized vegetation", percentage of considered vegetation type at its best radius was computed through "focal" function of the package RASTER (Hijmans 2018) in R, permitting to have for each 10 m x 10 m pixel the percentage of considered vegetation type within its best radius.

We built pie-charts with proportion of suitable habitat and unsuitable habitat per territory to see if random absence and historical absence territories have the same amount of suitable

habitat. To reach this goal, we computed a binary projection based on the previous predictive model, hence telling for each pixel if it was suitable or not for the Scops owl. We then calculated the percent of suitable pixels per territory within a 250 m radius.

The whole framework for Scops owl distribution model was done twice: once with all presences of Scops owl (single singer males and pairs) as response variable and once with only presences of pairs as response variables, thus considering territories with only single singer males as absence territories. Both responses followed a binomial distribution.

Meadow intensification and the Scops owl

Knowing that the Scops owl is a farmland bird (Sierro & Arlettaz 2013) and thus depends on open vegetation (Arlettaz 1990; Šušmelj 2011), we focussed on the vegetation intensification model built previously. Within all studied territories, we extracted DCA axis 1 values attributed to each 10 m x 10 m pixel of open vegetation and plotted the histogram of these values according to the presence/absence status of territories. With Student t-tests, we tested the difference between presence and absence territories considering all Scops owl presences and the difference between presence and absence territories considering only pair presences.

Tettigonia viridissima importance for the Scops owl

Acoustic monitoring

On 33 presence territories (from them, 26 were used by pairs) and on 32 historical ones, *T. viridissima* surveys were conducted. Between 9:00 PM and 1:00 AM, when they sing actively (Jeliazkov *et al.* 2016), three roughly 600m long transects were walked by foot to assess the number of singing males. Tettigonids were mapped on the field. As song can be heard up to 50 m or even 200 m in clear environments (Bellmann & Luquet 1995; Baur *et al.* 2006), a buffer of 40 m was used to take into account the effect of natural elements or building walls which could affect the sound transmission. Transects had a length of about 600 m so that the acoustic surveys covered between 46% and 78% of territories (average: 69%). Minimum is linked to a presence territory crossed by the Rhône river and containing an inaccessible gravel quarry.

Three acoustic surveys were conducted during the whole breeding season of the owls (**Table S3**) to have a global overview of *T. viridissima* abundance. Surveys were conducted only on

nights where the weather was good, meaning no wind, no rain and temperatures above 15°(Arak *et al.* 1990; Schirmel & Fartmann 2013).

Analysis

For each territory, we summed the three surveys to assess the food abundance throughout the season. We then normalised this final count by the percentage of total territory area covered by the 40 m buffer around transects.

To test whether the abundance of *T. viridissima* could explain the presence of Scops owls, we followed the same process as for the Scops owl to assess variable importance: we compared bivariate models and ranked the predictors thanks to the MuMIn package in R (Barton 2018). For this, we used only the 65 territories on which counts of singers were done and added the normalised total count to the previously selected predictors (indicated by the columns “in MuMIn all” and “in MuMIn pairs” of **Table 1**). As a subset of the territories was used in this analysis, correlation between variables was checked again and only uncorrelated variables were kept (correlation <0.7) to run all bivariate models and rank the predictors.

A detailed study of structure preferences for males *T. viridissima* is provided in supplementary methods (**Text S1**).

Results

Model results and scale selection

Using a multi-scale approach instead of a single-scale one improved the predictive power of the models. AUC for the ESMs with variables at their best scale were 0.88 when we considered all presences of Scops owl (**Figure 2A**) and 0.93 when we considered the presence of pairs. (**Figure 2B**). Both ESMs were also good to excellent if the single-scale at 250 m was selected: AUC for all presences was 0.84 (**Figure 2A**) and AUC for presence of pairs was 0.93 (**Figure 2B**) but the standard deviations around AUC were greater in both cases compared to ESM with variables at their best scale.

Specificity and sensitivity were also the highest when the best-scale for each predictor was selected.

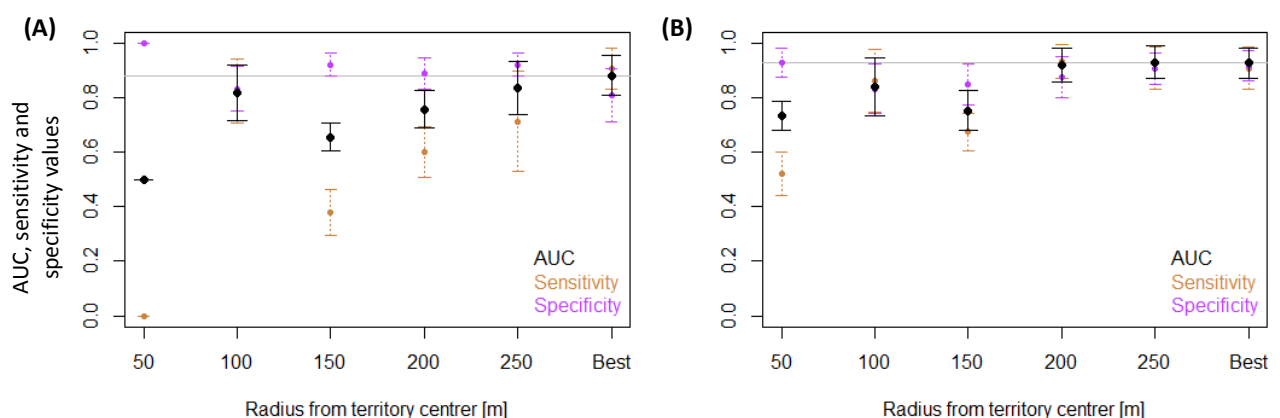


Figure 2. ESMs evaluation depending on single or multi-scale. (A) ESMs built with all presences of Scops owl as response. **(B)** ESMs built with only presences of pairs as response. For both **(A & B)**, mean and standard deviation for AUC, sensitivity and specificity are shown for all 5 single-scale ESMs and the multi-scale one, containing each variable at its best scale. The scale of predictors is indicated by the x-axis and label “Best” means that predictors were selected at their best scale to build the ESM.

Important variables for the Scops owl

When all Scops owl presences were considered, *precipitation* and proportion of *Mesobromion within 100 m radius* were the most important predictors. Increase in *precipitation* trends to decrease the probability of Scops owl presence (**Figure 3A**). Increases in proportion of *Mesobromion within 100 m radius*, which was the second most important predictor (**Figure 3B**), increases the probability of Scops owl presence. Proportion of *Arrhenatherion within 100 m radius* showed an optimum around 35% (**Figure 3C**). Probabilities of observing a Scops owl are increased when area of *Arrhenatherion* ranges

from 20% to 60% within 100 m radius from its nest. The probability also increases linearly with increasing amount of *grassland within 50 m radius* from the nest and increasing *GDD* (**Figure 3D-E**). The proportion of *wooded hem within 100 m radius* showed an optimum around 13% (**Figure 3F**).

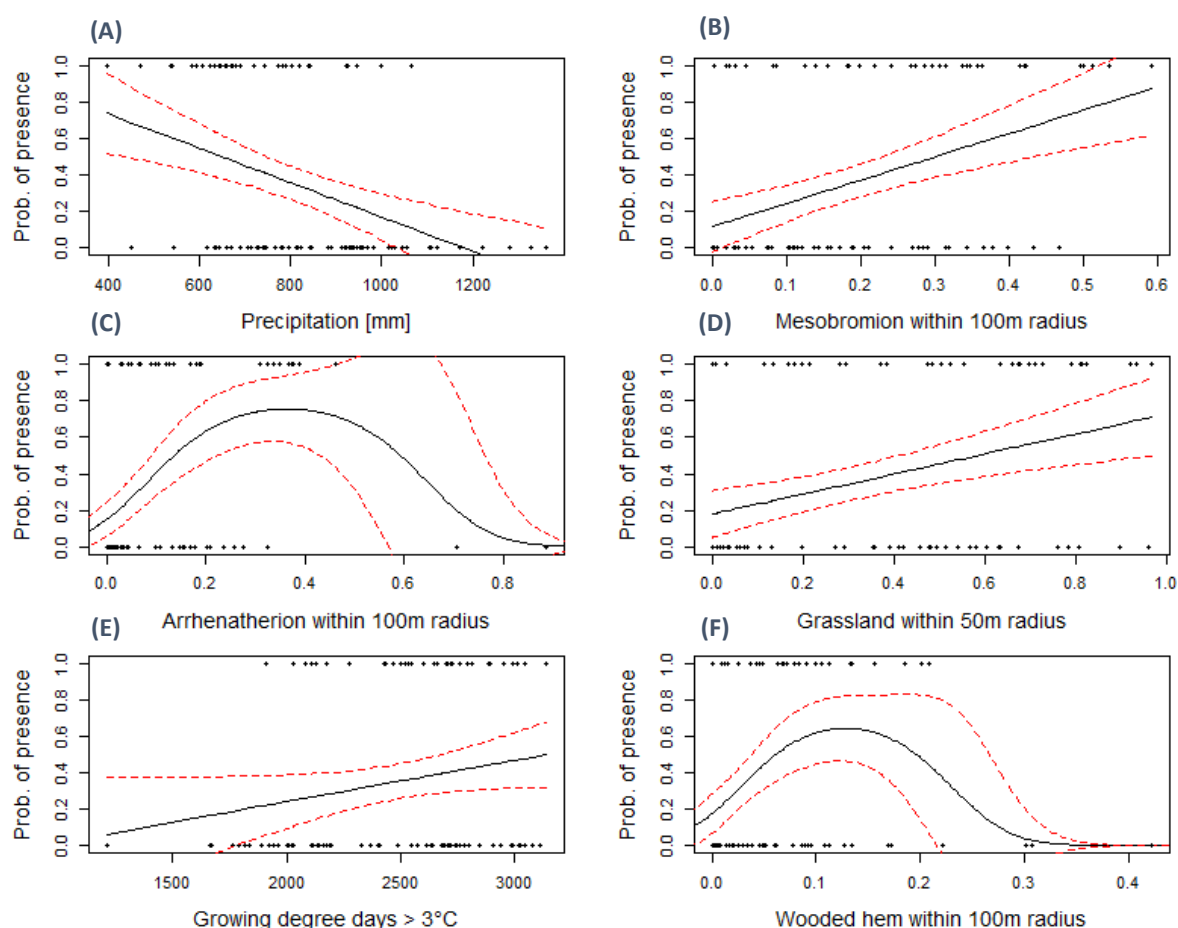


Figure 3. Plots of all Scops owl presences and absences according to the six most important predictors given by the MuMIn analysis. Y-axis represents for each plot the probability of Scops owl presence.

(A) Precipitation showed a relative importance (RI) of 0.78 (lm: F-stat = 15.21 on 1 and 95 DF, p-value > 0.001).

(B) Mesobromion within 100 m radius showed a RI of 0.78 (lm: F-stat = 19.15 on 1 and 95 DF, p-value > 0.001).

(C) Arrhenatherion within 100 m radius showed a RI of 0.03 (glm: Null deviance: 125.67 on 96 DF, Residual deviance: 104.07 on 94 DF, z-value = -2.54, p-value = 0.011, AIC= 110.07).

(D) Grassland within 50 m radius showed a RI of 0.03 (lm: F-stat = 13.95 on 1 and 95 DF, p-value > 0.001).

(E) Growing degree days >3°C showed a RI of 0.02 (lm: F-stat = 3.77 on 1 and 95 DF, p-value = 0.055).

(F) Wooded hem within 100 m radius showed a RI of 0.01 (glm: Null deviance = 125.67 on 96 DF, residual deviance = 111.01 on 94 DF, z-value = -2.46, p-value = 0.014, AIC = 117.01).

They are all expressed in linear term, except Arrhenatherion (C) and wooded hem (F) that are expressed in quadratic term.

When considering only presence of pairs (**Figure 4**), open vegetation (proportion of *Arrhenatherion within 100 m radius*, proportion of *grassland within 50 m radius*) and *precipitation* also played a strong role as they represented the three most important

predictors (**Figure 4A-C**). They showed the same trend as for *all Scops owls* (**Figure 3A, 3C & 3D**). The *distance to Grimisuat* showed that two clusters of Scops owl pairs exist: one close to Grimisuat and one about 45 km away (**Figure 4D**). The proportion of *single crop farming within a 100 m radius* also seemed to be important (**Figure 4E**). In the sixth position, the proportion of *Mesobromion within a 150 m radius* (**Figure 4F**) followed the same trend as the one for the *Mesobromion within 100 m radius* when all presences of Scops owl were considered (**Figure 3B**).

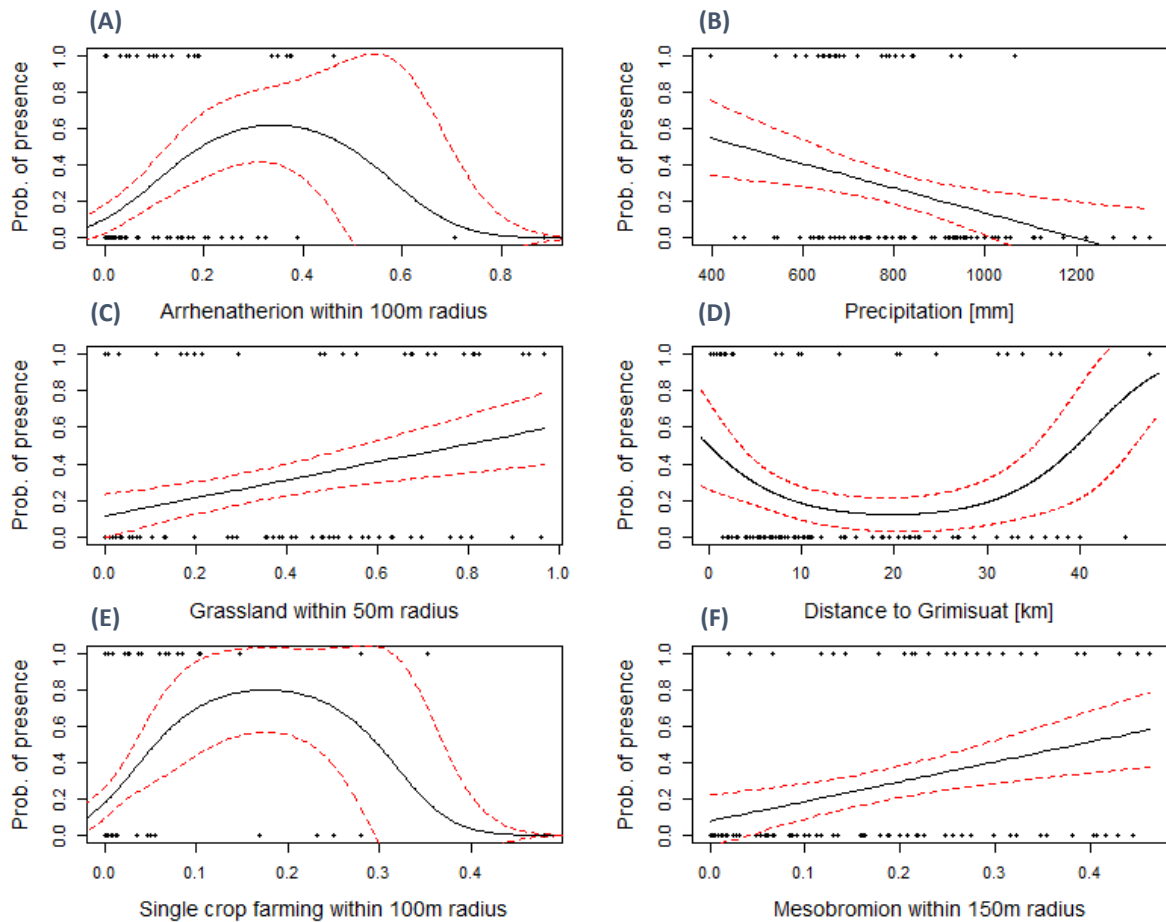


Figure 4. Plots of only pair presences and absences according to the six most important predictors given by the MuMIn analysis. Y-axis represents for each plot the probability of Scops owl presence.

(A) Proportion of Arrhenatherion within 100 m radius showed a RI of 0.3 (glm: Null deviance: 112.77 on 96 DF, Residual deviance: 95.40 on 94 DF, z-value = -2.03, p-value = 0.043, AIC = 101.4).

(B) Precipitation showed a RI of 0.28 (lm: F-stat = 8.63 on 1 and 95 DF, p-value = 0.004).

(C) Proportion of grassland within 50 m radius showed a RI of 0.19 (lm: F-stat = 13.02 on 1 and 95 DF, p-value > 0.001).

(D) The distance to Grimisuat showed a RI of 0.16 (glm: Null deviance: 112.77 on 96 DF, Residual deviance: 102.16 on 94 DF, z-value = 2.93, p-value = 0.003, AIC = 108.16).

(E) The proportion of single crop farming within 100 m radius showed a RI of 0.16 (glm: Null deviance: 112.77 on 96 DF, Residual deviance: 99.29 on 94 DF, z-value = -2.38, p-value = 0.018, AIC = 105.29).

(F) The proportion of Mesobromion within 150 m radius showed a RI of 0.15 (lm: F-stat = 10.98 on 1 and 95 DF, p-value = 0.001).

Precipitation, grassland and Mesobromion are expressed in linear term, the other three are expressed in quadratic term.

Meadow intensification and the Scops owl

As vegetation is one of the major drivers of Scops owl presence, we checked for distribution of open vegetation along the DCA 1 axis (**Figure 5**). Territories with presence of pairs contained significantly more *Arrhenatherion* and *Mesobromion*, and less intensive meadows or steppe than absence territories (Student's t-test, $t = 3.56$, $df = 1136.5$, $p\text{-value} < 0.001$). Pairs of Scops owls showed a bigger selective behaviour compared to all Scops owl presences, where the trend was also highlighted but this difference was not significant (Student's t-test, $t = 2.10$, $df = 1133.3$, $p\text{-value} = 0.04$. Bonferroni correction for multiple testing, here two tests, implied that p-value became significant at a 0.025 threshold). Scops owls promote territories with *Arrhenatherion* and *Mesobromion* and hence show a preference for these two types of vegetation compared to intensive meadows and steppes. This result was congruent with previous ones showing the importance of *Arrhenatherion* and *Mesobromion* (**Figures 3 & 4**) and their contributions to ESMs and final projections (**Tables 2 & 3**).

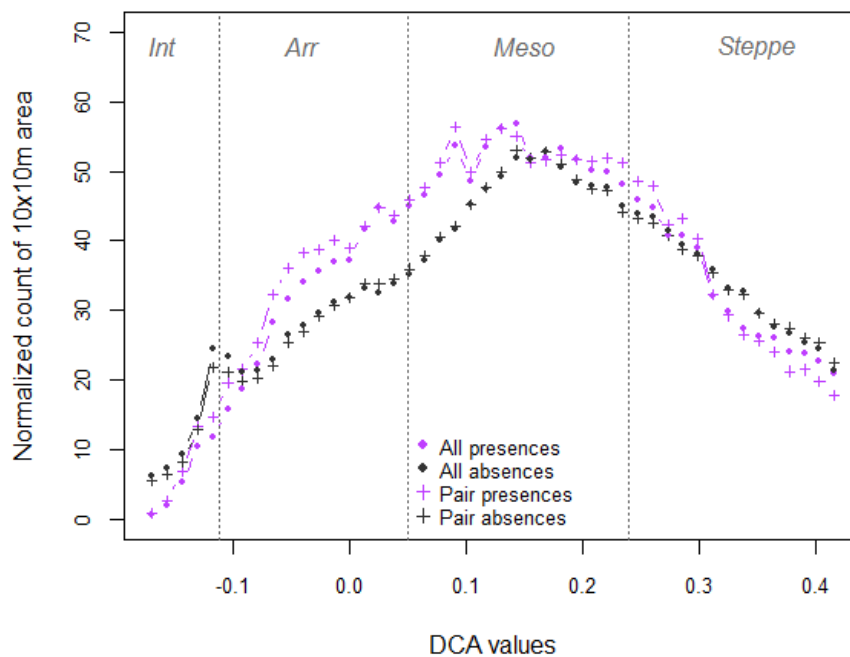


Figure 5. Distribution of open vegetation along DCA axis 1. Defined spatialized vegetation types are shown by the dotted vertical line, with the type written at the top of the box. Int: intensive meadows, Arr: Arrhenatherion, Meso: Mesobromion, Steppe. X-axis represents DCA axis 1 values and Y-axis represents the counts of pixels, normalized by the proportion of open vegetation area covering all the considered type of territories.

Scops owl distribution

Final projections of Scops owl distribution were both accurate. Predictions of all Scops owl presences (**Figure 6**) showed an AUC of 0.90 and the model of pair presences (**Figure 7**) showed an AUC of 0.85. The contribution of each of the four used predictors is shown in **Table 2**.

Table 2. Contribution in percentage of each predictor to the ESMs for projection built with the four most important predictors covering the whole study area at a 10 m x 10 m resolution.

All Scops owl presences		Pair presences	
Predictors	%	Predictors	%
<i>Arrhenatherion within 100 m radius</i>	37.49	<i>Precipitation</i>	50.00
<i>Precipitation</i>	31.45	<i>Arrhenatherion within 100 m radius</i>	25.72
<i>Mesobromion within 100 m radius</i>	24.87	<i>Mesobromion within 150 m radius</i>	24.28
<i>GDD > 3°</i>	6.19	<i>GDD > 3°</i>	0

The prediction of pair presences is less accurate than the prediction of all Scops owl presences, and only GLMs were used in the ESM for pairs, the two others modelling methods (GAM and RF) were always excluded from the ensemble forecasting falling below the 0.8 AUC threshold.

Figure 6. Habitat suitability projection for all Scops owls. Black circles show historical territories and blue circles show presence territories.

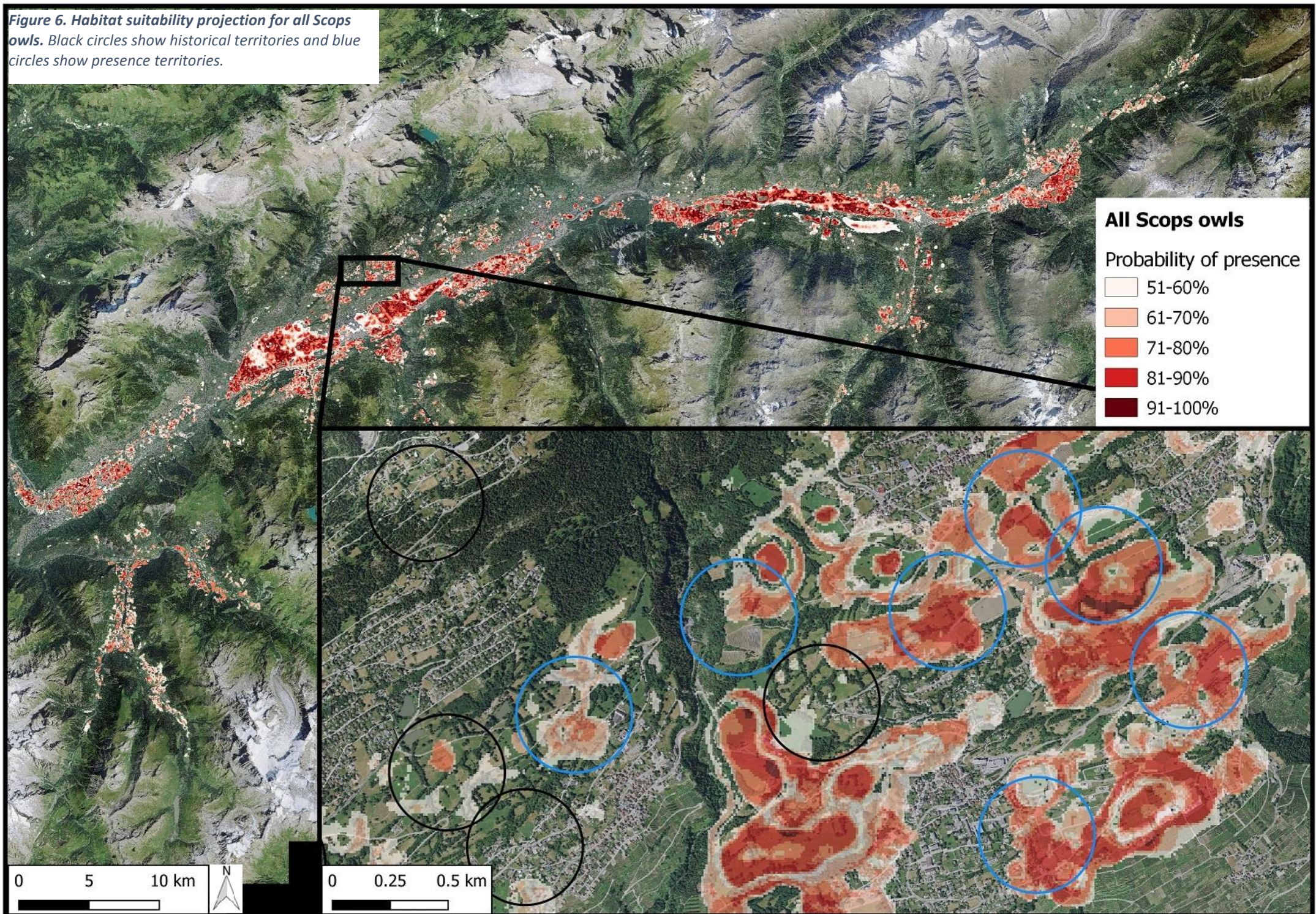
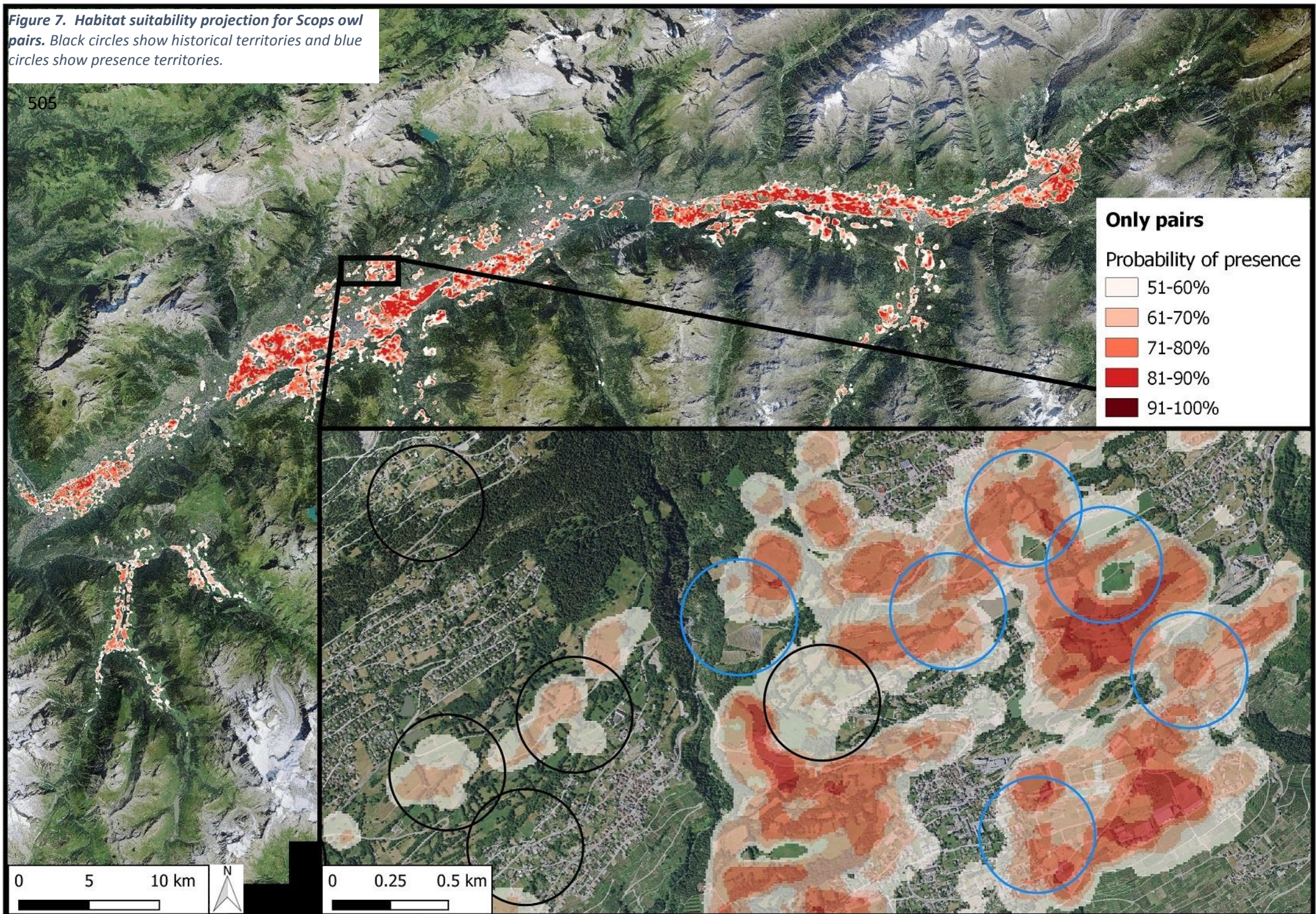


Figure 7. Habitat suitability projection for Scops owl pairs. Black circles show historical territories and blue circles show presence territories.



When both projections were compared through pie-charts (**Figure 8**), pairs of Scops owls showed territories with higher amount of suitable habitat (increase of approximately 20% compared to all Scops owls' presences territories). They seemed to be thus more selective in their nesting choice than if single male singers were included. The historical absence territories showed less favourable habitat than territories with presence. Random absences territories turned out to be globally less suitable than historical absences territories.

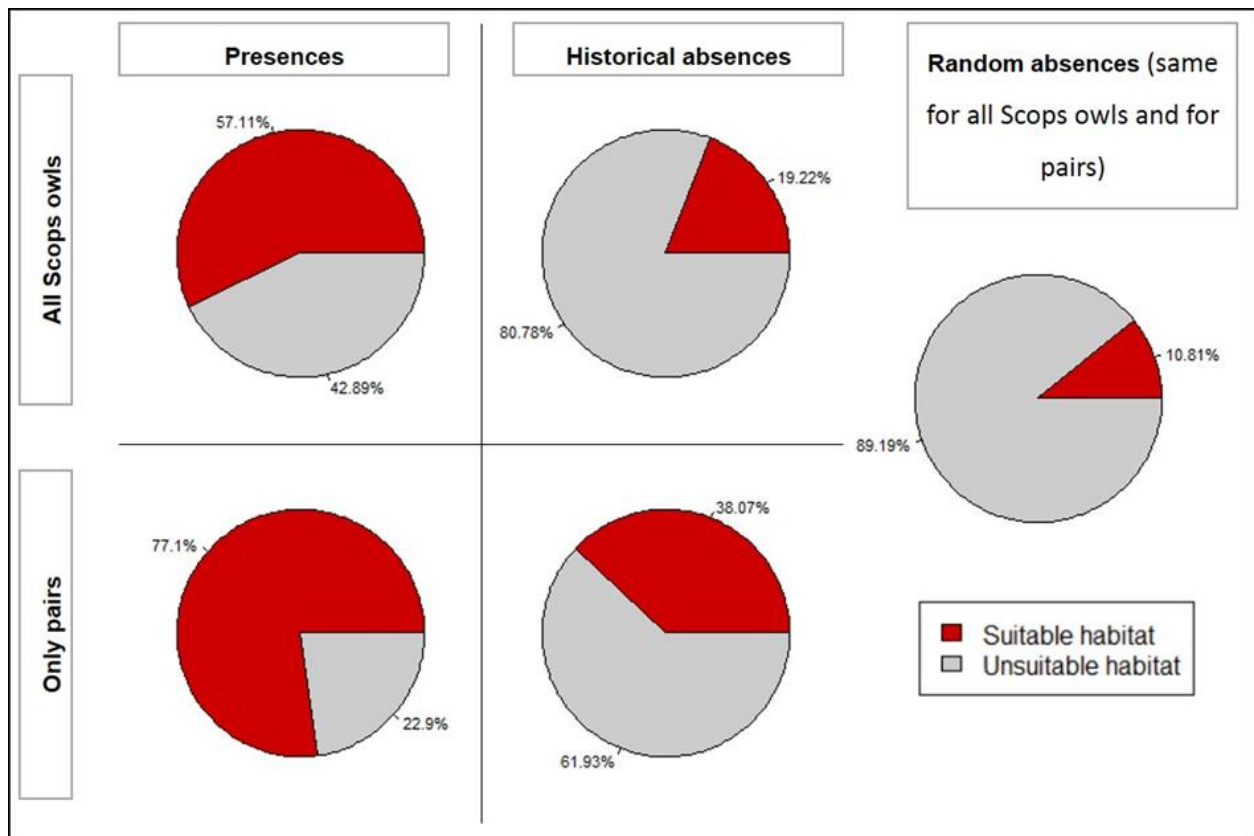


Figure 8. Pie-charts showing the suitability of territories depending on their use by the Scops owl.

When explicative ESMs were built with the 10 most important predictors, the AUC for all Scops owl presences was 0.92 and the AUC for pair presences was 0.87. Contributions of each predictor to build these ESMs are shown in **Table 3**. Thus, using only the four most important predictors that are projected to the whole Valais to build projections (**Table 2**) did not significantly decrease the predictive power of the projected ESMs (**Figures 6 & 7**).

519 **Table 3. Contribution in percentage of each predictor to the explicative ESMs with the 10 most important**
520 **predictors from MuMIn.**

All Scops owl presences		Pair presences	
Predictors	%	Predictors	%
<i>Arrhenatherion within 100 m radius</i>	23.93	<i>Intensive meadows within 200 m radius</i>	25.23
<i>Grassland within 50 m radius</i>	16.67	<i>Distance to Grimisuat</i>	25.03
<i>Dirt track within 200 m radius</i>	16.52	<i>Arrhenatherion within 100 m radius</i>	24.77
<i>GDD > 3°</i>	14.36	<i>Trees within 250 m radius</i>	12.66
<i>Precipitation</i>	9.57	<i>Single-crop farming within 250 m radius</i>	12.31
<i>Wooded hems within 100 m radius</i>	7.15	<i>Precipitation</i>	0
<i>Edges of bushes, wooded hems and forest within 100 m radius</i>	4.78	<i>Mesobromion within 150 m radius</i>	0
<i>Mesobromion within 100 m radius</i>	4.69	<i>GDD > 3°</i>	0
<i>Canopy of young trees within 100 m radius</i>	2.33	<i>Wooded hems within 100 m radius</i>	0
<i>Solar radiation</i>	0	<i>Grassland within 50 m radius</i>	0

521 *T. viridissima* and the Scops owl

522 The MuMIn showed that the normalized count of *T. viridissima* had a RI of 0.004 for all
523 presences and 0.019 for pair presences, thus ranking after 30 other predictors for all Scops
524 owl presences and after 12 other ones in the case of pair presences.

525 Absence territories tended to have higher *T. viridissima* counts than occupied territories in
526 both cases of presence (**Figure 9**). (Student's t-test, *all Scops owls*: $t = 1.96$, $df = 59.77$, $p =$
527 0.05 , mean in group "Presences" = 339 ± 152 , mean in group "Absences" 421 ± 187 (**Figure**
528 **9A & 9C**); *pairs of Scops owls*: $t = 1.95$, $df = 59.54$, $p\text{-value} = 0.06$, mean in group "Absences"
529 = 412 ± 182 , mean in group "Presences" = 330 ± 152 (**Figure 9B & 9D**)).

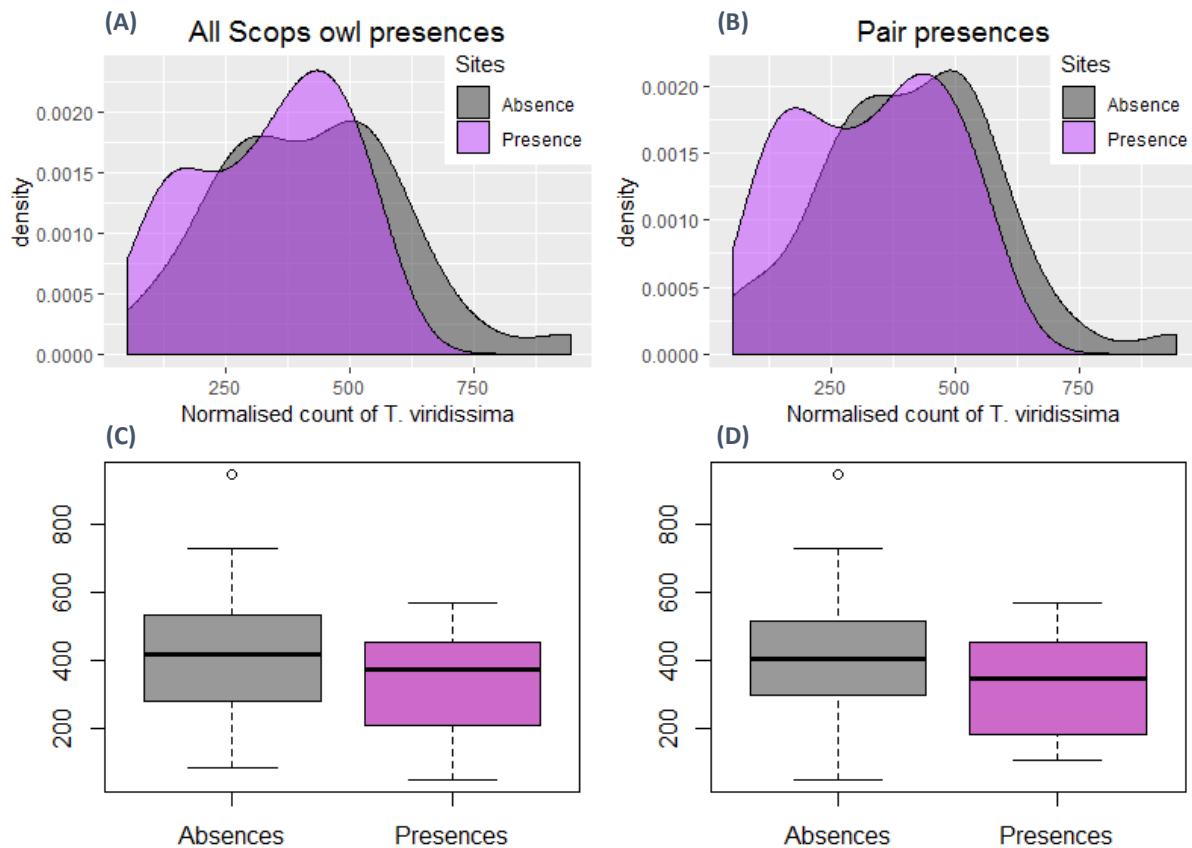


Figure 9. Distribution of normalized counts of *T. viridissima*. (A) Density of normalized counts when considering all Scops owl presences. (B) Density of normalized counts when considering only pair presences. (C) Boxplots of normalized counts according to the use of territories by all Scops owls. (D) Boxplots of normalized counts according to the use of territories by pairs.

A detailed study of structure preferences for males *T. viridissima* is provided in supplementary results (Text S2, Figures S2 & S3).

Discussion

What drives Scops owl presences?

Habitat preferences

In this study, we highlighted the main drivers of Scops owl presences and their best spatial scale. The two vegetation alliances representing extensive and semi-extensive meadow managements (*Mesobromion* and *Arrhenatherion*) in the proximity of the nest showed to be in the three most important factors explaining Scops owl presences (for all Scops owl presences as well as for pair presences). The third most important predictor is *precipitation*. Scops owl presences are indeed promoted by dryness, showing a decrease of presence probability with the increase of precipitation amount. Similarly, *Mesobromion* is a vegetation

alliance of species driven by mesophilic to arid conditions as well as *Arrhenatherion*, in a less extreme way (Delarze *et al.* 2015).

The importance of semi-intensive and dry meadows has already been highlighted through Europe (Denac 2009; Sergio *et al.* 2009; Šušmelj 2011) and in previous local studies (Arlettaz 1990; Sierro & Arlettaz 2013) as chasing habitats mostly used by Scops owls. This main preference could also be interpreted as avoidance of forest where their predators, such as the Tawny owl, nest (Sergio *et al.* 2009). However, the strength of this study was to quantify the requirements of Scops owls in different vegetation types that are often merged in current literature. The Scops owl needs about 1.1 ha of *Arrhenatherion* within the 100 m radius from his nest. This represents an optimum of about 35% of its territory within 100 m radius. Larger surfaces could be a limitation for the bird, and slightly more rapidly for pairs, as *Arrhenatherion* is often linked to more intensive management than *Mesobromion*. The Scops owl also requires at least 1.1 ha of *Mesobromion* within the same radius. Concerning *grassland* in general (see **Table 1**, to have the full list of which habitats are included in this merged category), the bird needs at least 60% of open meadows in a 50 m radius, which means about 0.5 ha. This considerable amount of open meadows close to the nest also shows that the Scops owl does not nest in forests or along clearings, but rather in single trees or isolated stands, showing similar behaviour as in other European countries. (Arlettaz *et al.* 1991; Martinez *et al.* 2007; Denac 2009; Šušmelj 2011). The others important predictors are dominated by structural factors and the bird needs between 10% and 20% of *wooded hems* within 100 m radius from its nest. This finding converges towards previous studies that showed the requirement of such structures as a feeding area (Sierro & Arlettaz 2013) but also as perches to hunt (Arlettaz 1990; Sierro & Arlettaz 2013) and as trees to nest (Arlettaz 1990; Denac 2009; Šušmelj 2011). Finally, the analysis of *T. viridissima* preferences (See Supplementary results, **Text S2, Figures S2**), clearly demonstrated that structures are essential as male Tettigonids mainly sing from high positions in vegetation, like trees or bushes (Schirmel & Fartmann 2013).

Vegetation intensification model

Coupling remote sensing data to field sampling allowed to create an accurate model of grassland management for the first time. The very fine resolution (10 m x 10 m) of the model was powerful to describe grassland types and thus intensification and obtain satisfying

prediction maps. With this new approach, we successfully projected intensive meadows, *Arrhenatherion* and *Mesobromion* over the whole study area. This vegetation intensification model allowed for the first time the creation of a distribution model of the Scops owl not only based on topo-climatic data but also on habitat quality and surface in the context of recent land-use changes. Indeed, the quality of the grasslands is a major factor shaping the distribution of this owl and the models used so far could only distinguish open vegetation from forest areas. The suitable areas were then far too important and not a reflection of the actual situation (Ramella 2017).

Spatial autocorrelation and recolonization

The major difference between predictors that drove all Scops owl presences and only pair presences was the importance of *the distance to Grimsuat*, the last breeding territory during the population's collapse in the nineties. This is the fourth most important variable that managed pair presences while it did not appear beyond the 10 most important predictors when we considered all presences of Scops owl. It showed a cluster close to Grimsuat, and another approximately 45 km further with only few pair presences in-between. This pattern could arise from two different hypothesis (or a mix of both): as this population is recolonizing the area, birds could have not reached suitable areas in-between these two clusters yet due to low population density and high breeding site fidelity of males (Grieco 2018). The second hypothesis is linked to a possible aggregation behaviour (Wagner 1997; Grieco 2018). Considering favourable area (good quality of some historical sites or sites highlighted by the predictive models) between both clusters, this strange pattern toward *distance to Grimsuat* and spatial correlation for pairs could disappear in future if the population carries on its recovery and new pairs colonize new areas.

We also highlighted the poor suitability of historical presence territories (named as historical absences, pie-charts in **Figure 8**). We could have expected an intermediate suitability of historical absence sites between random sites and presence sites, but the amount of suitable habitat was closer to random sites. This probably shows that part of them are thus not as suitable as they used to be when the Scops owls previously selected them as territories. The loss of suitability is probably directly linked to the land-use change toward intensive meadows or crop farming management and to the increase of the human population, which has expanded constructed zones in the whole study area.

T. viridissima implication for the Scops owl

Regarding the availability of the main prey, we were not able to detect a limitation in *T. viridissima*. As opposed to Arak et al. (1990) who showed that singing *T. viridissima* males in the wild were found 100 m away from each other, we observed greater densities (up to 16.5 ind./ha). We see two potential explanations for this. First, a part of the historically used territories could have been deserted because of the crash in Scops owl's population and not because of a significant loss in habitat quality or prey's quantity. The historical territories showed very high densities of *T. viridissima*, sometimes even higher than occupied territories (**Figure 9**). However, the historical sites could contain a higher coverage of structures, permitting a greater amount of *T. viridissima* but reducing the surface of open vegetation and thus being less favourable for the Scops owl. Moreover, considering the variability in food amounts in presence territories, the Scops owl could compensate for lower densities of *T. viridissima* with other preys or by longer chasing distance as recently revealed for the little owl (Grüebler et al. 2018). Nevertheless, several historical sites could host suitable territories for the Scops owl both in terms of habitat quality (**Figures 6 & 7**) and of main prey availability (**Figure 9**), new pairs could recolonize some suitable historical sites.

Scops owl models

Projections of all Scops owl presences and only pair presences were both accurate with AUC greater than 0.85, meaning that the four predictors used in the final ESMs are enough discriminant to assess a fair model (Fernandes et al. In press). Hence, the purpose of having available predictions for the whole area is reached without significant loss of accuracy compared to the explicative models with 10 predictors (a very low decrease of 0.02 in the AUC). Globally, we also proved that pairs chose slightly higher suitable surfaces for breeding: they are more sensitive to meadow types (**Figure 5**) and they select territories with higher suitable area (**Figure 8**). Working with these two kinds of presences (all Scops owls or only pairs subset) allowed to identify and remove bias from potential solitary male Scops owls. The unpaired males without a territory can sing in unfavourable habitats and create noise in the presence data. However, the differences in preference between both types of presences are very low and both samplings (all Scops owl or only pair presences) showed satisfying results. The habitat suitability projection in both cases turned out to be reliable and could

help in the selection of best area for the Scops owl breeding pairs and thus the best places to set action for the preservation of this bird.

Limitations and conservation implications of this study

The main limitation was directly linked to the status of the Scops owl. As this is the most threatened and the least studied owl in Europe (Ayé & Spaar 2015; Knaus *et al.* 2018), only little data was available. The low number of presence sites was reflected in ESMs results. In the 10 most important predictors, the contributions of the variables were not always congruent with their rank of importance in the MuMIn (**Table 3** vs **Figures 3 & 4**). During the ESMs process, depending on the random data split (80-20%), some variables with a limited amount of data could be removed because of a too low model quality due to the split sampling. This weakness also highlights the limitations inherent to working with rare species. Nevertheless, this study allowed us to highlight major requirements of Scops owls in terms of habitat quality and also to quantify them in terms of surface (ha), which provides essential data for setting conservation measures. Moreover, we were able to produce two fine scale spatial projections (at 10 m x 10 m resolution) of their presence based on bioclimatic predictors, a newly developed vegetation intensification model which matched the same fine resolution and a selection of predictors at different scales. With their high accuracy, these Scops owl projections can be used as a tool to set conservation prioritization (Guisan *et al.* 2013; Tulloch *et al.* 2016). They tell which area should be maintained (the highly suitable places) and which could be promoted by the preservation of extensive meadows and the implementation of wooded hems. All measures insuring mosaic-like landscapes of natural meadows mixing *Arrhenatherion* and *Mesobromion* and maintaining structures will increase the suitable habitats for the Scops owl. This will provide nesting sites and ensure an appropriate density of prey.

Conclusion and perspectives

In this study, we showed the importance of semi-natural meadows regulated by temperature, precipitation (Moles *et al.* 2014) and extensive to semi-intensive managements (Blüthgen *et al.* 2012). These factors also have a direct impact on orthopteran diversity and density (Humbert *et al.* 2010; Eo *et al.* 2017), which are the main prey of the Scops owl (Šotnár *et al.* 2008; Latkova *et al.* 2012; Panzeri *et al.* 2014). We developed

prediction maps of fair accuracy that will be of potential use by conservationists. We see three future research avenues to carry on increasing our knowledge of the recovering Scops owls' population in the Valais. First, as *T. viridissima* are available only from mid-June (Muraoka 2009), to understand what the Scops owl eats early in the season could be determinant and could drive the selection by Scops owl of nesting habitats. Latkova et al. (2012) reviewed different methods to assess this diet and combining different ones, future analyses could investigate the early season food of this bird. Secondly, as Scops owl is shown to nest in single trees or traditional orchards (Arlettaz 1990; Denac 2009; Šušmelj 2011), it would be equally important to quantify the number of single trees, old nests or cavities. Especially since traditional orchards are increasingly difficult to find, another possibility of nesting would lay on cavity in single trees or magpie nests (Grieco 2018). Third and last, predation and interspecific relationships are also important as the Scops owl could be the prey of Tawny owl (Sergio *et al.* 2009) and even Eagle owl (Marchesi & Sergio 2005); data on both raptors that are shown to nest in the area (Swiss Ornithological Institute database; Maumary et al. 2007) could be used as predictors in Scops owl models.

To conclude, a whole ecosystem approach always needs to be adopted when the aim is to assess the preferences of a rare species. Especially when this species is both a prey and a predator, like the Scops owl, which encounters major land-use changes within its territory.

Acknowledgement

My most heart-felt thanks go to Dr. Jean-Nicolas Pradervand and Prof. Antoine Guisan for their help and supervision throughout the whole project. I am also grateful to Noëlle Klein, Sophie Ruefenacht and Sylvain Eichhorn for their collaboration and support for the whole summer field work. I would also like to thank Prof. Raphaël Arlettaz, who helped for the historical breeding sites list, Dr. Olivier Broennimann for his availability and support during analysis, Dr. Alain Jacot for all his valuable pieces of advice throughout all the work and Dr. Anne Litsios-Dubuis and Dr. Pascal Vittoz for sharing their knowledge about the vegetation in the Valais and their help to select the list of plants. At last, I am really grateful also to my family, who took part in the field work, especially my sister Emilienne Theux, Sarah Thurnheer for comments on previous versions of the report and Julia Wildi for doing the spelling check of the final version of the report.

699 This project was supported by the Swiss Ornithological Institute and the School of Biology
700 (Faculty of Biology and Medicine, University of Lausanne).

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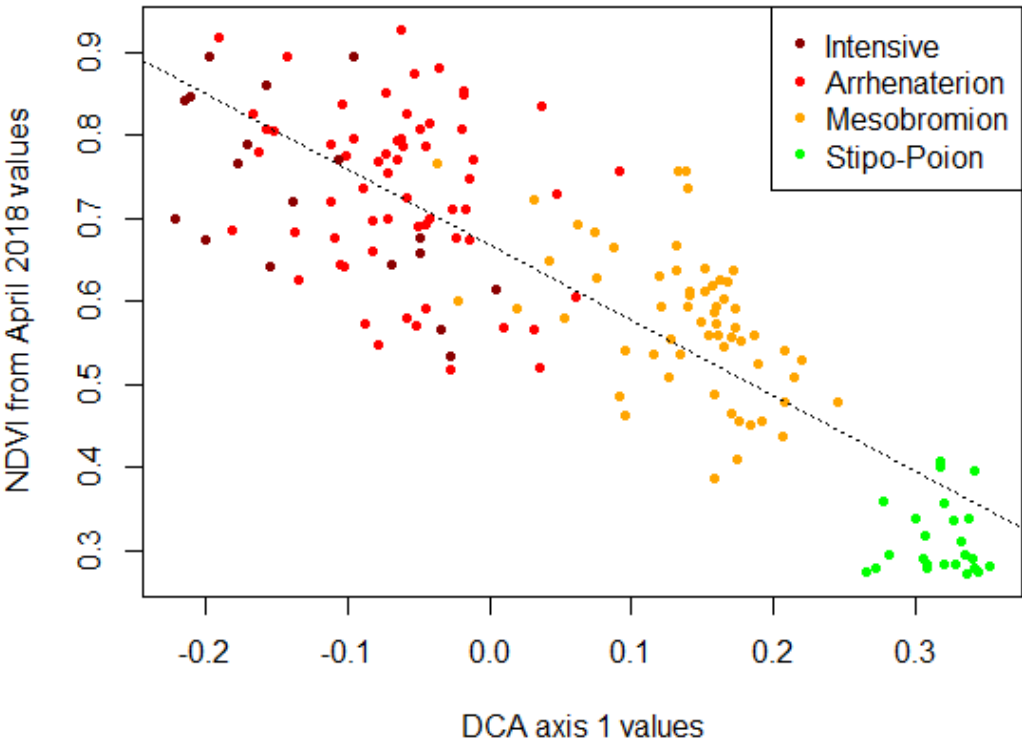
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922 **Supplementary methods**

923 *Table S1. Indicator species used for territory mapping and vegetation surveys.*

Type of meadow	Indicator species		
<i>Arrhenatherion</i>	<i>Arrhenatherum elatius</i> <i>Dactylis glomerata</i> <i>Crepis biennis</i> <i>Knautia arvensis</i> <i>Ranunculus acris</i> <i>Anthriscus sylvestris</i> <i>Galium album</i> <i>Trifolium repens</i> <i>Trifolium thalii</i> (high alt.) <i>Heracleum sphondylium</i> <i>Veronica chamaedrys</i> <i>Trisetum flavescens</i> <i>Holcus lanatus</i> <i>Rumex acetosa</i> <i>Bromus hordeaceus</i> <i>Cynosurus cristatus</i> <i>Festuca pratensis</i> <i>Teraxacum officinale</i> <i>Anthoxanthum odoratum</i> <i>Rhinanthus</i> <i>alectorolophus</i>		<i>Thymus serpyllum</i> <i>Ononis repens</i> <i>Gallium verum</i> <i>Helianthemum</i> <i>nummularium</i> <i>Koeleria pyramidata</i> <i>Pimpinella saxifraga</i> <i>Ranunculus bulbosus</i> <i>Trifolium montanum</i> <i>Daucus carota</i> <i>Sanguisorba minor</i> <i>Euphorbia cyparitia</i>
		<i>Stipo-Poion</i>	<i>Astragalus onobrychis</i> <i>Scabiosa trianda</i> <i>Silene otites</i> <i>Artemisia campestris</i> <i>Onobrychis arenaria</i> <i>Erysimum rhaeticum</i> <i>Euphorbia seguieriana</i> <i>Potentilla pusilla</i> <i>Stipa capillata</i> <i>Stipa pennata</i> <i>Carex liparocarpos</i> <i>Poa perconcinna</i> <i>Pulsatilla montana</i> <i>Scorzonera austriaca</i>
<i>Mesobromion</i>	<i>Bromus erectus</i> <i>Salvia pratensis</i> <i>Brachypodium pinnatum</i> <i>Hippocrepis comosa</i> <i>Carex caryophyllea</i> <i>Anthyllis vulneraria</i> <i>Onobrychis viciifolia</i> <i>Potentilla neumanniana</i> <i>Scabiosa columbaria</i>	Intensive meadows	<i>Lolium</i> sp. (multiflorum/ perenne) <i>Alopecurus pratensis</i> <i>Poa</i> sp. (pratensis/ trivialis) <i>Trifolium pratense</i> <i>Medicago sativa</i>

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Figure S1. Graph of correlation between DCA axis 1 values and NDVI from April 2018. Each point represents a plot of vegetation survey. The correlation was 0.84 (Pearson's product-moment correlation: $t = -19.62$, $DF = 162$, $p\text{-value} < 2.2e-16$; lm: $F\text{-stat} = 384.8$ on 1 and 162 DF , $p\text{-value}: < 2.2e-16$).

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Table S2. Results of Student's t-tests to compare area given by mapping to area given by the vegetation intensification model. As here 30 p -values are given, Bonferroni correction was applied and a $p\text{-value} < 0.0017$ was considered as significant.

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		50 m	100 m	150 m	200 m	250 m
Int	t.test p-value	0.67	0.60	0.21	0.11	0.06
Arr	t.test p-value	0.28	0.29	0.46	0.40	0.34
Meso	t.test p-value	0.0011	$1 \cdot 10^{-5}$	$1 \cdot 10^{-6}$	$6 \cdot 10^{-8}$	$2 \cdot 10^{-9}$
	Correlation p-value	$1 \cdot 10^{-13}$	$2 \cdot 10^{-14}$	$9 \cdot 10^{-15}$	$5 \cdot 10^{-14}$	$8 \cdot 10^{-12}$
	Correlation	0.657	0.672	0.678	0.663	0.617
Steppe	t.test p-value	$2 \cdot 10^{-10}$	$2 \cdot 10^{-16}$	$2 \cdot 10^{-16}$	$2 \cdot 10^{-16}$	$2 \cdot 10^{-16}$
	Correlation p-value	0.98	0.29	0.14	0.06	0.06

931

932 **Table S3. Date of *T. viridissima* survey.** Differences between total nights and working nights are explained by
933 bad weather conditions such storm or rain.

	Round 1	Round 2	Round 3
Starting date	20.06.2018	12.07.2018	03.08.2018
Ending date	01.07.2018	25.07.2018	15.08.2018
Total nights	12	14	14
Working nights	11	9	11

934 **Text S1 - Structure preferences of males *T. viridissima***

935 This last part of analyses focussed only on *T. viridissima* preferences. We aimed at
936 understanding what structures or habitats males Tettigonids prefer.

937 First, mapped habitat category was extracted for each *T. viridissima* point in qGIS. For each
938 habitat type, the sum of the three surveys was calculated and this final count per habitat
939 was normalized first by the percentage of each habitat type area covered by the 40 m buffer
940 around transects and, secondly, by the percentage that each habitat type represented
941 considering the total mapped area of the whole study. A simple plot was computed to
942 visualize the result.

943 Secondly, a set of 14 predictors from **Table 1** was selected (they are shown in the “T. viri.
944 GLMs” column). These are uncorrelated ($\text{cor} < 0.7$) predictors that screened the best their
945 gradient considering the 250 m scale. A MuMIn analysis on GLMs with all combinations of 6
946 of them, and normalized count per territory as response variable following a poisson
947 distribution, was run. We used all combinations of 6 predictors because 6 represents the
948 biggest number of variable that one can include using 65 sites; in respect to Harrell’s rule of
949 thumb (Harrell *et al.* 1996). Then, we selected the best model showing the smallest AIC and
950 thus the 6 predictors the most important for the night activity of male *T. viridissima*. For
951 each of these 6 most important predictors, we plotted the response curve.

952

Supplementary results

Text S2 - Structure preferences of males *T. viridissima*

Figure S2 showed from which structures males *T. viridissima* were singing during surveys. This revealed their preference for high vegetation such trees or high plants.

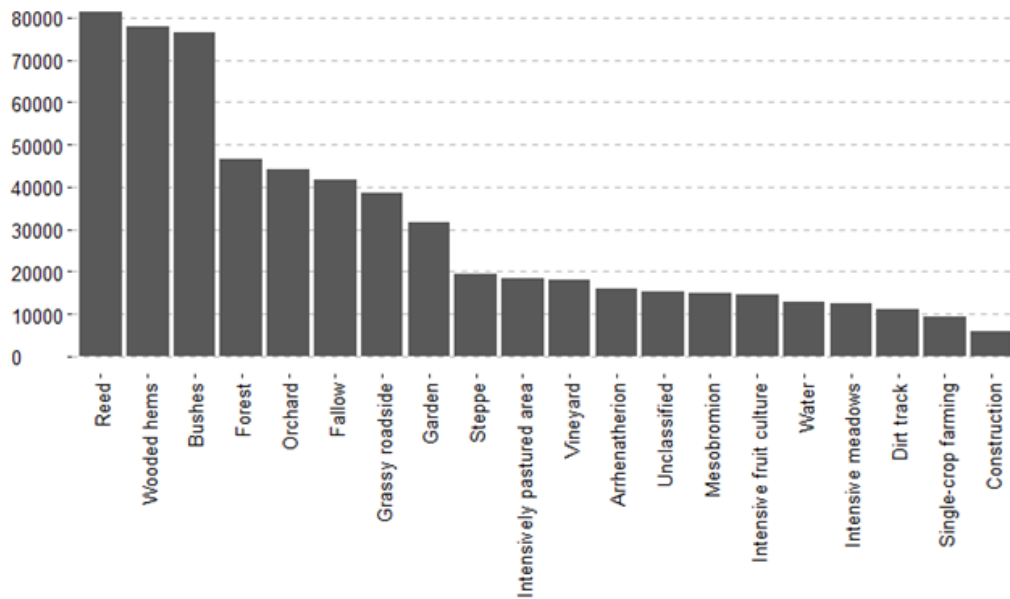


Figure S2. Plot of *T. viridissima* position while they were surveyed.

The GLM constructed according to its the lowest AIC contained the following predictors: *unsuitable area, grassland, single crop farming, precipitation, spatialized and mapped Mesobromion*. Response curves are shown in **Figure S3**. All these predictors had a significant effect (p -values < 0.001), and hence impacted the normalized count of *T. viridissima* per territories. The number of singers decreased with the increase of unsuitable area, showing the loveless from *T. viridissima* toward construction, human impacted area. Single crop farming area, highly managed by human, was also avoided. *T. viridissima* preferred territories with a part of grassland and *Mesobromion*. As for the Scops owl, open vegetation and precipitation played an important role but interestingly, *T. viridissima* reacts with opposite trend to the precipitation comparing to the Scops owl.

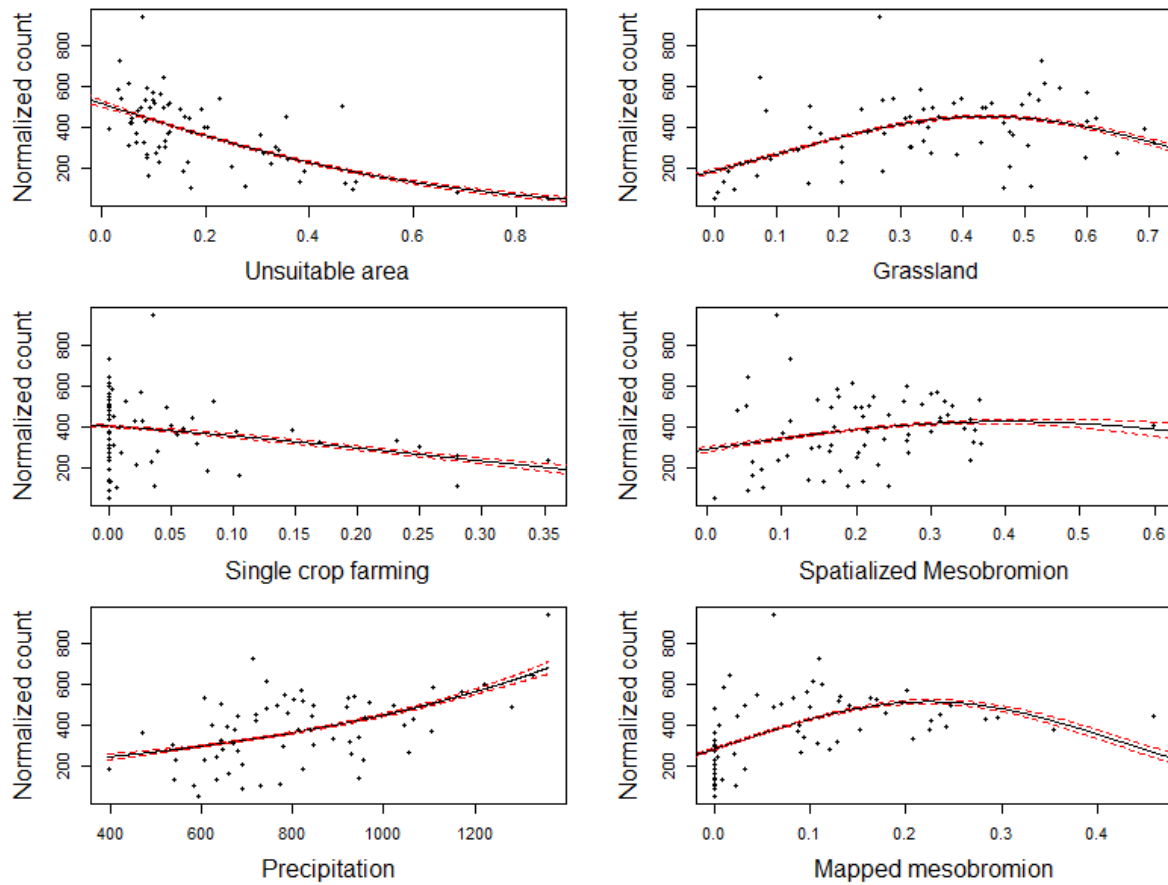


Figure S3. Plot of response curve of the *T. viridissima* toward the 6 predictors used in the GLM. Red dotted lines represent 95% confidence interval.