





# Food and habitats requirements of the Eurasian Scops Owl (*Otus scops*) in Switzerland revealed by very high-resolution multi-scale models

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In Europe, agricultural practices have progressively evolved towards high productivity leading either to the intensification of productive and accessible areas or to the abandonment of less profitable sites. Both processes have led to the degradation of semi-natural habitats like extensive grasslands, threatening species such as the Eurasian Scops Owl *Otus scops* that rely on extensively managed agricultural landscapes. In this work, we aimed to assess the habitat preferences of the Scops Owl using habitat suitability models combined with a multi-scale approach. We generated a set of multi-scale predictors, considering both biotic and abiotic variables, built on two newly developed vegetation management and orthopteran abundance models. To select the variables to incorporate in a 'best multi-scale model', we chose the best spatial scale for each variable using univariate models and by calculating their relative importance through multi-model inference. Next, we built ensembles of small models (ESMs) at 10 different scales from 50 to 1000 m, and an additional model with each variable at its best scale ('best multi-scale model'). The latter performed better than most of the other ESMs and allowed the creation of a high-resolution habitat suitability map for the species. Scops Owls showed a preference for dry sites with extensive and well-structured habitats with 30–40% bush cover, and relied strongly on semi-extensive grasslands covering at least 30% of the surface within 300 m of the territory centre and with high orthopteran availability near the centre (50-m radius), revealing a need for good foraging grounds near the nest. At a larger spatial scale within a radius of 1000 m, the habitat suitability of Scops Owls was negatively related to forest cover. The resulting ESM predictions provide valuable tools for conservation planning, highlighting sites in need of particular conservation efforts together with offering estimates of the percentage of habitat types and necessary prey abundance that could be used as targets in future management plans to ensure the persistence of the population.

**Keywords:** biotic factors, conservation, endangered species, ensemble of small models, habitat suitability models, orthopterans.

Over the past few decades, the landscape in Europe has evolved rapidly. On the one hand, the

mechanization of agricultural practices on productive lands has led to the homogenization of agricultural landscapes, the increased use of fertilizers, and the loss of structures such as hedges, orchards or groves (Laiolo *et al.* 2004). On the other hand, low productivity areas have been abandoned,

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leading to the expansion of forests (Hofstetter *et al.* 2015). The combination of these phenomena has been – and still is – leading to the degradation of semi-natural grasslands, making them some of the most threatened habitats in Europe (Canals & Sebastià 2000). All these gradual changes have already had a negative impact on many agricultural follower species (Donald *et al.* 2001), including several bird species such as the Whinchat *Saxicola rubetra*, Hoopoe *Upupa epops* and Eurasian Scops Owl *Otus scops* (hereafter referred to as Scops Owl), which depend on extensively managed areas rich in invertebrate food resources (Wilson *et al.* 1999). These species are showing a rapid decline, as reported in the recent French (Nidal & Muller 2015) and Swiss (Knaus *et al.* 2018) bird atlases, stressing the need to understand these birds' habitat preferences from large to fine spatial scales in order to make efficient conservation decisions.

Habitat suitability models (HSMs *sensu* Guisan *et al.* 2017) are increasingly being used to study and understand species' distributions and to quantify the effects of important factors on the presence or absence of a species. For several years, HSMs have been considered a key tool to set conservation measures based on habitat prioritization through probability maps and model response curves (Guisan *et al.* 2013, Meller *et al.* 2014). However, the use of HSMs is often hampered by low sample sizes, which frequently limit the use of such models for rare or endangered species (Lomba *et al.* 2010). A solution to this 'rare species modelling paradox' has recently been suggested through the use of ensembles of small models, a method where many small models which include few variables at a time are built and then averaged, often with performance-based weights, into a full model (ESM; Lomba *et al.* 2010, Breiner *et al.* 2018). This has enabled the application of HSMs to less frequent or rare species such as certain poorly documented bat species (Scherrer *et al.* 2019) and a rare Iberian endemic plant (Lomba *et al.* 2010).

Up to now, HSMs applied to mobile species with potentially large territories have used rather coarse resolutions (e.g. 1 km<sup>2</sup>), therefore ignoring the different fine-scale spatial requirements of the species (Banos-González & Terrer 2016). However, the spatial scale of influence of environmental predictors on ecological processes can vary (Vicente *et al.* 2014), and animal species often have specific and independent needs regarding, for

example, their nesting location and foraging areas (Jaberg & Guisan 2001, Xie *et al.* 2016). This raises the questions of how to select the best variables to describe a species habitat and how to find their best spatial resolution, which are two key steps for building efficient models for conservation planning (Guisan *et al.* 2013). In this context, the spatial scale of influence of predictors can be assessed using a multi-scale approach based on moving windows analysis (Bellamy & Altringham 2015, Bosco *et al.* 2018). This method enables the resolution to be kept as fine as possible while also investigating which spatial scale is best for each predictor (Bellamy & Altringham 2015, Scherrer *et al.* 2019).

A multi-scale approach, therefore, allows a better understanding of the species' requirements in different habitats, whether they are linked to small-scale preferences such as their nesting location, or larger scale determinants of their home-range or territory size such as food availability (Mateo-Tomás & Olea 2015). In particular, using a multi-scale approach allows a better understanding of bird species' ecology. For instance, this was used to define at which radius the fragmentation of the landscape in vineyards affects Woodlarks *Lullula arborea* (Bosco *et al.* 2018) and to model the habitat suitability of the Little Owl *Athene noctua* (Fatterbet *et al.* 2018). Multi-scale data in ecological studies are providing powerful information for assessing conservation measures (Seavy *et al.* 2009, Xie *et al.* 2016) and are starting to be increasingly used in modelling studies (McGarigal *et al.* 2016). However, they remain rarely used for HSMs and their spatial predictions.

The Scops Owl is an example of a bird species with ecological requirements that vary with spatial scale. It is a nocturnal bird that nests in old tree cavities or magpie nests (Denac *et al.* 2019). As a trophic specialist, the Scops Owl mainly feeds on orthopterans – especially Tettigonids – and moths, using other invertebrates or small vertebrates such as small birds or mammals as complementary resources (Panzeri *et al.* 2014). In Switzerland, the Scops Owl is known to forage in grassland with hedges, which is typical of extensive management (Sierra & Arlettaz 2013). Scops Owl populations declined sharply across Europe from 1970 to 1990 (Denac 2009, Sergio *et al.* 2009), and this long-distance migratory raptor is classified as endangered on the Swiss Red List (Ayé & Spaar 2015). It is now one of the rarest breeding birds in

Switzerland (Knaus *et al.* 2018). Understanding habitat and trophic preferences in relation to land-use changes and the intensification of grassland is a priority to counter the decline of this species, which is the least studied owl species in Europe (Marchesi & Sergio 2005). The Scops Owl's multi-trophic requirements make it a suitable species to test a multi-scale ESM framework, due to: (i) its scattered distribution in Switzerland; (ii) its habitat or diet preferences, investigated in previous studies, but without incorporating the respective spatial scales of influence; and (iii) its role as an umbrella species for other rare agricultural followers (Sergio *et al.* 2005, Denac *et al.* 2019). In this study, we expect a positive relationship between the Scops Owl's occurrence and the presence of invertebrate-rich extensive grasslands in the vicinity of the nest, but also a negative impact of dense forested areas within a larger neighbourhood around the territory centre, as these areas could potentially host predators such as the Tawny Owl *Strix aluco* or the Long-eared Owl *Asio otus*. Outputs from such multi-scale models should be precise enough to be used to synthesize the various requirements of the Scops Owl and provide recommendations for designing future conservation management strategies.

## MATERIALS AND METHODS

### Study area

The population of Scops Owls that was studied is located in the Valais (46°01'–46°34'N, 7°05'–8°01'E). This south-western Canton of Switzerland (Appendix S1: Fig. S1) shows an elevation ranging from 372 to 4634 m a.s.l. and covers 5224 km<sup>2</sup>. This region has a continental climate characterized by cold winters and hot, dry summers: for the city of Sion, 482 m a.s.l., the average temperature in 1980–2010 in January was –0.1 °C and in July 20.1 °C, and the average precipitation in January was 51 mm and in July 58 mm. As the Scops Owl breeds from the lowlands at 470 m up to 1200 m (Knaus *et al.* 2018), we did not consider areas above 1400 m in this study. Within this elevation range, the valley floor is covered by artificial meadows with very high management intensity, fruit cultures of mainly apples and pears or crop farming. South-exposed slopes are used for vineyards, which represent the predominant agricultural land-use type (Arlettaz *et al.*, 2019), whereas

north-exposed slopes are covered by fruit cultures such as 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 they are replaced with coniferous forests, as well as upstream from Leuk, where fruit cultures are absent.

### Scops Owl surveys and historical data

The Valais hosts the largest Scops Owl population in Switzerland, with an average of 25 singing males and around 15 breeding pairs detected between 2015 and 2019. The population showed a particularly steep decline in Switzerland until 2000, when only one breeding pair was detected (Sierro & Arlettaz 2013). Then, for reasons that remain unclear, the population started to recover slightly. To follow its evolution, a hybrid monitoring scheme combining data gathered by citizen science and an official monitoring scheme undertaken by the Swiss Ornithological Institute has been conducted yearly since 2006. To determine whether Scops Owls are present in the studied territories, acoustic surveys are conducted at night in all bird territories from 20 April to 20 June, between 21:00 and 02:00 h, when Scops Owls are most active (Panzeri *et al.* 2014). Monitoring only takes place under favourable weather conditions, on warm nights with no rain and little wind. Using the monitoring data (Swiss Ornithological Institute database), we selected 47 different territories in independent locations known to have hosted Scops Owls between the years 2000, when the population was at its lowest and therefore at the beginning of its recovery, and 2019. To understand the factors that caused the Scops Owl to almost disappear from the Valais, we used two types of absence: we used 31 territories where the species was present historically (between 1940 and 1999), but that have not been occupied since; then, to account for all available habitats in the Valais and increase the model power, we added 126 random territories, similar in size and shape to occupied territories but unoccupied, generated in Quantum GIS (Quantum GIS Development Team, 2018) with a minimal distance of 500 m to the centre of any other territory. This resulted in a total of 204 studied territories with presence and absence data. The important monitoring effort taking place in Valais ensures that the historical sites are no longer occupied by the species. Imperfect detection is always possible but

should not impact the results, as the data were pooled over a long period and most of the breeding territories from the past 15 years are known thanks to the ongoing monitoring scheme. Similarly, the chances of one of the random absence sites being occupied by a Scops Owl are very low, probably even null. The central position of each occupied territory corresponds either to an occupied natural or artificial nest, or to the location of singing individuals (either males and females duetting or lone singing males) whenever the exact location of the nest could not be determined.

### Scops Owl distribution models

#### *Spatial scale and resolution of the variables*

In the Valais, Scops Owls followed by radiotracking showed a variation of territory sizes 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 (Denac 2009, Panzeri *et al.* 2014). We therefore generated habitat predictors for different circular window sizes ranging from 50 m (0.2 ha) to 300 m (19.6 ha) radii in five steps of 50 m, completed then by larger radii of 400, 600, 800 and 1000 m. Using radii larger than 250 m generates some superpositions between territories but does not increase the spatial autocorrelation (SAC) of the focal variable significantly compared with smaller radii and is important to detect trends in spatial scales that are larger than the average territory size of 20 ha (250-m radius). We included four topo-climatic predictors, vegetation data from a vegetation model and a prey availability indicator from an orthopteran model. The climatic data were downscaled from coarser climatic maps using bilinear interpolation. Vegetation and orthopteran models were generated at a resolution of 10 × 10 m (Klein *et al.* 2020). All variables had a final resolution of 10 × 10 m in order to maintain as fine a resolution as possible in the scale analysis (see Table 1 for a list of the different variables). The framework used for the modelling is summarized in Fig. S2 of Appendix S1.

### Selected predictors

From all the predictors in Table 1, only 'Temp' and 'GDD' showed a correlation > 0.99 (Dormann *et al.* 2013); therefore, 'GDD' was kept for the next step of the analysis. Despite a correlation of

0.67 between the amount of semi-extensive meadows ('S-ext') and the estimated number of orthopterans ('Ortho'), we decided to keep both layers because they describe different ecological aspects of the Scops Owl territory and diet, and because 'S-ext' is also directly comparable to other vegetation layers (S-int). Finally, we had to remove the percentage of artificial meadows ('Art') due to inappropriate distribution of the data generating truncated response curves. We continued the analyses with eight variables ('GDD', 'Prec', 'SRad', 'S-ext', 'S-int', 'Bush', 'For', 'Ortho') listed in Table 1 and Appendix S1 (a detailed description of them is provided in Text S1). The following analysis was done using R version 3.5.1 (2 July 2018) (R Core Team, 2018).

### Variable selection and spatial scales

The high correlations among the variables at different spatial scales did not allow us to make a direct comparison of the variables in the same model through multivariate models or multi-model inference (MMI). Therefore, to select the best variables at the best scale, we ran univariate second order binomial-logit generalized linear models (GLMs) for each variable at each scale with Scops Owl (47 presences/126 absences + 31 historical absences) as the response variable. This allowed us to identify the best spatial scale for each variable according to the area under the receiver operating characteristic curve (AUC; Bellamy & Altringham 2015, Bosco *et al.* 2018, Scherrer *et al.* 2019). Within this new pool of variables, we tested the correlations among all variables; when a pair of variables showed a correlation > 0.7, we removed the variable showing the lowest AUC in order to limit collinearity and avoid overfitting the models (Lomba *et al.* 2010, Dormann *et al.* 2013). To avoid bias, we checked for SAC with Mantel tests, with 10 000 data permutations per predictor (Lichstein 2007), though SAC in predictors is usually not seen as a problem in models (Chevalier *et al.* 2021). We discarded two topo-climatic variables due to their overall low AUC at their best scale, 'GDD' with 0.58 and 'SRad' with 0.59, therefore only keeping 'Prec' in further analysis. We also discarded one biotic variable, 'Ste', which had a maximum AUC of 0.60. This left us with six variables to be used in the next steps and to build the final model.

**Table 1.** Environmental predictors. This table summarizes the origin of all used predictors, the way they are abbreviated throughout the work and how they were generated. The last column indicates whether the predictor was included in the Scops Owl ESMs or not

	Abbreviation	Origin	In ESMs
Spatialized vegetation (veg)			
Artificial meadows	'Art'	Reclassification of vegetation model (Klein <i>et al.</i> 2020)	No
Semi-intensive meadows	'S-int'	Reclassification of vegetation model (Klein <i>et al.</i> 2020)	Yes
Semi-extensive meadows	'S-ext'	Reclassification of vegetation model (Klein <i>et al.</i> 2020)	Yes
Steppe	'Ste'	Reclassification of vegetation model (Klein <i>et al.</i> 2020)	No
Bushes	'Bush'	Canopy model from digital surface model <sup>a</sup>	Yes
Forest	'For'	Canopy model from digital surface model <sup>a</sup>	Yes
Sum of orthopterans	'Ortho'	Orthopteran model (Klein <i>et al.</i> 2020)	Yes
Topo-climatic variables			
Temperature	'Temp'	Mean of temperature from January 1981 to December 2010 <sup>b,e</sup>	No
Precipitation	'Prec'	Average of precipitation from January 1981 to December 2010 <sup>b,e</sup>	Yes
Growing degree days	'GDD'	Mean of GDD above 3 °C from January 2000 to December 2015 <sup>c,e</sup>	No
Solar radiation	'SRad'	Mean of solar radiation from April to September, vegetation growth period <sup>d,e</sup>	No

<sup>a</sup>See Text S1 (Appendix S1). <sup>b</sup>Daily MeteoSwiss Grid-Data Products at 1-km resolution for 1981–2010, means with a resolution of 25 × 25 m (Broennimann 2018). <sup>c</sup>Computed by year (Broennimann 2018). Average of the 15 last available years with a resolution of 25 × 25 m. <sup>d</sup>Computed by month (following Zimmermann & Kienast, 1999; Broennimann 2018). Averaged for the months of April to September, with a resolution of 25 × 25 m. <sup>e</sup>Resampled in ArcGIS to 10 × 10 m resolution, using bilinear interpolation.

We then quantified the relative importance (RI) of the six variables and determined their best focal scale using univariate GLMs with the variable expressed as linear (lin) or linear and quadratic (qua) terms, using the 'poly' function in the R package 'stats'. To compare the univariate models and to rank the predictors, the MMI R package 'MuMin' (Barton 2018) was used to compute the Akaike information criterion corrected for small sample-size (AICc) for each model. These AICc scores enable the RI of each variable to be calculated (Burnham *et al.* 2011), therefore providing a ranking of the variables. This ranking was then used for the selection of each variable at its best scale for the final 'best multi-scale model'.

## HSM and projection

We used the ensemble of small models (ESM; Breiner *et al.* 2018) approach to model the distribution of the Scops Owl in the Valais using the six selected variables indicated in Table 1. The ESM strategy was developed to deal with small sample sizes, by creating many small models, using different modelling methods, for all possible combinations of predictors, then assembling and weighting all models according to a given evaluation metric obtained by repeated cross-validation (Lomba *et al.* 2010). To limit the number of variables and avoid overfitting, we built bivariate models each time with three different

techniques commonly used to build species distribution models (SDMs): general linear model (GLM), general additive model (GAM) and random forest model (RF) (Elith *et al.* 2006; Lomba *et al.* 2006) with the R package 'ecospat' (Di Cola *et al.* 2017). For the repeated split-sample validation, each model was run 150 times with 70% of the data to train the model and with the remaining 30% to evaluate it. We weighted each bivariate model, from each run and each model type, by its cross-validated true skill statistic (TSS) to obtain an ensemble of forecasting results including all models but weighted by their predictive accuracy.

Following this process, we built 11 different kinds of ESMs: 10 ESMs including the six variables at the 10 different scales (50, 100, 150, 200, 250, 300, 400, 600, 800, 1000 m) and one ESM (the 'best multi-scale model') with the variables at their respective best scale as identified by the univariate models and the RI of the MMI ('S-int 100', 'S-ext 300', 'Ortho 50', 'Bush 50', 'For 1000', 'Prec 150'). We evaluated each final ESM with maximizations of the TSS, specificity and sensitivity (Guisan *et al.* 2017) to compare the performance of the different ESMs. The final habitat suitability map was created by projecting over the study area the best model among the 11 different ESMs. To estimate the coverage of suitable habitats, we used the binarization threshold based on the TSS from the ESM function of the 'ecospat' package. This creates a binary (presence/absence) map based on

maximization of the TSS. To consider either all potentially suitable habitats or only highly suitable habitats for conservation guidelines, we measured the available surfaces according to the 100% of the binarized map, and also to the best 50%.

## RESULTS

### Single or multi-scale models

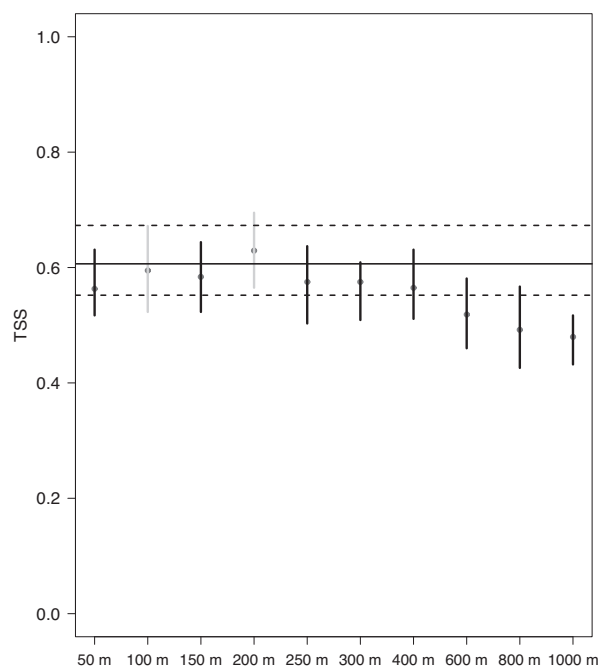
Using a multi-scale (best radius per predictor) approach instead of a single-scale one (same radius for all predictors) improved the predictive power of the ESM. The TSS of the best multi-scale ESM (0.602) was significantly higher than most of the single-scale ESMs (pairwise Wilcoxon tests:  $P > 0.001$ ) except for the 100- and 200- m radii (TSS = 0.594 and 0.620; Fig. 1). The 1000-m single-scale ESM showed the worst TSS (pairwise Wilcoxon tests:  $P < 0.001$ ) (Fig. 1), but also the worst specificity (Fig. S3). Overall, the best sensitivity relied on small-scale data (50 m) and larger scales (300, 400 and 800 m), whereas the best specificity was found at 100, 150 and 200 m. The best multi-scale ESM therefore produced intermediate results with a better specificity than most of the models, but with a lower sensitivity compared with some other scales. The 200-m single-scale ESM was the only one that performed better than the best multi-scale ESM, but it did not show a significant difference in TSS value (0.620 vs. 0.602). The median TSS across all scales was 0.567 (9.39% lower than the best model), and the median sensitivity and specificity were 0.857 (similar to the best scale) and 0.681 (7.22% lower than the best scale), respectively.

### Variable importance from ESM

The RI of variables from the best scale ESM was highest for bushes ('Bush 50': 36%), followed by yearly precipitation ('Prec 150': 17%), sum of orthopterans ('Ortho 50': 16%), semi-extensive and semi-intensive meadows ('S-int' and 'S-ext': 13%), and finally forest ('For 1000': 5%) (Fig. 2). The response curves are shown in Fig. 3.

### Habitat preferences

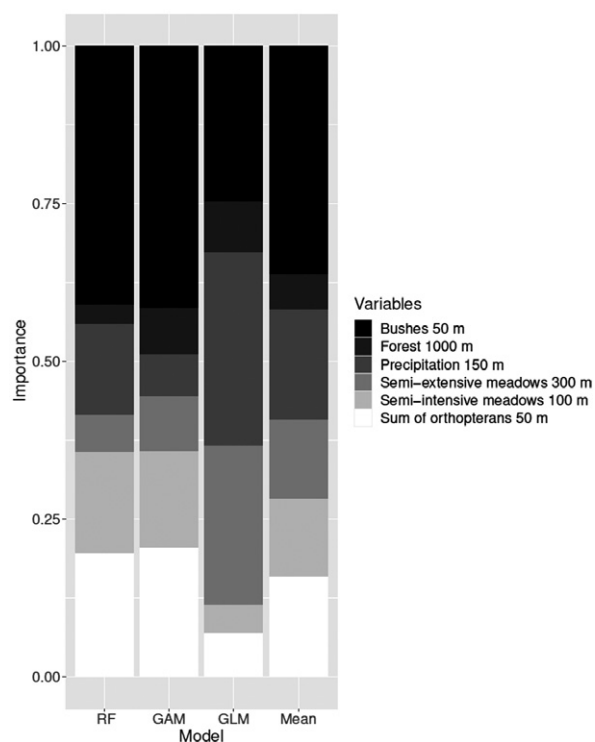
Before interpreting the results, it is important to remember that given a maximum habitat amount of 100%, a high percentage of good habitat will



**Figure 1.** ESM evaluation at each scale. The TSS values are shown for each ESM built with single-scale variables ranging from 50 to 1000 m. For comparison, the mean of the ESM built with variables at their best scale (multi-scale ESM) is represented by the continuous line, and the dotted lines represent the 25% and 75% quartiles. The multi-scale ESM is significantly different from all single-scale ESMs (pairwise Wilcoxon tests:  $P < 0.01$ , correction for multiple testing: Bonferroni) except for those at 100 and 200 m. The multi-scale, 100-m scale and 200-m scale ESMs perform better overall than the ESMs at all other scales.

often be correlated with a low percentage of bad habitat. This is, however, partly mediated by the different window sizes but can influence the results and should be kept in mind when interpreting them.

The most important predictor was 'Bush 50', which represents the openness of the habitat and the presence of structures (Fig. 3a); this showed an optimum between 20% and 40% coverage. The second predictor was 'Prec 150', a climatic predictor representing both the elevation gradient (with more precipitation at high elevations) and the continentality of the study area. Habitat suitability decreased with an increase of precipitation (Fig. 3b). Habitat suitability for Scops Owl increased when the sum of orthopterans, 'Ortho 50', increased, with a potential hump-shaped curve, though note high uncertainties at high values (Fig. 3c). Scops Owl habitat suitability also



**Figure 2.** Variable importance. This figure shows the relative importance of the variables used in the ESMs, each shade of grey representing a different variable. A summary of the variables is presented in Table 1. The three columns on the left represent the relative importance calculated for each of the three modelling techniques used to build the ESMs separately, and the last column represents the mean variable importance calculated for the three techniques.

increased with the proportion of semi-extensive meadows, 'S-ext 300', but again with a large uncertainty for high values (Fig. 3d). Semi-intensive meadows, 'S-int 100', showed an optimum for Scops Owl habitat suitability between 15% and 30% coverage (Fig. 3e). Finally, the coverage of forest, 'For 1000', showed a negative relationship with habitat suitability for Scops Owl (Fig. 3f).

### HSM and historical sites

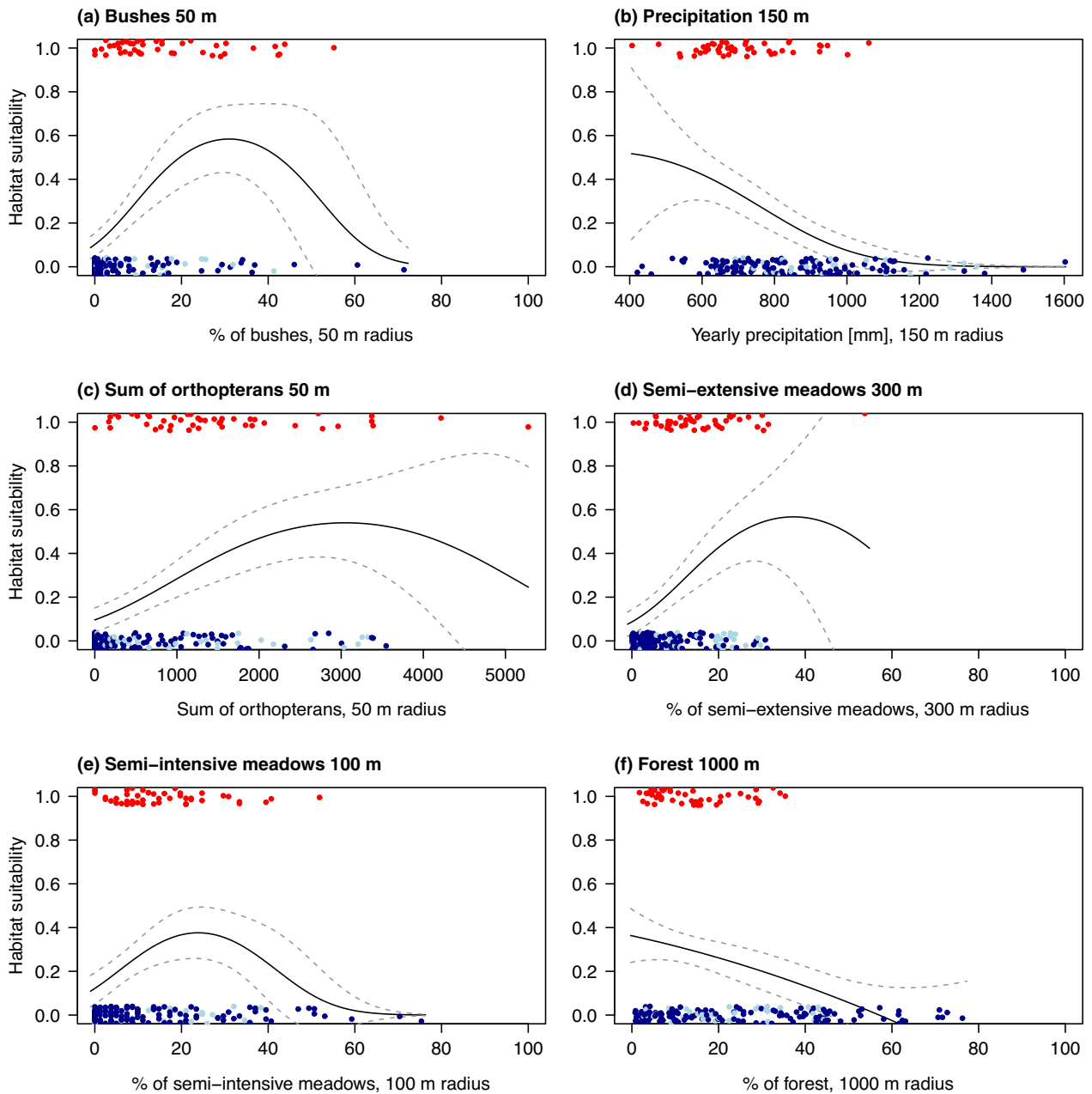
The presence points showed very suitable ensemble forecasting values (median = 0.719). These values were significantly lower for the random sites (median = 0.184). The values for historical sites (previously occupied sites but now vacant), however, were significantly higher than for random sites (median = 0.339), with several sites showing

values higher than 0.600. Overall, the historical sites did not show significant differences in terms of bush, semi-extensive or semi-intensive meadow coverages and of sum of orthopterans. However, the historical sites were more densely covered with forests and showed more precipitation (pairwise *t*-test,  $P < 0.01$ , Appendix S1: Fig. S4).

## DISCUSSION

In this study, we have developed a framework based on HSMs, MMI and focal windows at different spatial scales to understand and model the relationships between the presence of a rare species and environmental factors. We first tested the importance of key landscape and biotic variables at different spatial scales. We then used ESMs, a modelling method designed to deal with small datasets, to rank and model a species' distribution, and finally drew response curves for the selected variables. We found a hump-shaped relationship between Scops Owl habitat suitability and bush coverage within a 50-m radius from the nest, with an optimum between 15% and 30% coverage, and a decrease in the habitat suitability for the Owl as forest coverage increased within a 1000-m radius. A higher amount of semi-extensive meadows within a 300-m radius increased the suitability of the habitat for the Scops Owl, whereas semi-intensive meadows seem to have a negative impact when their coverage was not between 15% and 30%. The suitability also increased with the increase of orthopterans within 50 m of the territory centre. Finally, habitat suitability decreased with higher precipitation levels, with Scops Owls mostly avoiding sites at higher altitudes and selecting those with a more continental climate. Using this innovative mix of methods provides a deeper understanding of the different factors that shape the Scops Owl's distribution, especially through the selection of the scales at which these variables are most relevant. Finally, this study highlights important habitat requirements of the species that should be included in future conservation plans.

The use of climatic predictors in HSMs is a very powerful way to understand species distributions at relatively large scales (Martinez *et al.* 2003, Bellamy & Altringham 2015); however, their use at finer scales is often less efficient (Austin & Van Niel, 2011). The discriminatory power of climatic variables tends to decrease at smaller scales, whereas other variables such as land-use, food



**Figure 3.** Response curves of the six variables used to predict Scops Owl presence. Each panel represents a predictor used in the best-scale ESM. The x-axis represents the variable and the y-axis represents Scops Owl habitat suitability. Presence data are depicted in red, random absence data in light blue and historical data in dark blue. Presence data are scattered around 1 and absence data around 0 for visual purposes. The dotted lines represent the 95% confidence interval. All variables are expressed as quadratic terms. (a) Bush coverage within a 50-m radius of the territory centre ('Bush 50'). (b) Yearly precipitation within a 150-m radius of the territory centre ('Prec 150'). (c) Sum of orthopterans within a 50-m radius of the territory centre ('Ortho 50'). (d) Semi-extensive meadow coverage within a 300-m radius of the territory centre ('S-ext 300'). (e) Semi-intensive meadow coverage within a 100-m radius of the territory centre ('S-int 100'). (f) Forest coverage within a 1000-m radius of the territory centre ('For 1000'). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

availability and even stochasticity are becoming more important (Baudraz *et al.* 2018), consistent with our observations.

Adding the use of finer-scale predictors such as biotic variables often enables strong refinement of the models, increasing their predictive power



(Meier *et al.* 2010, Pellissier *et al.* 2010). A question remains: how to choose the most appropriate spatial scale? Using a multi-scale approach enabled us to identify the most appropriate scale and to confirm that selecting the best spatial scale for each predictor further increased the models' predictive power while providing a refined picture of the main habitat preferences of our species of interest (Bellamy *et al.* 2013, Scherrer *et al.* 2019), even though two fixed fine-scale models (100 and 200 m) also showed very good results.

### Biotic vs. abiotic predictors

The accuracy of climatic predictors often declines at smaller spatial scales (usually smaller extents at higher resolutions; Guisan & Zimmermann, 2000, Austin & Van Niel, 2011) where biotic variables, such as prey availability or interspecific competition, can overtake climate constraints (Guisan *et al.* 2017, Baudraz *et al.* 2018). This typically applied to the Scops Owl in Valais, where climate played only a minor role in its scattered and rather localized distribution within the Rhone valley. The only climatic variable retained in the models was yearly precipitation, which set elevational and longitudinal boundaries for the species. In our study, it corresponded to the lowlands and south-exposed slopes up to the mountain belt. Within the species' environmental niche, land-use and extensive agricultural practices overrode climate in terms of impact on the species' presence at a local scale, as shown by the predictors used as proxies for the intensity of vegetation management and abundance of orthopterans. This usually occurs when the modelling is going towards small scales and very fine resolutions, where the distribution of a species is often driven by land use, food resources, competition or just stochasticity (see Baudraz *et al.* 2018). Local factors can thus change drastically the suitability of habitats sharing similar top-climatic conditions making biotic variables very important at small scales. They are, however, seldom used in HSMs due to the difficulty of obtaining datasets over large surfaces (but see Meier *et al.* 2010, Pellissier *et al.* 2010). Biotic data such as vegetation coverage or prey availability are often measured directly in the field and are therefore hard to interpolate or model (Wisiz *et al.* 2013). Despite this, biotic predictors at different trophic levels such as the modelled degree of vegetation management intensification or orthopteran

abundance (*sensu* Klein *et al.* 2020) used in this study can be key variables to understand patterns of species distributions and biodiversity over large surfaces. This is especially true for mesopredators such as insectivorous birds that are highly dependent on meadow type, the presence of structures and prey availability (Pereira *et al.*, 2013).

### A multi-scale framework

Although using variables that reflect the type or quality of a given habitat is of primary importance, the effects of such variables on HSMs will also vary greatly depending on their spatial scale of influence or resolution (Bellamy *et al.* 2013, Vicente *et al.* 2014), especially for mobile species with large home-ranges (Schindler *et al.* 2013). When precise knowledge on the foraging territory is missing, the use of multi-scale analysis becomes mandatory to avoid misinterpreting the species' ecology and using irrelevant variables. For instance, our analysis suggests that Scops Owls avoided high proportions of bush and semi-intensive meadow coverage around the territory centre and preferred areas with high modelled orthopteran densities, with an average of 40 orthopterans per 100 m<sup>2</sup>. This average number accounts for the whole surface whatever the type of vegetation or structure and could therefore possibly be much higher in reality. Both variables (orthopterans and semi-intensive meadows) showed a high influence in the vicinity of the nest (100- and 50-m radii around the territory centre, respectively), whereas forest cover seemed to limit Scops Owl presence at larger scale (1000-m radius). As Scops Owls nest in tree cavities, working with small-scale forest data could bias model projections by suggesting forests as a key habitat when, in fact, the species tends to avoid densely forested areas and prefers to use isolated trees, probably to escape the Tawny Owls and the Long-Eared Owls, their main predators. The use of a multi-scale framework, which enables the selection or inclusion of each variable at its best spatial scale, showed an increase in predictive power of the ESMs (9.39% on average: Fig. 1) and potentially helped to avoid the misinterpretation of certain aspects of the species' ecology. However, the selection method does not take into account interactions between the variables that could lead to different results in the ESMs, as demonstrated with the fixed 100- and 200-m ESMs performing as well as the best multi-scale

ESM. Interestingly, the scales between 100 and 250 m produced very good models, which probably indicates that approximating Scops Owls territories with circles of 100- to 250-m radii could be appropriate. This also corresponds to the situation that can be observed in the field, where singing individuals are often separated by a few hundred metres in densely inhabited areas, typically between 200 and 300 m.

### Scops Owl conservation planning

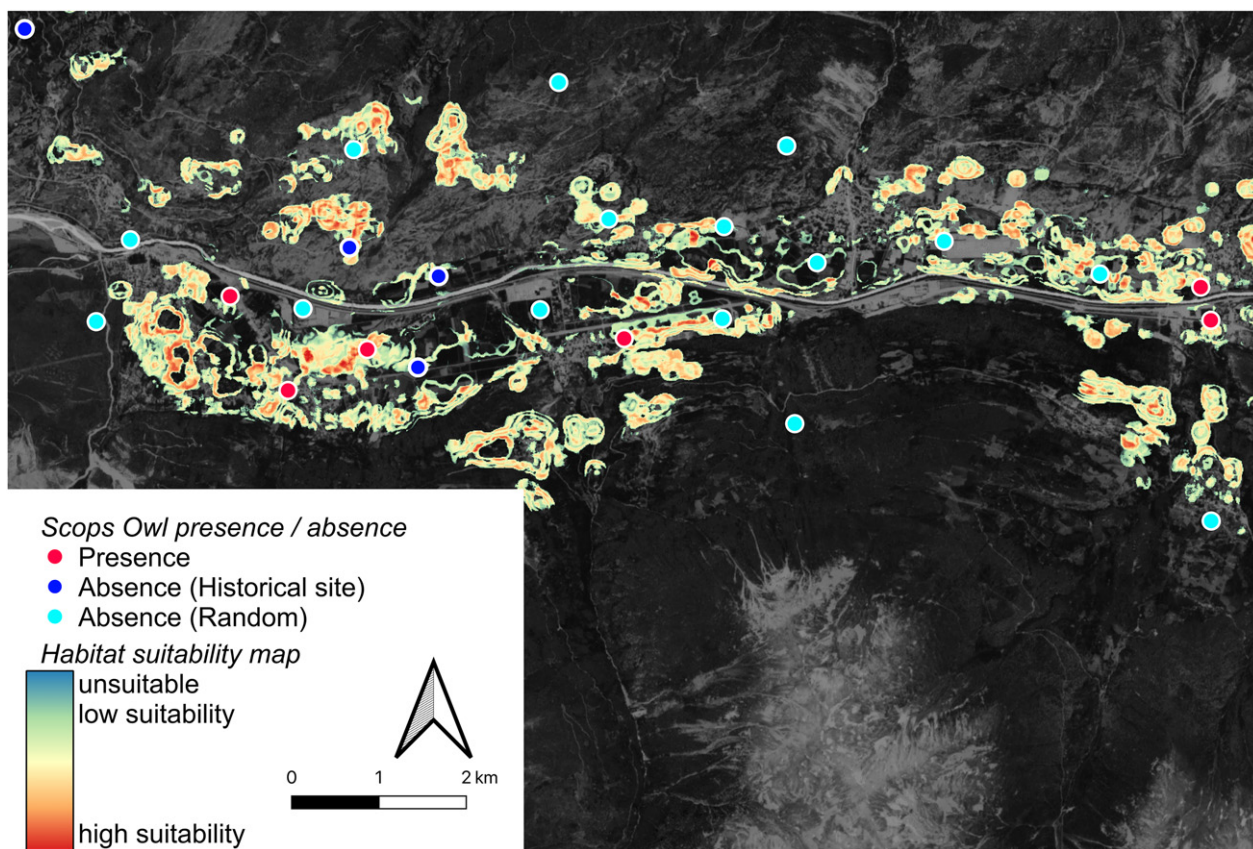
Modelling habitat suitability to predict species distributions offers two advantages for species conservation (Guisan *et al.* 2013). First, the final model outputs can be visualized as a map of the favourable/unfavourable locations for the species of interest, highlighting the best locations in which to focus conservation efforts to preserve the Scops Owl (Fig. 4). Our results showed that the area where habitat suitability for the Scops Owl was predicted to be high by the ESMs, or in other words the portion of the Valais that shows a high probability of presence for the Scops Owl, covers 1.34% of the study area and only 0.66% if we consider only the best 50% of these areas. Such maps may be of direct use to practitioners in conservation management.

Secondly, the statistics associated with the models and prediction maps provide information on the response of the species to the different predictor variables. Semi-intensive and semi-extensive meadows have already been shown to be habitats that are favoured by Scops Owls throughout Europe (Denac 2009, Sergio *et al.* 2009, Denac *et al.* 2019) and in previous local studies in Switzerland (Arlettaz 1990, Sierro & Arlettaz 2013). However, the exact spatial scale of influence of these variables, as shown here, has never been assessed before, especially the avoidance of areas with more than 30% of semi-intensive meadows. The approach proposed here should be applicable to many other species and should therefore prove to be a useful tool to increase ecological knowledge on endangered species and improve conservation planning, as has previously been shown for certain bat species (Bellamy & Altringham 2015, Scherrer *et al.* 2019).

In this study, we shed light in particular on the importance of semi-extensive to semi-intensive management practices in the vicinity of Scops Owl nests (within a radius of 100–300 m around the

territory centre), stressing the importance of preserving semi-natural meadows with low mowing regimes and low nitrogen inputs (Blüthgen *et al.* 2012) in their direct surroundings. The negative impact of forest coverage and the hump-shaped relationship with bush coverage also point to the need for extensive and well-structured open habitats away from forests. The positive effects of extensive grassland management on orthopteran diversity and density is well known (Humbert *et al.* 2010) but here we show that it also has a direct effect on the distribution of the Scops Owl, which selected areas with higher orthopteran densities.

The two most important biotic variables – bush coverage and orthopteran availability – were at their best scale within a radius of 50 m from the territory centre. For both of these predictors, Scops Owls presence showed a hump-shaped relationship, although with a high amount of uncertainty for orthopteran abundance. This would tend to indicate that, when possible, the Owls hunt in the direct vicinity of their nest. A proportion of bushes greater than 40% would be typical of a closed habitat, whereas a very low proportion of bushes would be indicative of a more homogeneous landscape, which tend to be more intensively cultivated and host fewer food resources. In a similar way to bush coverage, the area covered by forests at a scale of 1000 m around the territory centre also proved to be a limiting factor. This was a typical case of land abandonment with forest covering old extensive meadows. On the opposite end, low bush coverage indirectly points to areas with more intensive land-use management, often reducing small extensive zones such as uncut refuges for orthopterans. However, the habitat suitability increase with the amount of semi-extensive meadows but the presence of semi-intensive meadows, often less attractive for orthopterans, is a limitation when covering more than 30% of the area surrounding the territory centre (100 m). Even though Scops Owls prefer to catch large orthopteran prey (Panzeri *et al.* 2014), a high abundance of this taxonomic group indicates that a meadow is managed extensively (alternate cuts, absence of irrigation, uncut refuges; Humbert *et al.* 2010). Moreover, structure-rich habitats with high orthopteran abundance will most often host a high density of Tettigonidae, which are the main prey of nesting Scops Owls. The possible decrease of the habitat suitability



**Figure 4.** Partial map of the Scops Owl HSM. This map is part of the projection of the ESM built with the six predictors at their respective best scale. It shows the suitability of Scops Owl habitat on a colour gradient from blue (low suitability) to red (high suitability). Coloured points represent the presence/absence sites used to build the models. This map only shows suitable areas based on the binarization of the projection map based on maximization of the TSS. Base map: Very high-resolution Image Mosaic, Copernicus Land Monitoring Program. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

when shifting to higher numbers of orthopterans could be explained by these areas becoming more and more open and not presenting enough trees or structures to host Scops Owls.

The key strength and novelty of this study was the quantification of the best spatial scale of influence of each variable for the Scops Owl (Bosco *et al.* 2021) in a multi-scale HSM robust to small sample sizes (ESMs), in particular the inclusion of the vegetation management intensity and orthopteran abundance projections based on Klein *et al.* (2020). From a conservation point of view, measures ensuring mosaic-like landscapes of semi-intensive (max. 30%) and semi-extensive grasslands (at least 30–60%) separated by hedges or similar bushy structures with patches of trees or single trees big enough to host large cavities (max. 20%) will maximize the amount of suitable habitat

for the Scops Owl and its prey (Humbert *et al.* 2010, Theux 2019).

### Limitations

Working with a rare species that is either recolonizing its past habitats or using new ones shows analogies to expanding species dynamics. When modelling a species distribution, one usually assumes that the species is in a pseudo-equilibrium within its suitable environment (Guisan & Zimmermann 2000, Guisan *et al.* 2017). However, the efficiency of distribution models varies according to the stage of colonization or recolonization (Meentemeyer & Václavík 2011). The model therefore reflects the current potential habitat for the species but should be updated regularly to see whether new habitats that had not previously been

identified may also provide suitable conditions for the species and be incorporated in the species' niche quantification in a next step of the modelling process (Guisan *et al.* 2006, Le Lay *et al.* 2010). This could also explain why some historical absence sites could be suitable for the species in our HSM but have not yet been recolonized, thus lowering the sensitivity of our best models.

The second limitation with such sampling is linked to the amount of rare habitat types. Some particular or rare habitat types can occasionally be used as alternative foraging sites by the Scops Owl, e.g. insect-rich vineyards (Denac *et al.* 2019). However, as these elements are seldom encountered in the landscape, they can hardly be taken into account when fitting HSMs, even when using ESM. A study on Great Green Bush-Crickets *Tettigonia viridissima* similarly showed that some of these rare or localized habitat types, such as reeds or fallows, could host a high prey density (Theux 2019). One should always keep in mind that high-quality secondary foraging habitats could sometimes replace more common ones, e.g. extensive meadows, and provide nesting opportunities outside traditional sites. Therefore, HSM outputs that provide areas of interest for conservation actions should ideally be validated by experts in the field – and in this way iteratively improved – before any model-based conservation measures are taken (Guisan *et al.* 2006).

Finally, the use of orthopteran abundance as a proxy for insect biomass and extensively managed habitats could be questioned. The main prey of the Scops Owl during the nesting time in the Valais – the Great Green Bush-Cricket (Heller & Arlettaz 1994) – did not seem to be a limiting factor in this region (Theux 2019). However, monitoring Tettigonidae species is quite complex as they leave the meadows to sing from high vegetation, such as bushes. The relationship between Tettigonidae abundance and the distribution of Scops Owls should be investigated in future studies to understand their relationship along the season in both occupied and abandoned sites.

## CONCLUSIONS

Using a robust multi-scale analysis and modelling approach incorporating new essential variables for the species, we were able to model the Scops Owl's habitat suitability and refine its habitat requirements for conservation planning. This work has created two

valuable tools for conservationists and practitioners. First, the high accuracy of the Scops Owl HSM predictions can serve as a basis to assign conservation prioritization in Valais by showing the highly suitable areas that could be maintained, and which ones could be promoted by the preservation or restoration of semi-extensive meadows. Secondly, the calculated percentages of the different habitat types required by the species can be used as concrete recommendations to help practitioners take optimal conservation measures for this rare owl species. Finally, in 2020 and 2021, the very positive population dynamics of the species revealed some recolonization of historical absence sites, suggesting that the HSM suitability map is an appropriate tool to understand the requirements of the species in Valais. However, several years of monitoring will be needed to confirm this trend.

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## AUTHOR CONTRIBUTIONS

**Coralie Theux:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Project administration (equal); Software (equal); Writing-original draft (lead); Writing-review & editing (equal). **Noëlle Klein:** Data curation (equal); Formal analysis (supporting); Investigation (equal); Writing-review & editing (equal). **Elodie Garibaldi:** Formal analysis (supporting); Investigation (supporting). **Alain Jacot:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing-original draft (supporting); Writing-review & editing (equal). **Sylvain Eichhorn:** Investigation (equal). **Antoine Guisan:** Methodology (supporting); Project administration (supporting); Writing-review & editing (equal). **Jean-Nicolas Pradervand:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Project administration (lead); Supervision (lead);

Writing-original draft (equal); Writing-review & editing (equal).

### Data Availability Statement

The Scops Owl data are sensitive and cannot be made freely available; however, they can be obtained from the corresponding author upon reasonable request. The habitat suitability map and the vegetation and orthopteran maps are available at coarser scales in Zenodo, <https://doi.org/10.5281/zenodo.4943482>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1** Map of the Canton Valais (46° 01'–46°34' N, 7° 05'–8°01' E), our study area.

**Figure S2** Pipeline to build Scops Owl distribution models.

**Figure S3** Evaluation of ESMs. Sensitivity and specificity are shown for each ESM built with single-scale variables ranging from 50 m to 1000 m.

**Figure S4** Boxplots of the two variables showing a significant difference between presence and historical territories.

**Table S1** Used sites, whether they are mapped, unmapped and used for Great Green Bush-Cricket *Tettigonia viridissima* assessment.

**Table S2** Results of the Student's t-tests to compare the area given by mapping to the area given by the spatialized vegetation and ortho-teran models.