Alpine Entomology 6 2022, 25–38 | DOI 10.3897/alpento.6.83730

PENSOFT

Alpine Entomology

# Modeling the distribution of coprophagous beetle species in the Western Swiss Alps

Vivien Cosandey[1], Olivier Broennimann[1,2], Antoine Guisan[1,2]

1 *Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland*
2 *Institute of Earth Surface Dynamics, University of Lausanne, Lausanne, Switzerland*

*https://zoobank.org/D418EF00-49AA-4FED-8830-BFFEAF4D6367*

Corresponding author: Vivien Cosandey (vivien.cosandey@bluewin.ch)

Academic editor: Marco Moretti ♦ **Received** 13 March 2022 ♦ **Accepted** 2 June 2022 ♦ **Published** 6 July 2022

## Abstract

Coprophagous beetles are essential for fecal matter removal and are thus considered key ecosystem services providers. Yet, our knowledge of these beetles' distribution and ecology remains very limited. Here, we used Species Distribution Models (SDM) to investigate the species-environment relationships (i.e. their niche) and predict the geographic distribution of coprophagous beetles in the Western Swiss Alps. We used our own sampled data and existing national data from the Swiss faunal database to calibrate, for each species, a regional and a national SDM respectively. In both models, the best predictors were temperature and rock cover proportion, while a soil characteristic ($\partial^{13}C$) indicating its organic content and texture was important in the regional models and precipitations in the Swiss models. The model performed better for species specialized on low or high altitudes than for generalist species occurring in a large altitudinal range. The model performances were neither influenced by the size, nor by the nesting behavior (laying eggs inside or below the excrements) of the species. We also showed that species richness decreased with altitude. This study opens new perspective for a better knowledge of coprophagous beetle's ecology and a useful tool for their conservation in mountain regions.

## Key Words

Dung beetles, Species distribution modeling (SDM), Ensemble of Small Models (ESMs), Hydrophilidae, Geotrupidae, Scarabaeidae

## Introduction

Coprophagous beetles are part of a specialized entomofauna feeding on the droppings of mammals (Hanski 2016). Some taxa have coprophagous adults and predaceous larvae, which are chasing fly larvae from dung patches (Hydrophilidae, Sphaeridinae), while other have coprophagous adults and larvae. In the latter case, some species lay their eggs directly in the dung (non-nesters: Scarabaeidae, Aphodiinae) and other dig simple wells or sophisticated network of tunnels and rooms where they stock dung and lay their eggs (paracoprids: Geotrupidae and Scarabaeidae, Scarabeinae) as a strategy to avoid the harsh intra- and inter-specific competition to exploit dung patches before they dry (Hanski 2016). By feeding on excrements and burying it, coprophagous beetles are essential for dung decomposition (Gittings et al. 1994). They avoid the accumulation of excrements, preventing pasture surface loss (Beynon et al. 2012b) and supplementary expenses for dung removal (Fincher 1981; Losey and Vaughan 2006; Beynon et al. 2015) and are therefore considered as key "Ecosystem Service Providers" (Nichols et al. 2008). In addition, coprophagous beetles represent a part of the food for some insectivorous animals such as birds (in particular corvids) (Lumaret and Stiernet 1990) or mammals (e.g. greater horseshoe bat (*Rhinolophus ferrumequinum*)) (Beynon et al. 2015). The economic and ecological importance of coprophagous beetles coupled with the possibility to characterize the whole species assemblages found at a given location (dung patch) in a given time point (Finn and Giller 2000; Hanski 2016) make them an adequate group to study biogeography (Lumaret 1979) and animal communities (Hanski and Koskela 1977). In Europe, the species

assemblages of coprophagous beetles and their relative abundance have already been investigated (Lumaret and Stiernet 1984; Lumaret and Stiernet 1989; Errouissi et al. 2004; Negro et al. 2011) and the importance of climatic and edaphic factors have been shown at a coarse level (Hortal et al. 2001; Lobo and Martin-Piera 2002; Lumaret and Jay-Robert 2002). However, ecological needs and fine geographic distribution of single coprophagous beetle species remains an understudied topic.

The study of the realized environmental niche of species, adaptation to local conditions and interspecific interactions (Hutchinson 1957) allows a better understanding of the distribution of species (see Niche-Geography duality: Colwell and Rangel 2009), which is crucial to overcome Wallacean (knowledge about the geographical distribution of species) and Hutchinsonian (knowledge about the tolerance of species to abiotic factors) shortfalls concerning biodiversity (Hortal et al. 2015). The development of statistical species distribution models (SDM; also called 'habitat suitability' or 'ecological niche' models; see Franklin 2010; Peterson et al. 2011; Guisan et al. 2017) to quantify the niche and derive geographic predictions have brought powerful perspectives to better understand, compare and quantify the relationship between organism and their environment (i.e. their environmental niche), but also to predict their distribution in space and time (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). These tools can therefore bring essential knowledge about the ecology of understudied taxonomical groups like most arthropods (Hochkirch et al. 2021). SDMs have been used to study various groups of insects (Pellissier et al. 2012; Pradervand et al. 2014; D'Amen et al. 2015; Descombes et al. 2016; Mata et al. 2017) but there are only few examples of single modeled coprophagous beetles (e.g. Chefaoui et al. 2005; Lobo et al. 2010).

The aim of this study was to bring a better understanding of the factors influencing the distribution of coprophagous beetle species in temperate mountain environments using a SDM approach. In order to obtain a sufficient number of accurate species data to quantify species-environment relationships, we sampled coprophagous beetles throughout the Western Swiss Alps in a random stratified manner. We additionally obtained all the occurrences available in Switzerland for the beetles of interest (Hydrophilidae, Geotrupidae and Scarabaeidae) from the Swiss national database (www.cscf.ch). This allowed us to compare fine-scale models calibrated in the study area using our precisely sampled data (regional model) and large-scale models calibrated at the Swiss level using national occurrences and our data (Swiss model). We expected the latter to reduce the risk, while calibrating the SDMs, of truncating the species' environmental niche, which can happen when the complete extent of the species' geographic distributions and environmental requirements are not covered in an analysis (Pearson et al. 2004; Thuiller et al. 2004; Hannemann et al. 2016; Guisan et al. 2017; El-Gabbas and Dormann 2018; G. Mateo et al. 2019; Chevalier et al. 2021). Here, we particularly focused on the climatic, land-use and edaphic factors as environmental predictors of the species' presence. In addition, we investigated the effects of species characteristics such as the altitudinal amplitude where they occur, their nesting behavior and their body size on the SDMs performances. Finally, we assessed whether the stacking of all species predictions produced meaningful richness maps of coprophagous beetles in the study area.

# Materials and methods

## Study area

The study was conducted in Western Switzerland, in the alpine region of the Canton of Vaud, which goes from Vevey to Bex and to Rougemont (Fig. 1). It spans a wide altitudinal gradient, from 372 to 3051 meters above sea level. Since the lower part of the region is dedicated to crop fields and its slopes are covered by forests, we only considered the upper part of the area, starting from an altitude of 1000 meters above sea level (Fig. 1), where pastures grazed by domestic livestock (principally cows and sheep) and alpine grasslands inhabited by big wild herbivores, like Alpine chamois (*Rupicapra rupicapra*), Alpine ibex (*Capra ibex*) and Red deer (*Cervus elaphus*) occur. The study region is of particular interest for interdisciplinary research as it constitutes a priority region for research (http://rechalp.unil.ch; Reynard et al. 2020; von Däniken et al. 2014) and is also a priority region for biodiversity conservation (Lassen and Savoia 2005).

## Sampling

From the 31 of May to the 12 September 2020, we collected beetles in 132 sampling plots (Fig. 1) of 20 meters radius located in a random stratified manner (Guisan and Hirzel 2002) in open habitats (excluding the forests and built areas). We stratified the study region in 10 strata according to altitude (every 300 meters, from 1000 to 2500 meters) and the yearly sum of solar radiations (two levels: lower and higher than the mean radiation observed in the study area). In order to perform a sampling representative of the environment variability of the study area, we sampled a number of random points in each stratum proportional to its size. This could ensure optimizing the number of species to be found (according to the species-area relationship; Lomolino 2001) while still allowing good species-environment relationships to be fitted (Hirzel and Guisan 2002). To avoid bias due to the phenology of the beetles, we sampled the whole altitudinal gradient regularly through time.

We choose to perform active sampling over trapping in order to minimize the logistics and maximize the number of sampling stations. Each plot was sampled once. There, 20 minutes were dedicated to the manual search of beetles

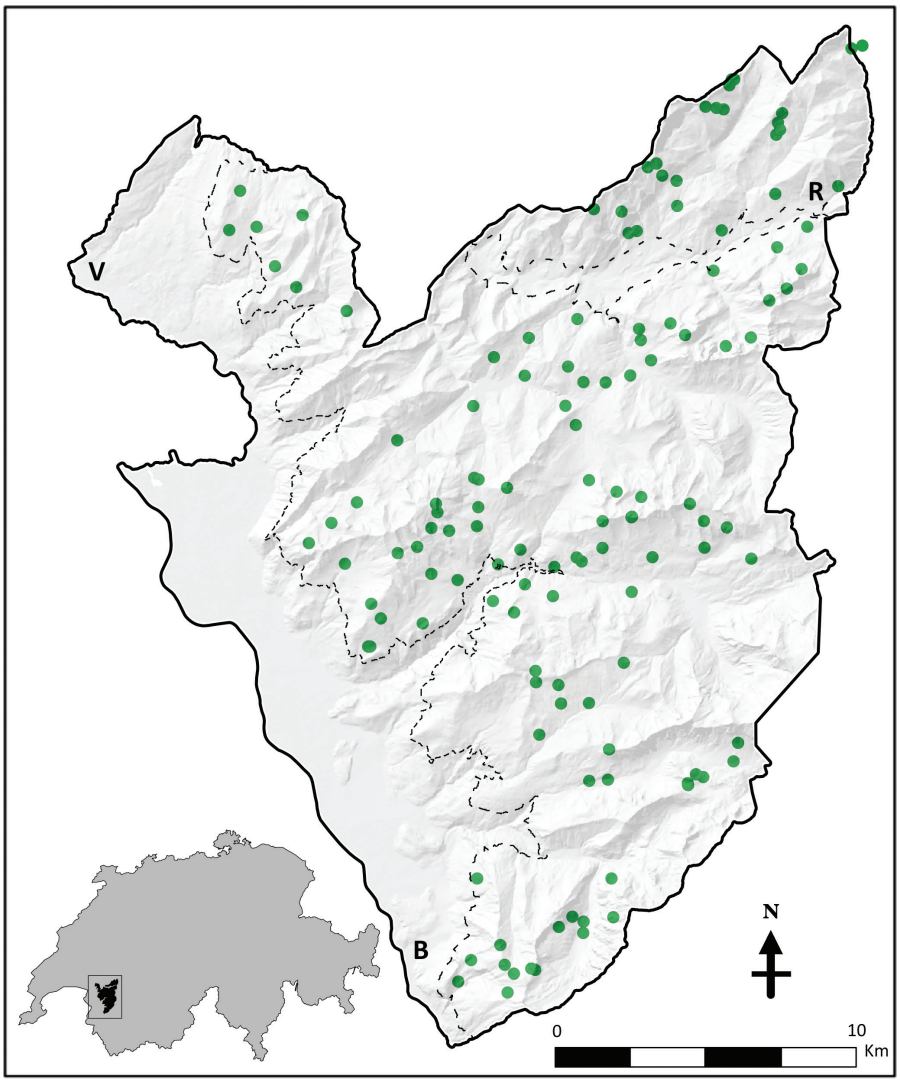


**Figure 1.** Map of the study area situated in the alpine region of the Canton of Vaud above 1000 meters above sea level (dashed line) with three of its the major localities: Bex (B), Rougemont (R) and Vevey (V). The 132 plots where coprophagous beetles were sampled in 2020 are represented by the green circles.

inside of the dung using a little shovel with the goal to catch the maximum number of species. We identified the collected beetles with the help of a binocular and based on identification keys found in the specialized literature (Baraud 1992; Fikáček 2006; Vorst 2009; Klausnitzer 2011). For the statistical analyses, *Amidorus immaturus* and *A. obscurus* were pooled together since these two species were erroneously not distinguished at the Swiss scale (Cosandey et al. 2017). The species were recorded as present or absent in each sampling plot. We classified the Scarabaeidae and Geotrupidae species according to their nesting behavior in 'non-nesters' (laying eggs in the dung), 'paracoprids' (laying eggs in dung buried under the excrement) with the help of the specialized literature (Klemperer 1980; Rojewski 1983; Zunino and Barbero 1990; Hanski 2016) and the revisions proposed by Tonelli (2021). All the data were transmitted to the Swiss database (info fauna-CSCF; distributional maps available here: https://lepus.unine.ch/carto/).

## Swiss beetle data

In addition to our sampling dataset, we received all the Swiss data (26'602 occurrences from museums and private collections) from the Swiss database (info fauna-CSCF; www.cscf.ch) for the species of coprophagous beetles we found during our sampling. For the statistical analyses, we discarded the duplicated occurrences and the imprecise old museum data (geographic accuracy of less than 250 meters) ending with a 5359 occurrences dataset (20.15% of all occurrences).

## Environmental data

To depict the species' niche and to fit our models, we used 13 predictors (Table 1): (i) land-use variables originating either from the Swiss Federal Office of Statistics (2004) - alpine pastures, lowland pastures, cultivations, human

**Table 1.** The 13 predictors used in our models. For each of the variables, we provide its category, name, a short description and the model in which it was used: Swiss and/or regional.

| Category | Name | Description |
|---|---|---|
| **Swiss models** | | |
| Bioclim | Bio10 | Mean temperature of the warmest year quarter in a 250 meter focal window |
| Bioclim | Bio16 | Mean precipitation in the wettest year quarter in a 250 meter focal window |
| Bioclim | Bio17 | Mean precipitation of the driest quarter of the year in a 250 meter focal window |
| Land use | Alpine pastures | Proportion of alpine pastures (situated above the permanent habitation area) area in a 250 meter focal window |
| Land use | Cultivations | Proportion of cultivated area in a 250 meter focal window |
| Land use | Forest edges | Proportion of forest edges area in a 250 meter focal window |
| Land use | Human infrastructures | Proportion of human infrastructures cover in a 250 meter focal window |
| Land use | Humid habitats | Proportion of humid habitats area in a 250 meter focal window |
| Land use | Lowland pastures | Proportion of lowland pastures (situated in the permanent habitation area) area in a 250 meter focal window |
| Land use | Rock | Proportion of rocks and bare soils area in a 250 meter focal window |
| **Regional models** | | |
| Bioclim | Solar radiation | Sum of the total radiation over one year |
| Soil | C13 | Predicted carbon isotope composition $\partial^{13}C$ of the soil in the study region |
| Soil | pH | Predicted soil pH in the study region |

infrastructures (at a 50 meters resolution) - or from the Swiss Federal Office of Topography (Topographic Landscape Model 3D catalogue, 2012); - humid habitats, forest edges, rock and bare soil covers (25 meters resolution); and ii) climatic variables (at a 25 meters resolution) calculated from the bioclimatic data of Switzerland (Hijmans et al. 2005; Broennimann 2018) - mean temperature of the warmest quarter of the year (Bio10), precipitation in the wettest year quarter (Bio16), and precipitation in the driest year quarter (Bio17). Elevation was not included as predictor, as it is not a causal variable for species (Guisan et al. 2017) and is driving many other variables already included as predictors (e.g. temperature). To take into account the precision of the data at the Swiss level, we ran, for each variable focal window (Bellamy et al. 2013; Scherrer et al. 2019), which summarized the proportion of each land-use variables (i) and the mean climatic condition (ii) in a 250 meters radius around every pixel of 25 meters. These predictors were used to calibrate the Swiss models.

For all species recorded at least 15 times in our sampling (Table 2), we calibrated regional models with the land-use, bioclimatic variables and fine scale predictors with a 25 meters resolution (Table 1) such as the yearly sum of solar radiation (Zimmermann and Kienast 1999) and edaphic factors; soil pH (Buri et al. 2017) and the carbon isotope composition $\partial^{13}C$, which is an indirect measure of soil texture and organic matter content (Bird et al. 2003; Buri et al. 2020). We verified that the correlations between the variables were not too high (<0.7) as proposed by Dorman et al. (2013).

## Statistical analyses

All the statistical analyses were performed with R Studio version 1.0.153. (R core team, 2017). The models were built using the biomod2 (Thuiller et al. 2009) and ecospat package (Di Cola et al. 2017). Among the techniques available to fit Species Distribution Model (SDM) (Elith et al. 2006; Guisan et al. 2017), we choose to use Ensemble of Small Models (ESMs; Lomba et al. 2010; Breiner et al. 2015, 2018). In this approach many small (here bivariate) models are fitted and averaged in a weighted way within a single Ensemble model in order to avoid overfitting of the models and is thus very useful in the case of species with few occurrences in a dataset (Lomba et al. 2010; Breiner et al. 2015), like ours.

For each species found at least 15 times (Scherrer et al. 2019) during our sampling, we calibrated a 'Regional' model with our presence-absence occurrences and all predictors (climatic, land use, edaphic and radiance; see Table 1). In parallel, we calibrated a 'Swiss' model for all species found in the study area and known from at least 15 accurate occurrences in Switzerland (originating from info fauna-CSCF and our sampled data) and background points, also called 'pseudo-absences' (or 'background points'; same number as the number of presences) with climatic and land-use variables as predictors (see Table 1). As the region of interest is not an outlier compared to the main topo-climatic conditions in Switzerland, we are confident that the response curves of the Swiss models are not truncated and that the predictions in the regions of interest are not biased.

We calibrated all our models using two techniques (Breiner et al. 2015). More precisely, we choose to use Generalized Linear Models (GLM) and Generalized Additive Models (GAM), to represent both parametric (GLM) and semi-parametric (i.e. more data-driven; GAM) modeling approaches. Both models are calibrated using a binomial distribution with logit link function to accommodate the binary nature of the response (Warton and Hui 2011). Hundred runs were conducted with 70% of the dataset used for model calibration and 30% for model validation. The GLM and GAM models were separately merged in two Ensemble models (ESM-GLM and ESM-GAM) with the single bivariate runs weighted according

**Table 2.** Species of coprophagous beetles found in the study area. For the 47 species, we report the family, the subfamily, the number of occurrences in the study area (in brackets for species with less than 15 occurrences, for which no regional models were run) and the number of all existing precise occurrences in Switzerland (in brackets for species, with less than 15 occurrences), the nesting behavior (N – Non-nesters, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]) and the mean size in mm. The species are depicted in Suppl. material 3: Fig. S3.

| Family | Subfamily | Species | Occurrences in the study area | Occurrences in Switzerland | Nesting behavior | Size [mm] |
|---|---|---|---|---|---|---|
| Geotrupidae | Geotrupinae | Anoplotrupes stercorosus (Scriba, 1791) | 26 | 326 | P | 15.5 |
| Geotrupidae | Geotrupinae | Geotrupes spiniger (Marsham, 1802) | (9) | 77 | P | 22 |
| Geotrupidae | Geotrupinae | Geotrupes stercorarius (Linnaeus, 1758) | 17 | 76 | P | 20.5 |
| Geotrupidae | Geotrupinae | Trypocopris vernalis (Linnaeus, 1758) | (2) | 67 | P | 11 |
| Hydrophilidae | Sphaeridiinae | Cercyon haemorrhoidalis (Fabricius, 1775) | (8) | 90 | H | 2.8 |
| Hydrophilidae | Sphaeridiinae | Cercyon impressus (Sturm, 1807) | 88 | 206 | H | 3.15 |
| Hydrophilidae | Sphaeridiinae | Cercyon lateralis (Marsham, 1802) | 70 | 140 | H | 2.75 |
| Hydrophilidae | Sphaeridiinae | Cercyon melanocephalus (Linnaeus, 1758) | 23 | 81 | H | 2.6 |
| Hydrophilidae | Sphaeridiinae | Cercyon obsoletus (Gyllenhall, 1808) | (4) | 15 | H | 3.6 |
| Hydrophilidae | Sphaeridiinae | Cercyon pygmaeus (Illiger, 1801) | 46 | 110 | H | 1.45 |
| Hydrophilidae | Sphaeridiinae | Cercyon quisquilius (Linnaeus, 1761) | (7) | 6 | H | 2.25 |
| Hydrophilidae | Sphaeridiinae | Cryptopleurum crenatum (Kugelann, 1794) | (8) | 16 | H | 2 |
| Hydrophilidae | Sphaeridiinae | Cryptopleurum minutum (Fabricius, 1775) | 17 | 73 | H | 2 |
| Hydrophilidae | Sphaeridiinae | Megasternum concinnum (Marsham, 1802) | (1) | 55 | H | 1.95 |
| Hydrophilidae | Sphaeridiinae | Sphaeridium bipustulatum Fabricius, 1781 | 17 | 97 | H | 4.35 |
| Hydrophilidae | Sphaeridiinae | Sphaeridium lunatum Fabricius, 1792 | 78 | 188 | H | 5.65 |
| Hydrophilidae | Sphaeridiinae | Sphaeridium marginatum Fabricius, 1787 | (5) | 24 | H | 4.55 |
| Hydrophilidae | Sphaeridiinae | Sphaeridium scarabaeoides (Linnaeus, 1758) | 80 | 228 | H | 5.75 |
| Scarabaeidae | Aphodiinae | Acrossus depressus (Kugelann, 1792) | 76 | 268 | N | 7.5 |
| Scarabaeidae | Aphodiinae | Acrossus rufipes (Linnaeus, 1758) | 62 | 242 | P | 12 |
| Scarabaeidae | Aphodiinae | Agoliinus satyrus (Reitter, 1892) | (2) | 24 | N | 6 |
| Scarabaeidae | Aphodiinae | Agrlilinus convexus (Erichson, 1848) | (12) | 77 | N | 5 |
| Scarabaeidae | Aphodiinae | Amidorus obscurus s.l. (Fabricius, 1792) | 42 | 129 | N | 7 |
| Scarabaeidae | Aphodiinae | Ammoecius brevis (Erichson, 1848) | (1) | 18 | N | 4 |
| Scarabaeidae | Aphodiinae | Aphodius fimetarius aggr. (Linnaeus, 1758) | 16 | 231 | N | 6.5 |
| Scarabaeidae | Aphodiinae | Bodilopsis rufa (Moll, 1782) | 59 | 217 | P | 6 |
| Scarabaeidae | Aphodiinae | Calamosternus granarius (Linnaeus, 1767) | (8) | 249 | N | 4 |
| Scarabaeidae | Aphodiinae | Colobopterus erraticus (Linnaeus, 1758) | 82 | 207 | P | 6 |
| Scarabaeidae | Aphodiinae | Esymus pusillus (Herbst, 1789) | 20 | 130 | N | 4 |
| Scarabaeidae | Aphodiinae | Euheptaulacus carinatus (Germar, 1824) | (10) | 25 | N | 5 |
| Scarabaeidae | Aphodiinae | Nimbus contaminatus (Herbst, 1783) | (3) | 61 | N | 6 |
| Scarabaeidae | Aphodiinae | Oromus alpinus (Scopoli, 1763) | 27 | 133 | N | 5.5 |
| Scarabaeidae | Aphodiinae | Otophorus haemorrhoidalis (Linnaeus, 1758) | 47 | 156 | N | 4.5 |
| Scarabaeidae | Aphodiinae | Parammoecius gibbus (Germar, 1816) | 21 | 50 | N | 3.75 |
| Scarabaeidae | Aphodiinae | Planolinoides borealis (Gyllenhal, 1827) | (4) | (9) | N | 4.5 |
| Scarabaeidae | Aphodiinae | Planolinus fasciatus (A. G. Olivier, 1789) | (4) | 21 | N | 4.5 |
| Scarabaeidae | Aphodiinae | Rhodaphodius foetens (Fabricius, 1787) | (4) | 21 | N | 7.5 |
| Scarabaeidae | Aphodiinae | Teuchestes fossor (Linnaeus, 1758) | 64 | 203 | P | 10.5 |
| Scarabaeidae | Aphodiinae | Volinus sticticus (Panzer, 1798) | (5) | 141 | N | 4.5 |
| Scarabaeidae | Scarabaeinae | Copris lunaris (Linnaeus, 1758) | (1) | 72 | P | 17.5 |
| Scarabaeidae | Scarabaeinae | Euoniticellus fulvus (Goeze, 1777) | (5) | 55 | P | 9 |
| Scarabaeidae | Scarabaeinae | Onthophagus baraudi Nicolas, 1964 | 16 | 27 | P | 5.5 |
| Scarabaeidae | Scarabaeinae | Onthophagus coenobita (Herbst, 1783) | (3) | 123 | P | 8 |
| Scarabaeidae | Scarabaeinae | Onthophagus fracticornis (Preyssler, 1790) | 58 | 315 | P | 8.5 |
| Scarabaeidae | Scarabaeinae | Onthophagus illyricus (Scopoli, 1763) | (6) | 64 | P | 8.75 |
| Scarabaeidae | Scarabaeinae | Onthophagus joannae Goljan, 1953 | (10) | 128 | P | 5 |
| Scarabaeidae | Scarabaeinae | Onthophagus verticicornis (Laicharting, 1781) | (1) | 19 | P | 8 |

to their AUC scores. Finally, these two single-technique ESMs were included in a final Ensemble model (final ESM), weighted by their respective SomersD score. All the final models were projected over the study region. We evaluated the quality of our models, with a maximization of their True Skill Statistic score (TSS; Allouche et al. 2006; maxTSS; Jimenez-Valverde 2014; Guisan et al. 2017). The relative importance's of each variable in the models were also extracted using the ecospat.ESM VarContrib function of the ecospat package, which sums separately the weights of the bivariate models including each variable and compares them to the sum of all the

bivariate models. Finally, we used the probability value (or suitability value in the case of the Swiss presence/background model) providing the maxTSS as a cutoff to binarize species predictions into presence/absence maps.

### Swiss model performances in relation with species' biological traits

We tried to explain the performance differences between single species models with species characteristics such as the standard deviation of the altitudinal amplitude (i.e. difference between highest and lowest altitude where the species were recorded in Switzerland), the influence of the three different nesting behavior (species with coprophagous larvae: non-nesters and paracoprids; species with predaceous larvae: Hydrophilidae) and the body size of the beetles (according to the specialized literature; Baraud 1992; Allemand and Leblanc 2004; Vorst 2009; Klausnitzer 2011) on the quality of the Swiss models (max TSS). Using the package lme4 (Bates et al. 2015), we ran a Generalized Linear Model (GLM) with these three species characteristics as explanatory variables and the median maxTSS of the final models of each species as response variable.

### Species richness of coprophagous beetle communities

We summed all species' maps of environmental suitability (as proposed by Dubuis et al. (2011)) resulting of our Swiss models ESMs to get a map of the index of cumulated suitability reflecting the species richness in each pixel (25 meters resolution) of the study area. Because these models were based on presence-pseudoabsence, the predictions are not true probabilities (Guillera-Arroita et al. 2015) and accordingly their sum is not a true estimate of species richness but rather an index of cumulated suitability of coprophagous beetles that can reflect on the variations of species richness. We also summed the environmental suitability of the species with the same nesting behavior (non-nesters, paracoprids or non-nesting Hydrophilidae) to obtain predictions of the cumulative index per group.

## Results

### Coprophagous beetles inventory

During our sampling, we recorded 1120 occurrences of coprophagous beetles belonging to 48 species. We pooled the data of *A. immaturus* (20 occurrences) and *A. obscurus* (38 occurrences) together (see remark in the material and methods section) and considered for the statistical analyses 47 species (Table 2, Suppl. material 3: Fig. S3) belonging respectively to Scarabaeidae (21 Aphodiinae and 8 Scarabaeinae), Geotrupidae (4 species) and Hydrophilidae (14 species).

### Swiss models

Only one of the 47 species that we recorded in the study region had less than 15 occurrences at the Swiss level (*Planolinoides borealis*; Table 2) and was therefore not used to build ESMs. For the 46 other species, the models calibrated at the Swiss level ranged from a median maxTSS going from 0.27 (*Anoplotrupes stercorosus*) to 0.93 (*Ammoecius brevis*) (Fig. 2A). All specific maps are provided in the supplementary material (Suppl. material 1: Fig. S1). At the Swiss level the variables had not high differences in their contribution but it is still possible to observe that the most important were the mean temperature of the warmest quarter of year (Bio10), the proportion of rock and bare soils (Rock) the precipitation during the driest quarter of the year (Bio17) (Fig. 3A) and the forest edges proportion. The proportion of human infrastructure, wet habitats and cultivation had the lowest contribution (Fig. 3A).

### Regional models

On the 47 species recorded in the study area, 23 had enough occurrences (at least 15) to build ESMs. The regional models showed a high heterogeneity in their performances going from a median maxTSS of 0.40 (*Acrossus rufipes*) and 0.85 (*Parammoecius gibbus*) (Fig. 2B). All the maps are presented in the supplementary material (Suppl. material 2: Fig. S2). In the regional models, the variable with the highest contribution were the proportion of rock and bare soil cover (Rock), the carbon isotope composition of the soil ($\partial^{13}C$), the mean temperature of the warmest quarter of year (Bio10) and the forest edges proportion (Fig. 3B), while the cultivation proportion and the human infrastructure had the lowest contribution (Fig. 3B).

### Swiss model performances in relation with species' biological traits

We tested the influence of species' biological traits on the performances of the Swiss models. The altitudinal range of the species had a significant influence on the median maxTSS in the models (GLM result: p-value = $1.78\times10^{-10}$, t-value = -8.42; Fig. 4A). Neither the nesting strategies (GLM result: p-values = 0.94 and 0.25, t-values = 0.08 and -1.16; Fig. 4B), nor the mean size of the species had an influence on the performance of the models (GLM result: p-value = 0.81, t-value = 0.24; Fig. 4C). There was no significant interaction between variables.

### Species richness of coprophagous beetle communities

The sum of the environmental suitability resulting of our Swiss models predicted a global decrease in species richness from the low to the high altitudes (min = 11.45,

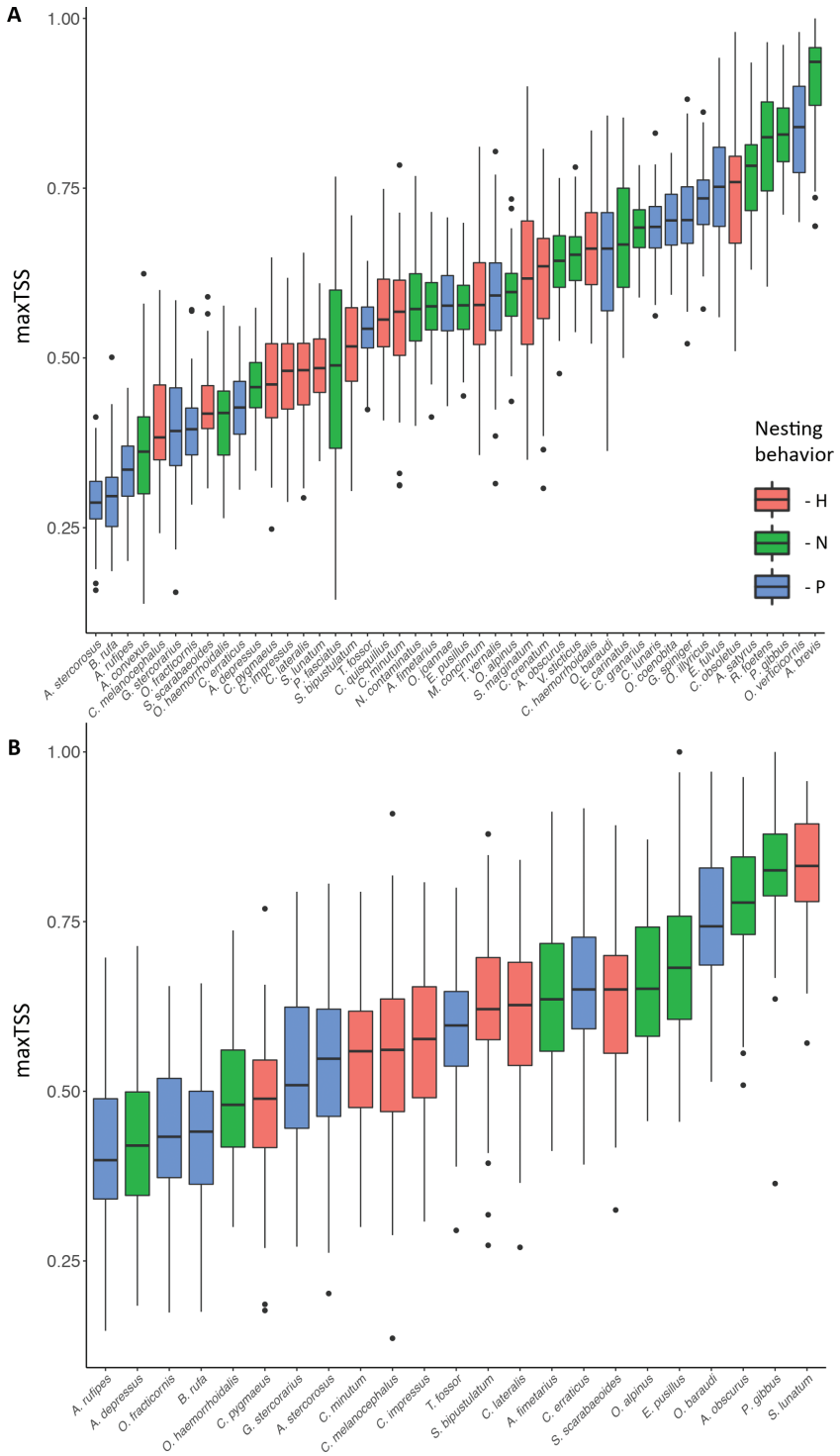


**Figure 2.** Results of the Ensemble of Small Models (ESMs) ordered by increasing median of max True Skills Statistics (maxTSS), calibrated (**A**) at the Swiss scale (46 species treated) and (**B**) at the Regional scale (23 species treated). The boxplots are colored according to the nesting behavior of the species (N – Non-nesters, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]). All the model projections are presented in Suppl. material 1: Fig. S1 and all the species are illustrated in Suppl. material 3: Fig. S3.

max = 24.59 species) (Fig. 5A). This trend was particularly sharp for the paracoprids (min =3.07, max = 9.28) (Fig. 5B) but much less for the non-nesters (min = 4.62, max = 7.18) (Fig. 5C). Hydrophilidae also showed a strong loss of species diversity with the increasing altitude (min = 2.51, max = 8.52 species). (Fig. 5D).

## Discussion

We investigated the influence of various factors on the distributions of single coprophagous beetle species in the Western Swiss Alps using correlative species distribution modeling (SDM) approaches based on quantifying

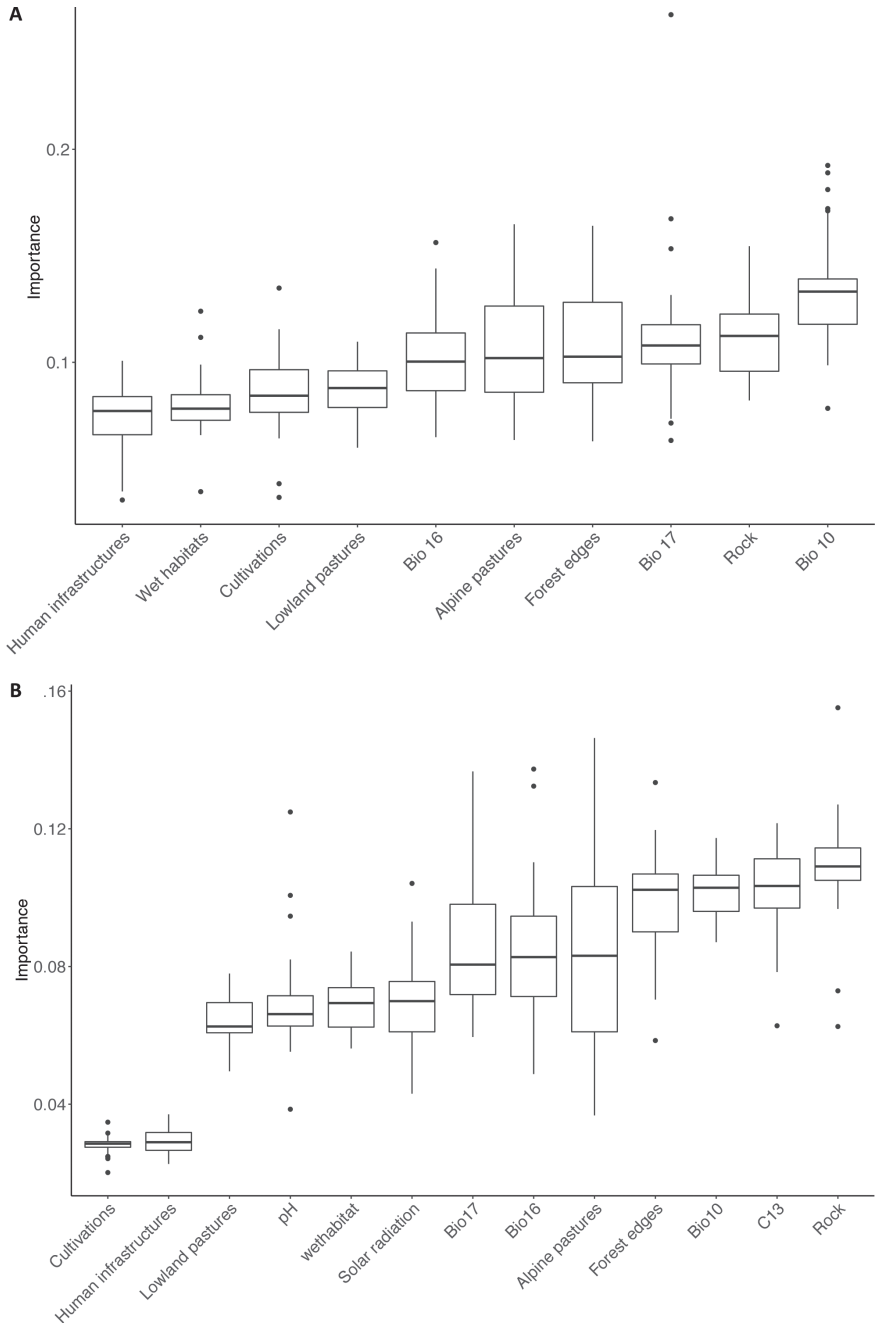


**Figure 3.** Relative importance of the variables used as predictors in the Ensemble of Small Models (ESMs) presented in increasing order of importance, for (**A**) the 46 models calibrated at the Swiss scale and (**B**) the 23 models calibrated at the Regional scale. For the full descriptions of the predictors, see Table 1.

habitat suitability (Guisan et al. 2017). Given the high number of species with small number of occurrences, we used a particular approach recently developed for small sample sizes: ensemble of small models (ESMs; Lomba et al. 2010; Breiner et al. 2015, 2018). In all our models, the predictors with the greatest importance included climatic variables (Fig. 3), like in many SDM studies (Austin and Van Niel 2011; Pradervand et al. 2013; Mod et al. 2016; Scherrer et al. 2019). Interestingly, in both models (i.e. Swiss, Fig. 3A and Regional, Fig. 3B) the proportion of rock and bare soil cover (Rock) was an important predictor. In the study region as in the rest of the Alps, the altitude is correlated with the proportion of rocky surfaces, which could act as a confounding factor. As specialized species are better modeled than the widespread species covering a large elevation range (Guisan and Hofer 2003), the importance of the rocky surface variable in the models might be artificially high. It is also possible that more species are present in pastures of high ecological value (i.e. with a high overall biodiversity) including grasslands with discontinuous vegetation cover (Delarze et al. 2015). Furthermore, the superficial rock cover proportion could be an indirect way of quantifying the heterogeneity of the landscape, such as the proportion

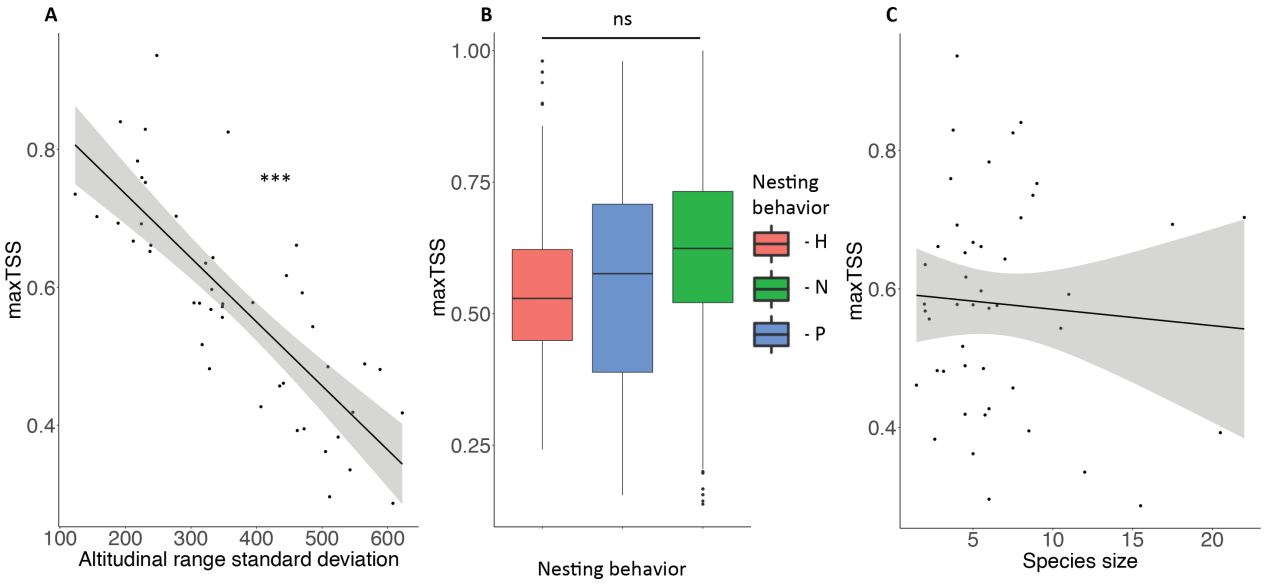


**Figure 4.** Model performances in relation to species characteristics. The median max True Skills Statistics (maxTSS) of each species are plotted (**A**) against the altitudinal amplitude standard deviation of the species in Switzerland; (**B**) according to the nesting behavior of the species (N – Non-nesters, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]); (**C**) against the species size. The grey area represents the confidence interval 95%.

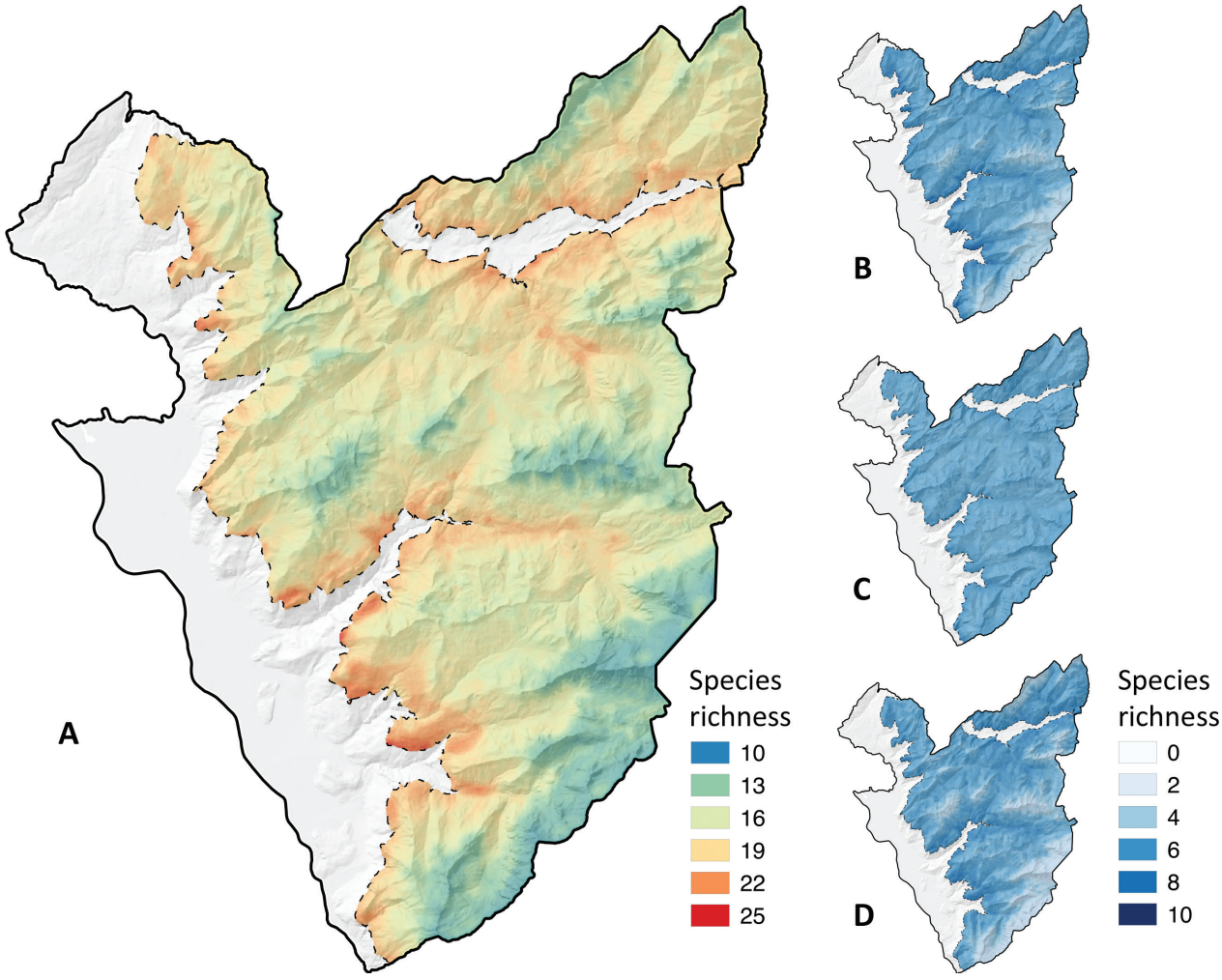


**Figure 5.** Expected species richness, based on the index of cumulated species suitability, in the Swiss Western Alps study area starting at 1000 meters above sea level according to the stacking of regional models considering (**A**) all species, (**B**) the Paracoprids, (**C**) the Non-nesters and (**D**) the Hydrophilidae.

of forest edges, which was also an important predictor (Fig. 3) in our model. Indeed, Negro et al. (2011) suggested that habitat heterogeneity, especially the presence of natural forested areas next to pastures, plays an important role in increasing coprophagous beetle species richness. In contrast, some variables had little influence in our models. These were often land cover or land use variables spatially restricted in Switzerland (e.g. wet habitats) or in the study area (e.g. cultivations) but it is difficult to know if it is the low frequency of these variables over the landscape that induces their smaller influence in the models or if they really do not have an influence on species distributions.

Our ESMs had very variable predictive performances as measured by the maximized TSS (see Jimenez-Valverde 2014; Guisan et al. 2017), with values ranging from 0.27 to 0.93 for the Swiss models (Fig. 2A) and from 0.40 to 0.85 for the regional models (Fig. 2B). Note that the use of threshold independent discrimination metrics, such as the maxTSS (or the classical AUC) for the evaluation of presence/absence models (i.e. our Regional models) may be problematic because of a non-linear asymptotic relationship between discrimination metrics and true model accuracy, and that it might be accordingly difficult to distinguish between models with high AUC value (Jimenez-Valverde 2014). Nonetheless, maxTSS from models calibrated in the same area can still correctly inform on the ranking of accuracy between models (e.g. between poor, useful or good models), except among very high TSS values (i.e. calling for caution in the ranking among good models). We found that ubiquitous species present over a wide altitudinal range had weaker models compared with specialized species occurring in narrower altitudinal amplitude (Fig. 4A). Our results are in line with those of Guisan and Hofer (2003) and Grenouillet et al. (2011), who showed that the distributions of generalist reptile and fish species, respectively, are more difficult to predict, and with those of Tessarolo et al. (2021), who found that niche marginality has a major influence on the models' quality for dung beetles in Spain. On the other hand, we found no influence of the nesting behavior (Fig. 4B) nor the size of the species (Fig. 4C) on the maxTSS of the models, meaning that these biological traits seem not relevant to explain models' quality.

When looking at the expected species richness of the coprophagous beetle communities based on the stacking of single species environmental suitability values over the study region, the global trend shows a diminution of the number of species with increasing altitude (Fig. 5). This result was also observed in other taxa in the same region (Dubuis et al. 2011 for plants; Pradervand et al. 2013 for orthopterans; Reymond et al. 2013 for ants; Pellissier et al. 2013 for butterflies; Scherrer et al. 2019 for bats; Seppey et al. 2020 for protists), for which the climatic predictors, especially temperature, were also of great importance. However, it is important to notice that for coprophagous beetles, the decrease in species richness depends on the nesting behavior: the paracoprids (Fig. 5B) and the Hydrophilidae (Fig. 5D) show a steep decrease with increasing elevations, while the non-nesters (Fig. 5C) show a gentler one. This latter group forms the biggest part of the coprophagous beetle diversity at high altitude where almost no paracoprids and Hydrophilidae are found (Fig. 5B, C). This result, consistent with those of Lobo et al. (2007) is explained by the ecology of non-nester beetles, which are more tolerant to cold and are outcompeted by paracoprids in thermophilous places (Hanski 2016).

Many of the studies focusing on the coprophagous fauna use dung-baited trap to get an exhaustive species list in addition to data on the phenology and abundance (see for example Lumaret 1978). No large-scale trapping campaign was performed in Switzerland where the ecology of coprophagous beetles is still poorly studied. As a first step in a better knowledge of these taxa and since we were not interested in phenological or abundance data, we made the choice to perform an active sampling, less constraining logistically (transport of traps and dung), more efficient to visit a large number of sites (what we needed to build models) and allowing to select the individuals to collect sparing identification time. Moreover, the active search has been shown to be a very efficient way to get species inventories for beetles traditionally caught with traps (Chittaro and Marggi 2016). Our active field sampling designed in a random stratified manner permitted to be representative of the various environment of the study area and likely allowed us to find most of the coprophagous beetle species known from the study area (*Agolius abdominalis* and *Neagolius montanus* only were missing). Nevertheless, it is possible that we missed the occurrence of some species with low detectability in some plots. Future studies aim to correct for this bias, for example by implementing methods to estimate the completeness of plot inventory, or combining models of $\alpha$- and $\beta$-diversity to predict the spatial community composition in a region, and areas of incompleteness within it (Mokany et al. 2011).

From a faunistical point of view, our study brings valuable new records for beetles, an under-sampled taxon in comparison to other insect groups such as orthopterans, butterflies, and even more vertebrates (Troudet et al. 2017), with the perspective to improve predictions of global change impact on biodiversity in mountain areas (Guisan et al. 2019) and better support conservation decisions (Guisan et al. 2013). Indeed, the data sampled in our study represents now 17.9% (N=1120, Swiss database info fauna-CSCF) of all precise occurrences existing for these 47 coprophagous beetle species in Switzerland (N=6258). An important part (42%) of all the coprophagous beetle species of Switzerland is found in the Vaud Alps (info fauna-CSCF), reinforcing the status of biodiversity hotspot of this study region in the European Alps (Lassen and Savoia 2005). Future studies should investigate more of such under-sampled taxa, like other invertebrate groups, to allow more robust comparative studies and produce better global biodiversity assessments within a same study area (Mod et al. 2020).

## Acknowledgements

We particularly thank: Yannick Chittaro and Andreas Sanchez for their advises in entomology, for providing us the Swiss occurrences dataset and for their comments on the manuscript; Tatiana Zingre for her help during the field sampling; Paul Béziers, Robin Séchaud and the reviewers for their constructive remarks on the manuscript, which permitted to improve it substantially. Finally, we thank the researchers/curators of the Natural History Museum of Geneva, Giulio Cuccodoro, Bernard Landry and Emmanuel Toussaint for providing the photographic material. AG received support from the Federal Office of the Environment through the ValPar.CH project.

## References

Allemand R, Leblanc P (2004) Identification des *Sphaeridium* de France (Coleoptera Hydrophilidae). L'Entomologiste 60: 125–131.

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Alves Da Mata R, Tidon R, De Oliveira G, Vilela B, Felizola Diniz-Filho JA, Rangel TF, Terribile CL (2017) Stacked species distribution and macroecological models provide incongruent predictions of species richness for Drosophilidae in the Brazilian savanna. Insect Conservation and Diversity 10: 415–423. https://doi.org/10.1111/icad.12240

Austin MP, Van Niel KP (2011) Improving species distribution models for climate change studies: variable selection and scale. Journal of Biogeography 38(1): 1–8. https://doi.org/10.1111/j.1365-2699.2010.02416.x

Baraud J (1992) Coléoptères Scarabaeoidea d'Europe. Fédération Française des Sociétés de Sciences naturelles & Société Linnéenne de Lyon, Lyon, 856 pp. https://doi.org/10.3406/linly.1992.11007

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: How, where and how many?: How to use pseudo-absences in niche modelling? Methods in Ecology and Evolution 3(2): 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01

Bellamy C, Scott C, Altringham J (2013) Multiscale, presence-only habitat suitability models: Fine-resolution maps for eight bat species. Journal of Applied Ecology 50(4): 892–901. https://doi.org/10.1111/1365-2664.12117

Beynon SA, Peck M, Mann DJ, Lewis OT (2012) Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning. Agriculture, Ecosystems & Environment 162: 36–44. https://doi.org/10.1016/j.agee.2012.08.010

Beynon SA, Wainwright WA, Christie M (2015) The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry: Economic benefits of dung beetles. Ecological Entomology 40: 124–135. https://doi.org/10.1111/een.12240

Bird M, Derrien D, Zhou Y (2003) The effect of soil texture and roots on the stable isotope composition of soil organic matter. Australian Journal of Soil Research 41: 77–94. https://doi.org/10.1071/SR02044

Breiner FT, Guisan A, Bergamini A, Nobis MP (2015) Overcoming limitations of modelling rare species by using ensembles of small models. Methods in Ecology and Evolution 6(10): 1210–1218. https://doi.org/10.1111/2041-210X.12403

Breiner FT, Nobis MP, Bergamini A, Guisan A (2018) Optimizing ensembles of small models for predicting the distribution of species with few occurrences. Methods in Ecology and Evolution 9: 802–808. https://doi.org/10.1111/2041-210X.12957

Broennimann O (2018) CHclim25: A high spatial and temporal resolution climate dataset for Switzerland. Ecospat Laboratory, University of Lausanne Switzerland.

Buri A, Cianfrani C, Pinto-Figueroa E, Yashiro E, Spangenberg JE, Adatte T, Verrecchia E, Guisan A, Pradervand J-N (2017) Soil factors improve predictions of plant species distribution in a mountain environment. Progress in Physical Geography: Earth and Environment 41(6): 703–722. https://doi.org/10.1177/0309133317738162

Buri A, Grand S, Yashiro E, Adatte T, Spangenberg JE, Pinto-Figueroa E, Verrecchia E, Guisan A (2020) What are the most crucial soil variables for predicting the distribution of mountain plant species? A comprehensive study in the Swiss Alps. Journal of Biogeography 47(5): 1143–1153. https://doi.org/10.1111/jbi.13803

Chefaoui RM, Hortal J, Lobo JM (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: A case study of Iberian *Copris* species. Biological Conservation 122(2): 327–338. https://doi.org/10.1016/j.biocon.2004.08.005

Chevalier M, Broennimann O, Cornuault J, Guisan A (2021) Data integration methods to account for spatial niche truncation effects in regional projections of species distribution. Ecological Applications 31(7): e02427. https://doi.org/10.1002/eap.2427

Chittaro Y, Marggi W (2016) Bilan d'une année de recherches ciblées de Carabiques en Suisse: découverte de *Notiophilus quadripunctatus* Dejean, 1826) et autres captures remarquables (Coleoptera, Carabidae). Entomologische Blätter und Coleoptera 112(1): 107–120.

Colwell RK, Rangel TF (2009) Hutchinson's duality: The once and future niche. Proceedings of the National Academy of Sciences 106(suppl. 2): 19651–19658. https://doi.org/10.1073/pnas.0901650106

Cosandey V, Chittaro Y, Sanchez A (2017) Liste commentée des Scarabaeoidea (Coleoptera) de Suisse. Alpine Entomology 1: 57–90. https://doi.org/10.3897/alpento.1.21179

D'Amen M, Pradervand J-N, Guisan A (2015) Predicting richness and composition in mountain insect communities at high resolution: A new test of the SESAM framework: Community-level models of insects. Global Ecology and Biogeography 24(12): 1443–1453. https://doi.org/10.1111/geb.12357

Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) Guide des milieux naturels de Suisse: Écologie, menaces, espèces caractéristiques. Rossolis, Bussigny, 440 pp.

Descombes P, Pradervand J-N, Golay J, Guisan A, Pellissier L (2016) Simulated shifts in trophic niche breadth modulate range loss of alpine butterflies under climate change. Ecography 39(8): 796–804. https://doi.org/10.1111/ecog.01557

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan, A (2017) ecospat: An R pack-

age to support spatial analyses and modeling of species niches and distributions. Ecography 40(6): 774–787. https://doi.org/10.1111/ecog.02671

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitã PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1): 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dubuis A, Pottier J, Rion V, Pellissier L, Theurillat JP, Guisan A (2011) Predicting spatial patterns of plant species richness: A comparison of direct macroecological and species stacking modelling approaches: Predicting plant species richness. Diversity and Distributions 17(6): 1122–1131. https://doi.org/10.1111/j.1472-4642.2011.00792.x

El-Gabbas A, Dormann CF (2018) Wrong, but useful: Regional species distribution models may not be improved by range-wide data under biased sampling. Ecology and Evolution 8: 2196–2206. https://doi.org/10.1002/ece3.3834

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loisells BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcC, Peterson AT, Philips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Sobéron J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2): 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Errouissi F, Jay-robert P, Lumaret J-P, Piau O (2004) Composition and Structure of Dung Beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) Assemblages in Mountain Grasslands of the Southern Alps. Annals of the Entomological Society of America 97(4): 701–709. https://doi.org/10.1603/0013-8746(2004)097[0701:CASODB]2.0.CO;2

Fikáček M (2006) Taxonomic status of *Cercyon alpinus*, *C. exorabilis*, *C. strandi* and *C. tatricus* and notes on their biology (Coleoptera: Hydrophilidae: Sphaeridiinae). Annalen Des Naturhistorische Museums in Wien 107(B): 145–164.

Fincher GT (1981) The potential value of dung beetles in pasture ecosystems [Texas]. Journal of the Georgia Entomological Society 16: 316–333.

Finn JA, Giller PS (2000) Patch size and colonisation patterns: An experimental analysis using north temperate coprophagous dung beetles. Ecography 23(3): 315–327. https://doi.org/10.1111/j.1600-0587.2000.tb00287.x

Franklin J (2010) Mapping species distributions: Spatial inference and prediction. Cambridge University Press, Cambridge, 320 pp. https://doi.org/10.1017/CBO9780511810602

Gittings T (1994) The community ecology of *Aphodius* dung beetles. PhD thesis, Cork, Ireland: National Univesity of Ireland.

Grenouillet G, Buisson L, Casajus N, Lek S (2011) Ensemble modelling of species distribution: The effects of geographical and environmental ranges. Ecography 34(1): 9–17. https://doi.org/10.1111/j.1600-0587.2010.06152.x

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, McCarthy MA, Tingley R, Wintle BA (2015) Is my species distribution model fit for purpose? Matching data and models to applications: Matching distribution models to applications. Global Ecology and Biogeography 24(3): 276–292. https://doi.org/10.1111/geb.12268

Guisan A, Broennimann O, Buri A, Cianfrani C, D'Amen M, Di Cola V, Fernandes R, Gray S, Mateo RG, Pinto E, Pradervand J-N, Scherrer D, von Däniken I, Yashiro E, Vittoz P (2019) Climate change impacts on mountain biodiversity. In: Lovejoy TE, Hannah L (Eds) Biodiversity and Climate Change: Transforming the Biosphere. Yale University Press, Yale, 221–233. https://doi.org/10.2307/j.ctv8jnzw1.29

Guisan A, Hofer U (2003) Predicting reptile distributions at the mesoscale: relation to climate and topography: Predicting reptile distributions at the mesoscale. Journal of Biogeography 30(8): 1233–1243. https://doi.org/10.1046/j.1365-2699.2003.00914.x

Guisan A, Thuiller W (2005) Predicting species distribution: Offering more than simple habitat models. Ecology Letters 8(9): 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan A, Thuiller W, Zimmermann NE (2017) Habitat suitability and distribution models with applications in R. Cambridge University Press, Cambridge, 462 pp. https://doi.org/10.1017/9781139028271

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. Ecology Letters 16(12): 1424–1435. https://doi.org/10.1111/ele.12189

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecological Modelling 135(2–3): 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hannemann H, Willis KJ, Macias-Fauria M (2016) The devil is in the detail: Unstable response functions in species distribution models challenge bulk ensemble modelling: Unstable response functions in SDMs. Global Ecology and Biogeography 25(1): 26–35. https://doi.org/10.1111/geb.12381

Hanski I, Koskela H (1977) Niche relations among dung-inhabiting beetles. Oecologia 28(3): 203–231. https://doi.org/10.1007/BF00751601

Hanski I, Cambefort Y (2016) Dung beetle ecology. Princeton University Press, Princeton, 514 pp.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25(15): 1965–1978. https://doi.org/10.1002/joc.1276

Hirzel A, Guisan A (2002) Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling 157(2–3): 331–341. https://doi.org/10.1016/S0304-3800(02)00203-X

Hochkirch A, Samways MJ, Gerlach J, Böhm M, Williams P, Cardoso P, Cumberlidge N, Stephenson PJ, Seddon MB, Clausnitzer V, Borges PAV, Mueller GM, Pearce-Kelly P, Raimondo DC, Danielczak A, Dijkstra KB (2021) A strategy for the next decade to address data deficiency in neglected biodiversity. Conservation Biology 35(2): 502–509. https://doi.org/10.1111/cobi.13589

Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2015) Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 46(1): 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Hortal J, Lobo JM, Martín-Piera F (2001) Forecasting insect species richness scores in poorly surveyed territories: The case of the Portuguese dung beetles (Col. Scarabaeinae). Biodiversity and Conservation 10: 1343–1367. https://doi.org/10.1023/A:1016624500023

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7(12): 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Jiménez-Valverde A (2014) Threshold-dependence as a desirable attribute for discrimination assessment: implications for the evaluation of species distribution models. Biodiversity and Conservation 23(2): 369–385. https://doi.org/10.1007/s10531-013-0606-1

Klausnitzer B (2011) Die Käfer Mitteleuropas, Band 3. Adephaga II, Palpicornia. Goecke & Evers, Krefeld, 367 pp.

Klemperer HG (1980) Kleptoparasitic behavior of *Aphodius rufipes* (L.) larvae in nests of *Geotrupes spiniger* Marsh. Ecological Entomology 5: 143–151. https://doi.org/10.1111/j.1365-2311.1980.tb01135.x

Von Däniken I, Guisan A, Lane S (2014) RechAlp.vd: Une nouvelle plateforme UNIL de support pour la recherche transdisciplinaire dans les Alpes vaudoises. Bulletin de la Société Vaudoise des Sciences Naturelles 94(2): 175–178.

Lassen P, Savoia S (2005) Ecoregion Conservation Plan for the Alps. WWF European Alpine Programme 1(62).

Lobo JM, Jiménez-Valverde A, Hortal J (2010) The uncertain nature of absences and their importance in species distribution modelling. Ecography 33(1): 103–114. https://doi.org/10.1111/j.1600-0587.2009.06039.x

Lobo JM, Martin-Piera F (2002) Searching for a Predictive Model for Species Richness of Iberian Dung Beetle Based on Spatial and Environmental Variables. Conservation Biology 16(1): 158–173. https://doi.org/10.1046/j.1523-1739.2002.00211.x

Lomba A, Pellissier L, Randin C, Vicente J, Moreira F, Honrado J, Guisan A (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. Biological Conservation 143(11): 2647–2657. https://doi.org/10.1016/j.biocon.2010.07.007

Lomolino MV (2001) The species-area relationship: New challenges for an old pattern. Progress in Physical Geography 25(1): 1–21. https://doi.org/10.1191/030913301666288491

Lumaret J-P (1978) Biogéographie et écologie des Scarabaéides coprophages du sud de la France. Vie et Milieu 18(1): 1–34.

Lumaret J-P, Jay-Robert P (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables: Dung beetle species richness variation. Global Ecology and Biogeography 11(4): 265–277. https://doi.org/10.1046/j.1466-822X.2002.00291.x

Lumaret J-P, Stiernet N (1984) Contribution à l'étude de la faune des Alpes suisses. Description de la larve d'*Aphodius* (*Neagolius*) *abdominalis* Bonelli, 1812 (Coleoptera, Aphodiidae). Bulletin de la Société Enomologique Suisse. 57: 193–228.

Lumaret J-P, Stiernet N (1990) Inventaire et distribution des coléoptères Scarabaéides coprophages dans le massif de la Vanoise. Travaux Scientifiques Du Parc National de La Vanoise 17: 193–228.

Mateo RG, Aroca-Fernández MJ, Gastón A, Gómez-Rubio V, Saura S, García-Viñas JI (2019) Looking for an optimal hierarchical approach for ecologically meaningful niche modelling. Ecological Modelling 409: e108735. https://doi.org/10.1016/j.ecolmodel.2019.108735

Mod HK, Scherrer D, Di Cola V, Broennimann O, Blandenier Q, Breiner FT, Buri A, Goudet J, Guex N, Lara E, Mitchel EAD, Niculita-Hirzel H, Pagni M, Pellissier L, Pinto-Figerosa E, Sanders IR, Schmidt BR, Seppey CVW, Singer D, Ursenbacher S, Yashiro E, van der Meer JR, Guisan A (2020) Greater topoclimatic control of above- versus below-ground communities. Global Change Biology 26(12): 6715–6728. https://doi.org/10.1111/gcb.15330

Mod HK, Scherrer D, Luoto M, Guisan A (2016) What we use is not what we know: Environmental predictors in plant distribution models. Journal of Vegetation Science 27(6): 1308–1322. https://doi.org/10.1111/jvs.12444

Mokany K, Harwood TD, Overton, JM, Barker GM, Ferrier S (2011) Combining α - and β -diversity models to fill gaps in our knowledge of biodiversity: Filling gaps in biodiversity knowledge. Ecology Letters 14(10): 1043–1051. https://doi.org/10.1111/j.1461-0248.2011.01675.x

Negro M, Palestrini C, Giraudo MT, Rolando A (2011) The effect of local environmental heterogeneity on species diversity of alpine dung beetles (Coleoptera: Scarabaeidae). European Journal of Entomology 108(1): 91–98. https://doi.org/10.14411/eje.2011.012

Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141(6): 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: A hierarchical integration of climate and land-cover data. Ecography 27(3): 285–298. https://doi.org/10.1111/j.0906-7590.2004.03740.x

Pellissier L, Alvarez N, Espíndola A, Pottier J, Dubuis A, Pradervand J-N, Guisan A (2013) Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in the western Swiss Alps. Ecography 36(5): 541–550. https://doi.org/10.1111/j.1600-0587.2012.07716.x

Pellissier L, Pradervand J-N, Pottier J, Dubuis A, Maiorano L, Guisan A (2012) Climate-based empirical models show biased predictions of butterfly communities along environmental gradients. Ecography 35(8): 684–692. https://doi.org/10.1111/j.1600-0587.2011.07047.x

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton, 328 pp. https://doi.org/10.23943/princeton/9780691136868.003.0003

Pradervand J-N, Dubuis A, Reymond A, Gelin A, Guisan A (2013) Quels facteurs influencent la richesse en orthoptères des Préalpes vaudoises? Bulletin de la Société vaudoise des Sciences naturelles 93(4): 155–173.

Pradervand J-N, Pellissier L, Randin CF, Guisan A (2014) Functional homogenization of bumblebee communities in alpine landscapes under projected climate change. Climate Change Responses 1(1): 1. https://doi.org/10.1186/s40665-014-0001-5

Pulliam HR (2000) On the relationship between niche and distribution. Ecology Letters 3(4): 349–361. https://doi.org/10.1046/j.1461-0248.2000.00143.x

Reymond A, Purcell J, Cherix D, Guisan A, Pellissier L (2013) Functional diversity decreases with temperature in high elevation ant fauna: Functional diversity in high elevation ant. Ecological Entomology 38(4): 364–373. https://doi.org/10.1111/een.12027

Reynard E, Otero I, Clivaz M (2020) The Interdisciplinary Centre for Mountain Research (CIRM): Fostering Transdisciplinarity for Transformation Research in Mountains. Mountain Research and Development 40(2): 1–3. https://doi.org/10.1659/MRD-JOURNAL-D-20-00051.1

Rojewski C (1983) Observations on the nesting behavior of *Aphodius erraticus* (L.) (Coleopera, Scarabaeidae). Bulletin Entomologique de Pologne 53: 271–279.

Scherrer D, Christe P, Guisan A (2019) Modelling bat distributions and diversity in a mountain landscape using focal predictors in ensemble

of small models. Diversity and Distributions 25(5): 770–782. https://doi.org/10.1111/ddi.12893

Seppey CVW, Broennimann O, Buri A, Yashiro E, Pinto-Figuerosa E, Singer D, Blandenier Q, Mitchell EAD, Niculita-Hirzel H, Guisan A, Lara E (2020) Soil protist diversity in the Swiss western Alps is better predicted by topo-climatic than by edaphic variables. Journal of Biogeography 47: 866–878. https://doi.org/10.1111/jbi.13755

Tessarolo G, Lobo JM, Rangel TF, Hortal J (2021) High uncertainty in the effects of data characteristics on the performance of species distribution models. Ecological Indicators 121: 107147. https://doi.org/10.1016/j.ecolind.2020.107147

Thuiller W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental range of data to project current and future species distributions. Ecography 27(2): 165–172. https://doi.org/10.1111/j.0906-7590.2004.03673.x

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32(3): 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tonelli M (2021) Some considerations on the terminology applied to dung beetle functional groups. Ecological Entomology 46: 772–776. https://doi.org/10.1111/een.13017

Vorst O (2009) *Cercyon castaneipennis* sp. n., an overlooked species from Europe (Coleoptera: Hydrophilidae). Zootaxa 2054: 59–68. https://doi.org/10.11646/zootaxa.2054.1.4

Warton IW, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 91(1): 3–10. https://doi.org/10.1890/10-0340.1

Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. Journal of Vegetation Science 10(4): 469–482. https://doi.org/10.2307/3237182

Zunino M, Barbero E (1990) Food relocation and the reproductive biology of *Aphodius fossor* (L.) (Coleoptera, Scarabaeidae, Aphodiinae). Ethology Ecology and Evolution 2: 334. https://doi.org/10.1080/08927014.1990.9525480

# Supplementary material 1

## Figure S1

Authors: Vivien Cosandey, Olivier Broennimann, Antoine Guisan

Data type: pdf file

Explanation note: Map of all the 46 species for which a model was run at the Swiss scale. The environmental suitability of each species is projected in the study area above 1000 meters above sea level (represented by a dashed line).



Link: https://doi.org/10.3897/alpento.6.83730.suppl1

# Supplementary material 2

## Figure S2

Authors: Vivien Cosandey, Olivier Broennimann, Antoine Guisan

Data type: pdf file

Explanation note: Map of the 23 species for which a model was run at the Regional scale. The environmental suitability of each species is projected in the study area above 1000 meters above sea level (represented by a dashed line).



Link: https://doi.org/10.3897/alpento.6.83730.suppl2

# Supplementary material 3

## Figure S3

Authors: Vivien Cosandey, Olivier Broennimann, Antoine Guisan

Data type: pdf file

Explanation note: Illustration of all the coprophagous beetle species found in the study region. Illustration: Vivien Cosandey.



Link: https://doi.org/10.3897/alpento.6.83730.suppl3