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Modelling the distribution of coprophagous beetle species in the Western Swiss Alps

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par

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Abstract

Dung beetles depend on mammal droppings as unique trophic resource and are thus considered key ecosystem services providers. Since our knowledge of dung beetles distribution and ecology is still limited, we chose to investigate it with Species Distribution Modeling (SDM), which allows quantifying the species-environment interactions (i.e. their niche) and predict the species' presence probability. We sampled coprophagous beetles in the Vaud Alps and calibrated for each species a regional SDM with our data and another one with all occurrences for Switzerland. In both cases, the best predictors were temperature and rock cover proportion, while a soil characteristic was important in the regional models and precipitations in the Swiss models. The model performances were influenced by the altitudinal range where the species occur but not by other species characteristics like their size or nesting behavior (laying eggs inside or below the excrements). We also showed that species richness decreased with altitude but that the species nesting in the dung represented a higher proportion of dung beetles at high altitude. Overall this study brought new data and insights for an ecologically important group of species, which is still poorly studied in Switzerland.

Résumé

Les bousiers dépendent exclusivement des excréments de mammifères pour se nourrir et fournissent donc des services écosystémiques essentiels. La connaissance de la répartition et de l'écologie des bousiers étant encore limitée, nous avons choisi de nous y intéresser en utilisant des Modèles de Distribution d'Espèces (Species Distribution Models - SDM) qui permettent de quantifier les besoins environnementaux des espèces (leurs niches) et de prédire leur répartition géographique. Nous avons échantillonné des bousiers dans les Alpes vaudoises et avons calibré pour chaque espèce un SDM régional avec nos données et un second en utilisant toutes les données disponibles au niveau suisse. Dans les deux modèles, les meilleures prédicteurs incluaient la température et la proportion de couverture rocheuse, tandis qu'une des caractéristiques du sol ($\partial^{13}C$) et les précipitations étaient importantes respectivement pour les modèles des Alpes vaudoises et les modèles suisses. Les performances des modèles étaient influencées par l'amplitude altitudinale occupée par les espèces alors que d'autres caractéristiques spécifiques telles que la taille ou le mode de nidification (ponte des œufs dans les excréments ou en dessous) n'avaient aucun effet. Nous démontrons également que la richesse spécifique des coléoptères coprophages décroit avec l'altitude mais que les espèces pondant leurs œufs dans les excréments étaient proportionnellement plus nombreuses en altitude. Dans cette étude, nous apportons de nouvelles données et connaissance écologiques sur des taxa peu étudiés en Suisse bien qu'écologiquement important.

Keywords
Dung beetles, Species distribution modeling, 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 species have coprophagous adult and predaceous larvae, which are chasing fly larvae from dung patches (Hydrophilidae, Sphaeridinae), while other have coprophagous adults and larvae. In this latter case, some species lay their eggs directly in the dung (endocoprids: 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) to avoid the harsh intra- and inter-specific competition to exploit dung patches before they dry (Hanski, 2016). By feeding and burying excrements, dung beetles are essential for dung decomposition (Gittings et al., 1994) and avoid the accumulation of excrements. Considered as key “Ecosystem Service Providers” (Nichols et al., 2008), dung beetles prevent the loss of 4.8% of the pasture surface per year in England (Beynon et al., 2012b) and allow sparing between 380 million (Losey and Vaughan 2006) and 2 billion (Fincher 1981) of USD in the USA and at least 367 million pounds in the UK (Beynon et al. 2015). In addition, dung beetles represent locally an important a part of the food for 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 dung 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) makes them an adequate group to study biogeography (Lumaret 1979) and animal communities (Hanski and Koskela, 1977). In Europe, the species assemblages of dung beetle and their relative abundance were already characterized (Lumaret and Stiernet, 1989; Errouissi et al., 2004; Lumaret and Stiernet, 1984; Negro, 2011) and the importance of climatic and edaphic factors have been shown by the study of the species richness of the dung beetles assemblages 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 individual dung 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 models to quantify the niche and derive geographic predictions, the Species Distribution Models (SDM; also called 'habitat suitability' or 'ecological niche' models; see Franklin, 2010; Peterson et al., 2011; Guisan et al., 2017), have brought powerful tools to better understand, compare and quantify the relationship between organism and environment (i.e. their environmental niche) but also to predict their distribution in space and time (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000), which can bring essential knowledge about the ecology of understudied taxonomical groups like arthropods (Hochkirch et al., 2020). SDMs have been used to study various groups of insects (Pradervand et al., 2014; D'Amen et al., 2015; Pellissier et al., 2012; Descombes et al., 2016; Mata et al., 2017) but there are few examples of individually modeled dung beetle species (Chefaoui et al., 2005; Lobo, 2010).

The aim of this study is to bring a better understanding of the factors influencing the distribution of individual dung beetle species in temperate mountain environments using an SDM approach, which was never done before to our knowledge. To do so, we sampled dung beetles throughout the Western Swiss Alps of the Vaud state in a random stratified manner with the aim of assessing which dung beetle species are present and obtaining a sufficient number of accurate species data to quantify species-environment relationships in SDMs. We additionally obtained all the occurrences available in Switzerland for the beetle families of interest (Hydrophilidae, Geotrupidae and Scarabaeidae) from the Swiss national database (infofauna-CSCF). This allowed us to compare fine-scale models calibrated in the study region using our precisely sampled data and larger-scale models calibrated at the Swiss level with the infofauna data. We expected the latter to reduce the risk, while calibrating the SDMs, of truncating the species' environmental niches, if not covering the complete extent of the species' geographic distributions and environmental requirements, as could expectedly be observed in the smaller extent (Chevalier et al., (In Review); 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). 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 the species are found, the nesting behavior and the species' size on the SDMs performances. We also interested us to the species richness of dung beetles patterns and the proportion of endocoprids compared to the other dung beetles throughout the study region.

Material & Methods

Study area

The study was conducted in Western Switzerland, in the alpine region of the Canton de Vaud, which goes from Vevey to Bex and to Rougemont (Figure 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 the slopes of the mountain basis are covered by forests, we only considered the upper part of the area, starting from an altitude of 1000 meters above sea level (Figure 1), where pastures grazed by domestic livestock (principally cows an sheeps) and alpine grasslands inhabited by big wild herbivores, like Alpine chamois (*Rupicapra rupicapra*), Alpine ibex (*Capra ibex*) and Red deers (*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)

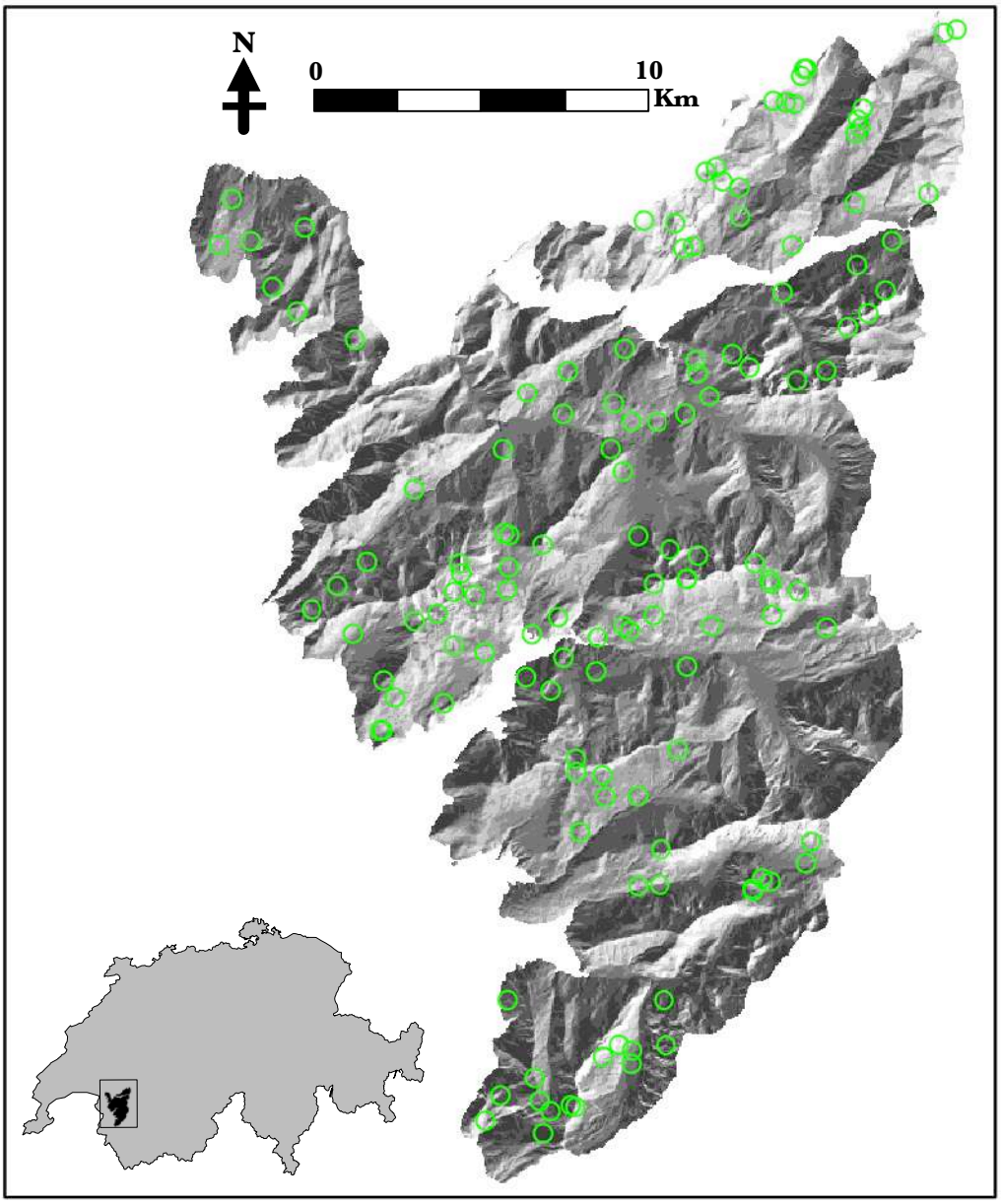

Figure 1. Map of the study region with the 132 sampling plots.

Sampling & beetle data acquisition

From the 31 of May to the 12 September 2020, we collected dung beetles in 132 sampling plots (Figure 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 until, 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 monitoring that represents the environment of the study area, we sampled a number of random points in each stratum proportional to its size. Since it is the first time such sampling is done for this beetle group, it should 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). The effective sampling plots were placed as close as possible to the point locations in the initial design, but their position was slightly shifted (maximum 200 meters, staying in the same strata) when the initial point was falling in places that had not been recently pastured by domestic or wild herbivores. In each sampling plot, 20 minutes were dedicated to the manual search of beetles inside of the dung using a little shovel with the goal to catch the maximum number of species. The sampled individuals were stored in Scheerpelz solution (55% water, 30% EtOH 96%, acetic acid 10%, acetic ether 5%). 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; Klausnitzer, 2011; Vorst, 2009). The species were recorded as present or absent in each sampling plot but the individuals were not counted because our sampling was not thought to reflect the abundance of these insects. We classified the Scarabaeidae and Geotrupidae species according to their nesting behaviour in 'endocoprids' (laying eggs in the dung), 'paracoprids' (laying eggs in dung buried under the excrement) with the help of the specialized literature (Hanski, 2016; Rojewski, 1983).

In addition to our sampling dataset, we received from the Swiss Center of Cartography of the Fauna (infofauna-CSCF) the complete dataset of occurrences (from museums and private collections) of coprophagous beetles for the whole territory of Switzerland. For the statistical analyses, we only kept the data that had a geographic accuracy of at least 250 meters.

Environmental data

To depict the species' niche and to fit our models, we used as predictors (see Table 1): (i) land-use variables originating either from the Swiss Federal Office of Statistics (2004) - alpine pastures, lowland pastures, cultivation, human 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 movement of the dung beetles and 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 models at the Swiss scale (Table 1).

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

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 scale		
Bioclim	Bio10	Mean temperature of the warmest quarter of year 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 altitude) 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 altitude) area in a 250 meter focal window
Land use	Rock	Proportion of rocks and bare soils area in a 250 meter focal window
Regional scale		
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

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 and al., 2017), we choose to use a particular approach developed for small sample sizes: Ensemble of Small Models (ESMs; Lomba et al. 2010; Breiner et al., 2015, 2018), a technique fitting many small (here bivariate) models and averaging them in a weighted way within a single Ensemble model. This approach avoids overfitting of the models and is thus very useful in the case of species with few occurrences

in a dataset (Breiner et al., 2015; Lomba et al., 2010), as was our case here. Using this modeling approach, we calibrated two models for the dung beetle species found in the Vaud Alps. First, and only for species found at least 15 times in the study area (Scherrer, et al., 2019), we calibrated a "Regional model" using presence-absence based on our accurately sampled species data and all predictors (climatic, land use, edaphic and radiance; see Table 1). Secondly, for all the species found at least once in the study region and at least 15 times in Switzerland, we calibrated a "Swiss model" using all occurrences available in Switzerland (from infofauna-CSCF and our sampled data) with climatic and land-use variables as predictors (see Table 1). We added to the "Swiss models" a same number of background points (also called 'pseudo-absences') as the number of presences and iterated the models many times.

We calibrated our 68 models (Regional and Swiss models) using only two techniques since the addition of several modeling techniques has a low impact on the quality of the ESMs predictions (Breiner et al., 2015). 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. 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 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; 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.

Model performances in relation with species characteristics

We investigated wherever species' characteristics impact the performances of the individual species' models. We tested the influence of the standard deviation of the altitudinal amplitude where the beetles are found in Switzerland (i.e. difference between highest and lowest altitude), the influence of the nesting behavior (endocoprid, paracoprid and non-nesting species: Hydrophilidae) and the body size of the beetles (according to the specialized literature; Baraud, 1992; Allemand and Leblanc, 2004; 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 the three species characteristics as explanatory variables and the median maxTSS of the final models of each species as response variable.

Species richness patterns of dung beetles

We wanted to obtain the expected species richness patterns of dung beetles in the study region, which can be approximated by summing the probabilities of presence of species (Dubuis et al., 2011). In order to include the highest number of potential species, we summed the maps of presence probabilities of the Swiss models ESMs to get a map of the global species richness. We also summed the presence probabilities for the species with the same nesting behavior (endocoprids, paracoprids or non nesting Hydrophilidae) to obtain predictions of species richness per group. Finally, we investigated the proportion of the coprophagous entomofauna represented by the endocoprids.

Results

Beetles

We recorded 1120 occurrences of coprophagous beetles for a total of 46 species (Table 2, Figure S3) belonging respectively to Scarabaeidae (28 species, 20 Aphodiinae and 8 Scarabaeinae), Geotrupidae (4 species) and Hydrophilidae (14 species).

Table 2. Species of coprophagous beetles found in the study area. For the 46 species, we report the name of the family, the number of sampled points where the species was present (in brackets the species with a too low number of occurences (less than 15), for which no regional models, were run) and the number of already existing precise occurrences in Switzerland (in brackets the species, for which no model was built since there were less than 15 occurences) and the nesting behaviour (E – Endocoprids, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]). The species are depicted in Figure S3.

Family	Subfamily	Species	Vaud Alps	Switzerland	Nesting
Geotrupidae	Geotrupinae	*Anoplotrupes stercorosus* (Scriba, 1791)	26	401	P
Geotrupidae	Geotrupinae	*Geotrupes spiniger* (Marsham, 1802)	(9)	124	P
Geotrupidae	Geotrupinae	*Geotrupes stercorarius* (Linnaeus, 1758)	17	76	P
Geotrupidae	Geotrupinae	*Trypocopris vernalis* (Linnaeus, 1758)	(2)	72	P
Hydrophilidae	Sphaeridiinae	*Cercyon haemorrhoidalis* (Fabricius, 1775)	(8)	82	H
Hydrophilidae	Sphaeridiinae	*Cercyon impressus* (Sturm, 1807)	88	115	H
Hydrophilidae	Sphaeridiinae	*Cercyon lateralis* (Marsham, 1802)	70	203	H
Hydrophilidae	Sphaeridiinae	*Cercyon melanocephalus* (Linnaeus, 1758)	23	82	H
Hydrophilidae	Sphaeridiinae	*Cercyon obsoletus* (Gyllenhall, 1808)	(4)	17	H
Hydrophilidae	Sphaeridiinae	*Cercyon pygmaeus* (Illiger, 1801)	46	69	H
Hydrophilidae	Sphaeridiinae	*Cercyon quisquilius* (Linnaeus, 1761)	(7)	162	H
Hydrophilidae	Sphaeridiinae	*Cryptopleurum crenatum* (Kugelann, 1794)	(8)	17	H

Hydrophilidae	Sphaeridiinae	*Cryptopleurum minutum* (Fabricius, 1775)	17	61	H
Hydrophilidae	Sphaeridiinae	*Megasternum concinnum* (Marsham, 1802)	(1)	131	H
Hydrophilidae	Sphaeridiinae	*Sphaeridium bipustulatum* Fabricius, 1781	17	83	H
Hydrophilidae	Sphaeridiinae	*Sphaeridium lunatum* Fabricius, 1792	78	134	H
Hydrophilidae	Sphaeridiinae	*Sphaeridium marginatum* Fabricius, 1787	(6)	19	H
Hydrophilidae	Sphaeridiinae	*Sphaeridium scarabaeoides* (Linnaeus, 1758)	80	189	H
Scarabaeidae	Aphodiinae	*Acrossus depressus* (Kugelann, 1792)	76	254	E
Scarabaeidae	Aphodiinae	*Acrossus rufipes* (Linnaeus, 1758)	62	304	E
Scarabaeidae	Aphodiinae	*Agoliinus satyrus* (Reitter, 1892)	(2)	30	E
Scarabaeidae	Aphodiinae	*Amidorus obscurus* (Fabricius, 1792)	42	88	E
Scarabaeidae	Aphodiinae	*Ammoecius brevis* (Erichson, 1848)	(1)	16	E
Scarabaeidae	Aphodiinae	*Aphodius fimetarius* aggr. (Linnaeus, 1758)	16	214	E
Scarabaeidae	Aphodiinae	*Bodilopsis rufa* (Moll, 1782)	59	335	E
Scarabaeidae	Aphodiinae	*Calamosternus granarius* (Linnaeus, 1767)	(8)	236	E
Scarabaeidae	Aphodiinae	*Colobopterus erraticus* (Linnaeus, 1758)	82	140	P
Scarabaeidae	Aphodiinae	*Esymus pusillus* (Herbst, 1789)	20	133	E
Scarabaeidae	Aphodiinae	*Euheptaulacus carinatus* (Germar, 1824)	(10)	30	E
Scarabaeidae	Aphodiinae	*Nimbus contaminatus* (Herbst, 1783)	(3)	90	E
Scarabaeidae	Aphodiinae	*Oromus alpinus* (Scopoli, 1763)	27	121	E
Scarabaeidae	Aphodiinae	*Otophorus haemorrhoidalis* (Linnaeus, 1758)	47	117	E
Scarabaeidae	Aphodiinae	*Parammoecius gibbus* (Germar, 1816)	21	48	E
Scarabaeidae	Aphodiinae	*Planolinoides borealis* (Gyllenhal, 1827)	(4)	(9)	E
Scarabaeidae	Aphodiinae	*Planolinus fasciatus* (A. G. Olivier, 1789)	(4)	21	E
Scarabaeidae	Aphodiinae	*Rhodaphodius foetens* (Fabricius, 1787)	(4)	19	E
Scarabaeidae	Aphodiinae	*Teuchestes fossor* (Linnaeus, 1758)	64	151	E
Scarabaeidae	Aphodiinae	*Volinus sticticus* (Panzer, 1798)	(5)	172	E
Scarabaeidae	Scarabaeinae	*Copris lunaris* (Linnaeus, 1758)	(1)	184	P
Scarabaeidae	Scarabaeinae	*Euoniticellus fulvus* (Goeze, 1777)	(5)	53	P
Scarabaeidae	Scarabaeinae	*Onthophagus baraudi* Nicolas, 1964	16	33	P
Scarabaeidae	Scarabaeinae	*Onthophagus coenobita* (Herbst, 1783)	(3)	125	P
Scarabaeidae	Scarabaeinae	*Onthophagus fracticornis* (Preyssler, 1790)	58	291	P
Scarabaeidae	Scarabaeinae	*Onthophagus illyricus* (Scopoli, 1763)	(6)	62	P
Scarabaeidae	Scarabaeinae	*Onthophagus joannae* Goljan, 1953	(10)	155	P
Scarabaeidae	Scarabaeinae	*Onthophagus verticicornis* (Laicharting, 1781)	(1)	22	P

Swiss model

One of the 46 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 45 other species, the models calibrated at the Swiss level ranged from poor to high quality with median maxTSS going from 0.27 (*Anoplotrupes stercorosus*) to 0.93 (*Ammoecius brevis*) (Figure 2). We present all the maps in the supplementary material (Figure S1). At the Swiss level the variable with the highest contribution in the models were the mean temperature of the warmest quarter of year (Bio10), the proportion of rock and bare

soils (Rock) and precipitation during the driest quarter of the year (Bio17) (Figure 3). The human infrastructure, wet habitats and cultivation had the lowest impact (Figure 3).

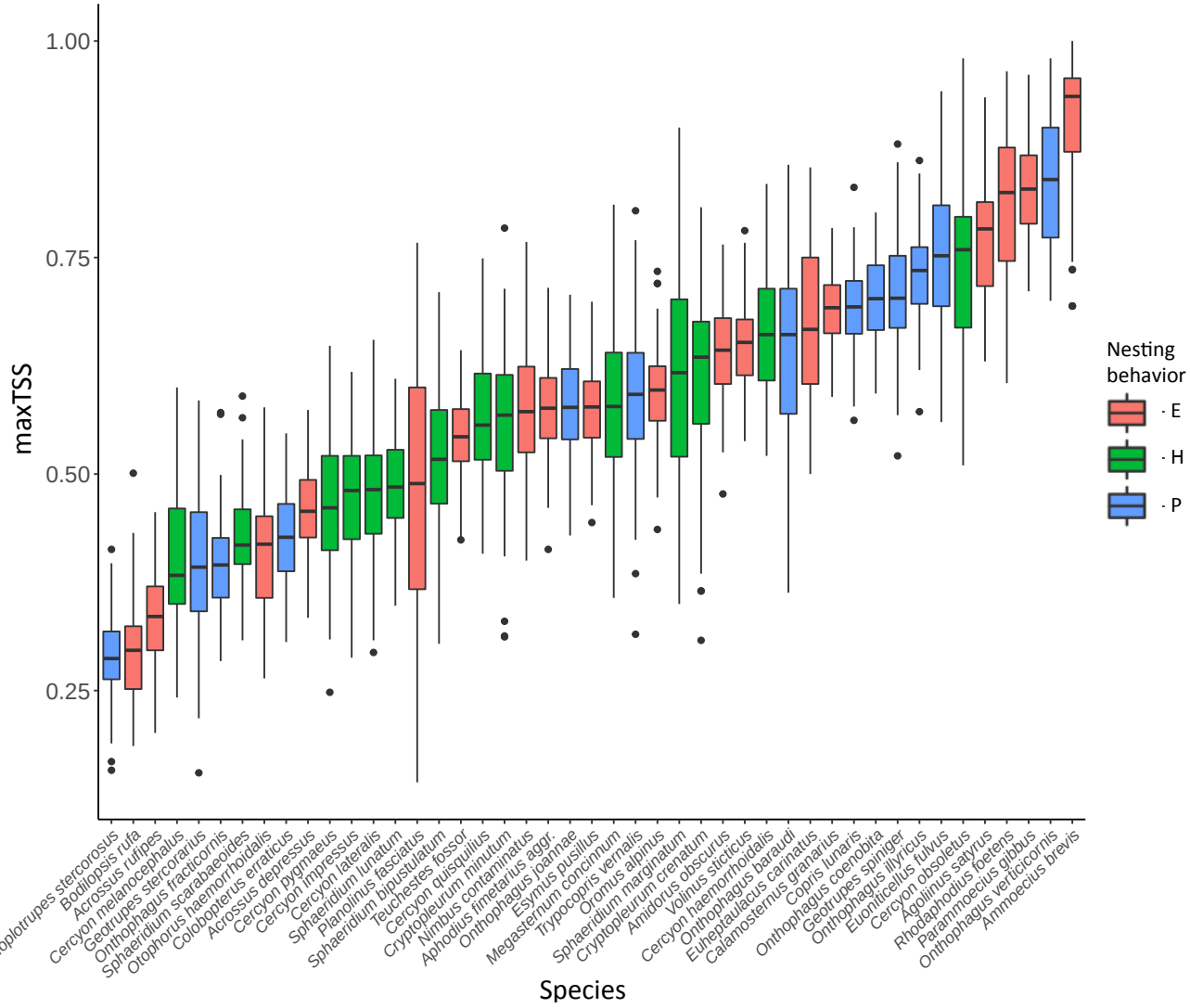

Figure 2. Results of the Ensemble of Small Models (ESMs) calibrated at the Swiss scale presented for each of the 45 species treated with the max True Skills Statistics (maxTSS) ordered by median. The boxplots are colored according to the nesting behavior of the species (E – Endocoprids, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]). All the model projections are presented in Figure S1 and all the species are illustrated in Figure S3.

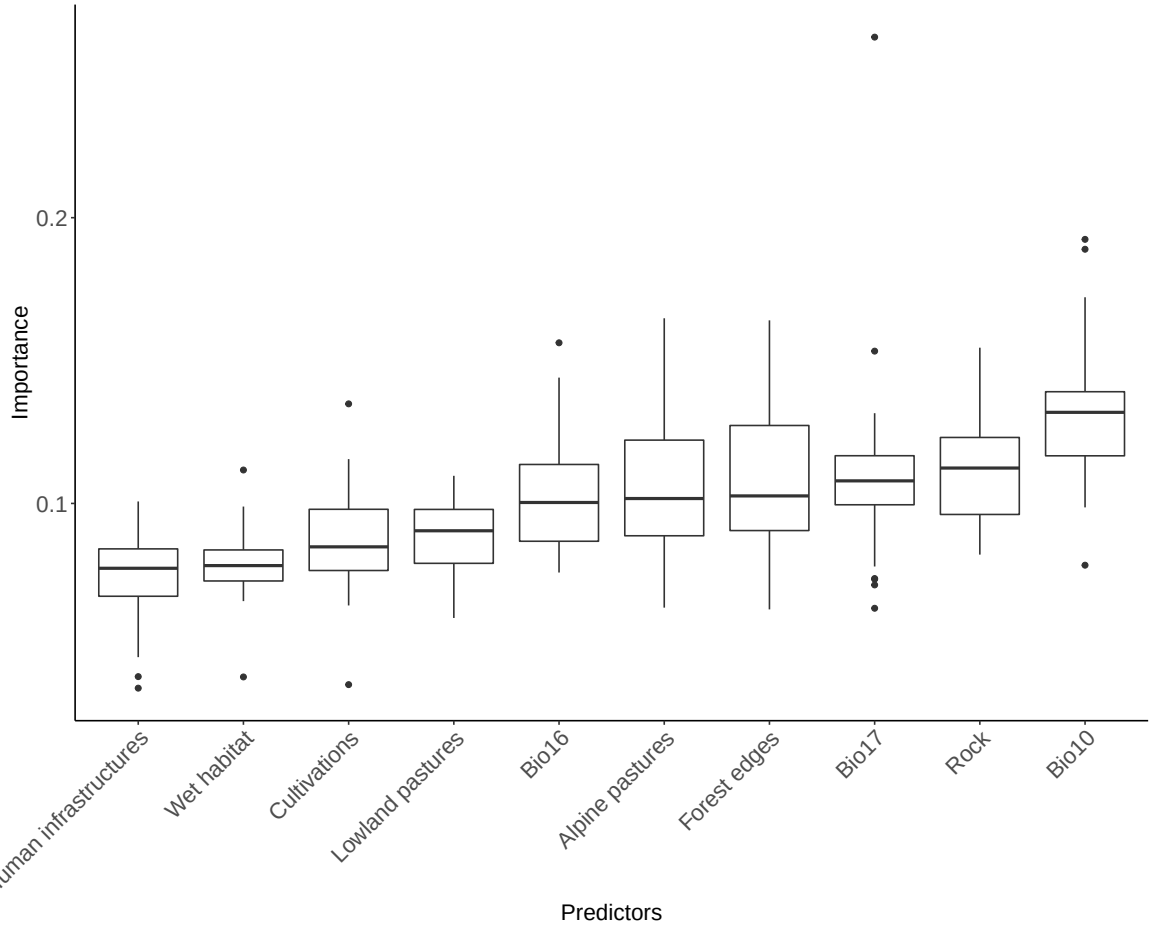

Figure 3. Relative importance of the variables used as predictors in the 45 Ensemble of Small Models (ESMs) calibrated at the Swiss scale presented in increasing order of importance. The climatic conditions are Bio 10 (temperature of the warmest quarter of year), Bio 16 (precipitation in the wettest year quarter) and Bio17 (precipitation of the driest quarter of the year). For the full descriptions of the predictors, see Table 1.

Vaud Alps model (Regional)

On the 46 species recorded in the study area, 23 had at least 15 occurrences and were therefore used to build ESMs. The regional models showed a high heterogeneity in their performances (worst model: *Acrossus rufipes*, median maxTSS = 0.40, best: *Parammoecius gibbus*, median maxTSS = 0.85) (Figure 4). We present all the maps in the supplementary material (Figure S2). At the level of the study region, the variable with the highest contribution in the models 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) (Figure 5), while the cultivation proportion, the human infrastructure and the solar radiation had the lowest contribution (Figure 5).

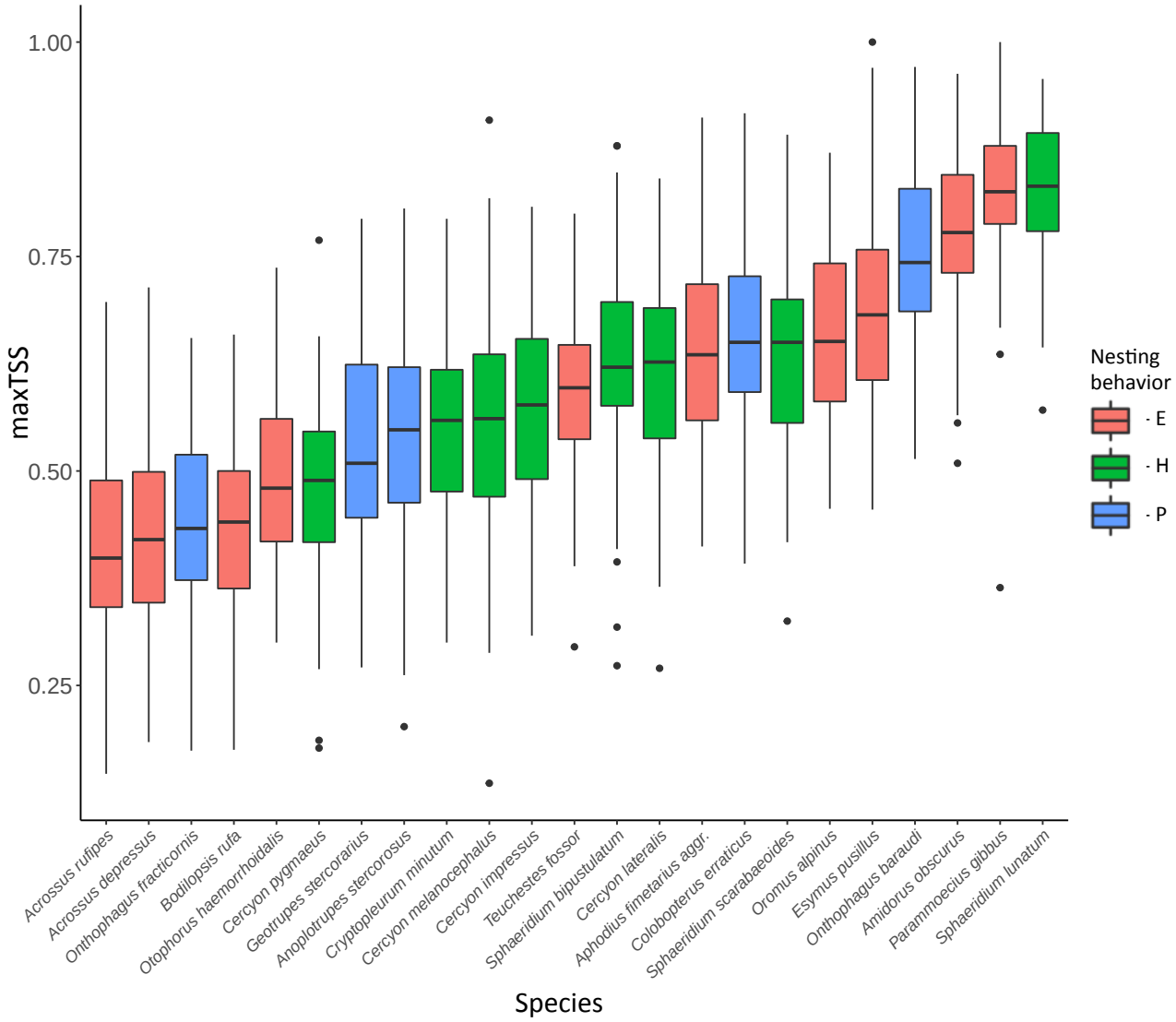

Figure 4. Results of the Ensemble of Small Models (ESMs) calibrated at the Regional scale presented for each of the 23 species treated with the max True Skills Statistics (maxTSS) ordered by median. The boxplots are colored according to the nesting behavior of the species (E – Endocoprids, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]). All the model projections are presented in Figure S2 and all the species are illustrated in Figure S3.

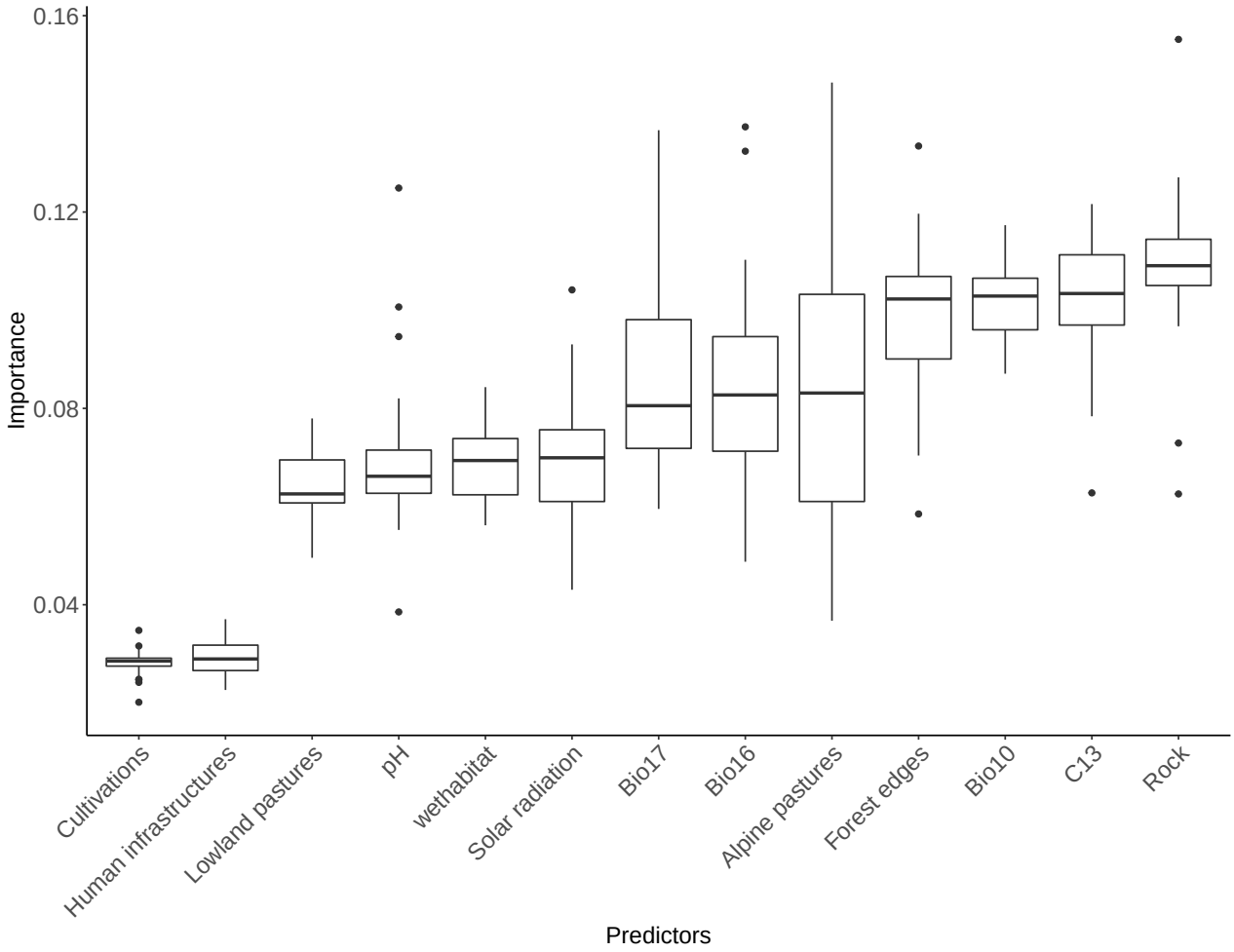

Figure 5. Relative importance of the variables used as predictors in the 23 Ensemble of Small Models (ESMs) calibrated at the Regional scale presented in increasing order of importance. The climatic conditions are Bio 10 (temperature of the warmest quarter of year), Bio 16 (precipitation in the wettest year quarter) and Bio17 (precipitation of the driest quarter of the year). For the description of the predictors see Table 1.

Model performances in relation with species characteristics

The altitudinal amplitude where the species occur had a significant influence on the median maxTSS in the models (GLM result: p-value = $1x10^{-9}$, t-value = -7.98; Figure 6A). Neither the nesting strategies (GLM result: p-values = 0.88 and 0.24, t-values = -0.16 and -1.20; Figure 6B), nor the size of the species had an influence on the performance of the models (GLM result: p-value = 0.89, t-value = 0.14; Figure 6C). There was no significant interaction between variables.

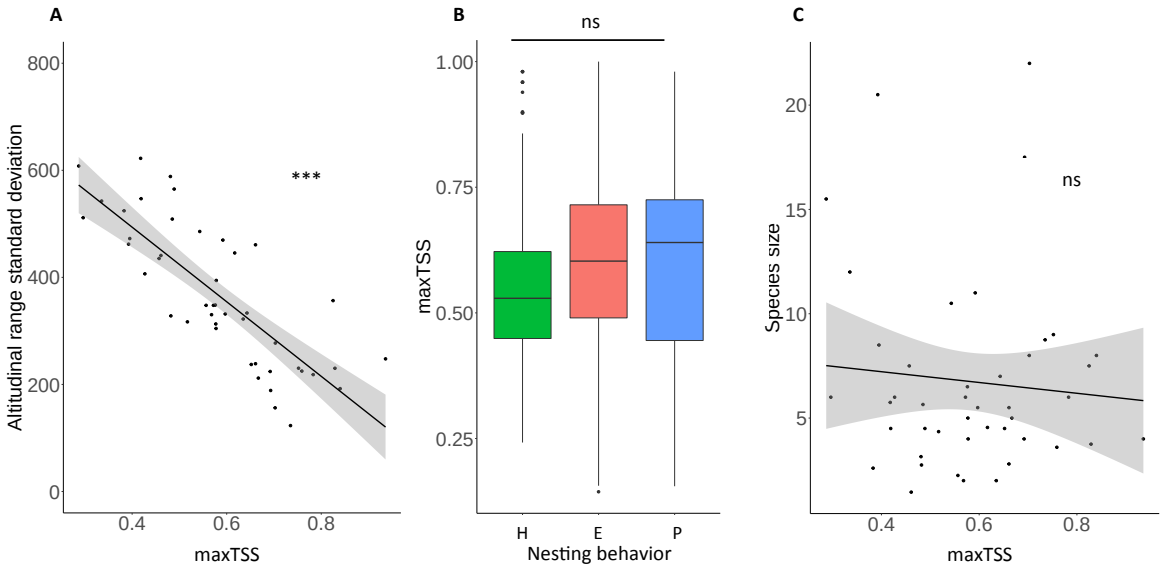

Figure 6 Model performances in relation with species characteristics. The median max True Skills Statistics (maxTSS) of each species are plotted (A) against the altitudinal amplitude standard deviation where the species are found in Switzerland; (B) according to the nesting behavior of the species (E – Endocoprids, P – Paracoprids, H – Hydrophilidae [predatory larvae, no nesting]); (C) against the species size. The grey area represents the confidence interval 95%.

Species richness models

Our models predicted a global decrease in species richness from the low to the high altitudes (min = 11.06, max = 24.58 species) (Figure 7A). This trend was particularly sharp for the paracoprids (min =2.39, max = 7.66) (Figure 7B) but much less for the endocoprids (min = 5.65, max = 8.85) (Figure 7C). Hydrophilidae also show a strong loss of species diversity with the increasing altitude (min = 2.51, max = 8.52 species). (Figure 7D). The highest proportion of endocoprid was observed at higher altitude (min = 0.33, max = 0.55) (Figure 7E).

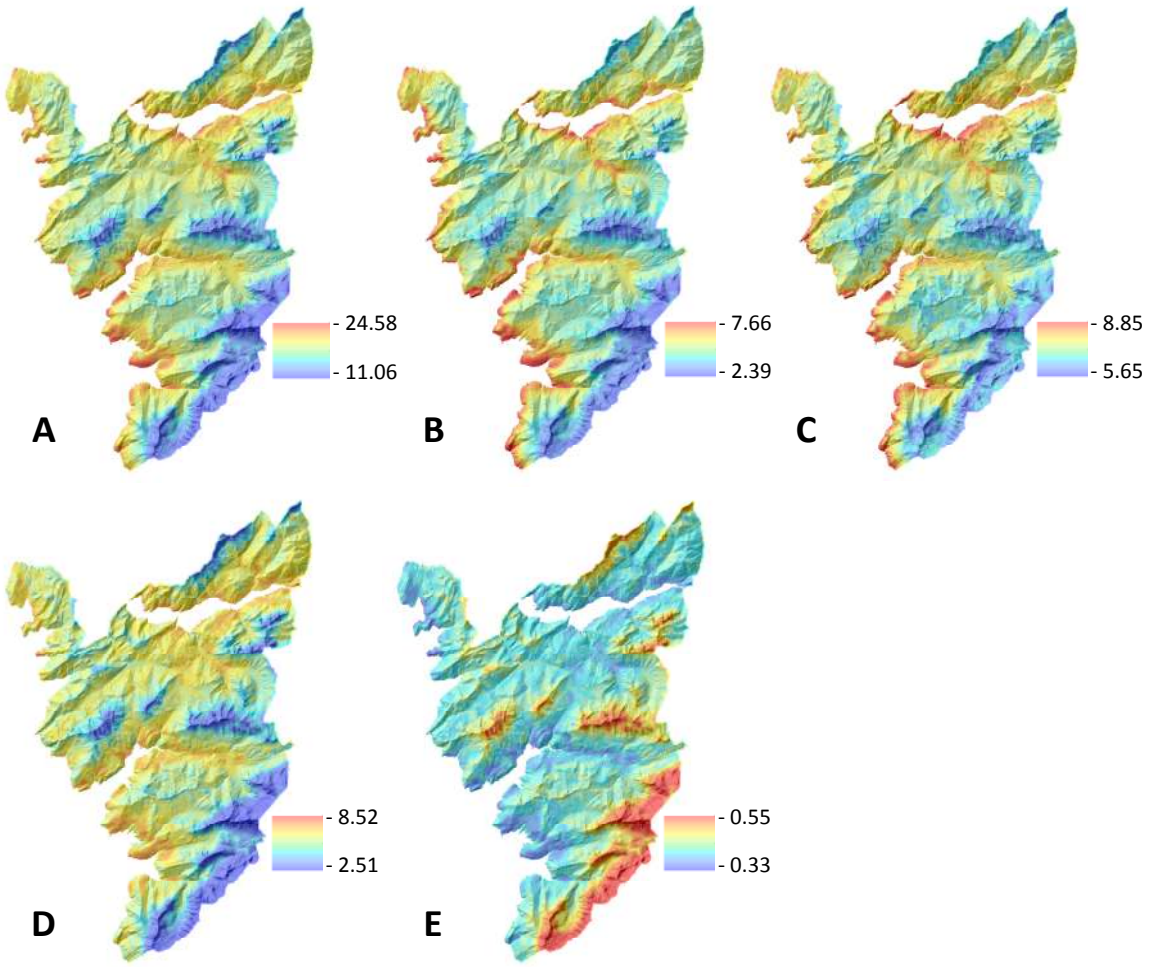

Figure 7. Predicted species richness in the study region starting at 1000 meters above sea level according to the models calibrated at the Swiss scale considering (A) all species, (B) the Paracoprids, (C) the Endocoprids, (D) the Hydrophilidae and (E) the proportion of the global diversity represented by Endocoprid.

Discussion

We investigated the influence of various factors on the distributions of coprophagous beetle species in the Western Swiss Alps using correlative species distribution modeling (SDM) approaches based on quantifying 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 our models, the predictors with the greatest importance always included climatic variables (Figure 3; Figure 5), like in many SDM studies (Pradervand et al., 2013; Scherrer et al., 2019), demonstrating once more the importance of those limiting factors. Interestingly, in both models (i.e. Swiss and Regional) the proportion of rock and bare soil cover (Rock) was an important predictor (Figure 3B, Figure 5B), which could be due

to a higher proportion of unvegetated surfaces at higher altitudes, where the species are also better modeled, artificially increasing the influence of species inhabiting these areas in the results. Another possibility could be that more species are expected in pastures of high ecological value (i.e. with a high overall biodiversity), which are grasslands with discontinuous vegetation cover due to low fertilization rate (Delarze et al., 2015). In addition, the superficial cover by rocks could be an indirect way of quantifying the heterogeneity of the landscape around the occurrence points. For instance, Negro et al. (2011) suggested that habitat heterogeneity, especially the presence of natural forested areas next to pastures, plays an important role in increasing dung beetle species richness. Forest edges brought an important contribution as predictor in our models even if this predictor was not in the top ones (Figure 3B; Figure 5B). In contrast, some variables had little influence in our models. These are often land cover or land use variables with small cover in Switzerland (e.g. wet habitats) or in the study region (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 Guisan et al., 2017), with values ranging from 0.27 to 0.93 for the Swiss models (Figure 2) and from 0.40 to 0.85 for the regional models (Figure 4). We tried to explain the variability of our model performances with species characteristics and found that species present over a wide altitudinal range had weaker models compared to the species occurring in a narrower altitudinal amplitude (Figure 6A). Our results are in line with those of Guisan and Hofer (2003) and Grenouillet et al. (2011), who showed that the distributions of generalist species are more difficult to predict. These results are also consistent 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 (Figure 6B) nor the size of the species (Figure 6C) on the maxTSS of the models meaning that these biological traits seems not being relevant to explain the models quality. However, further analyses could be performed to try to improve the predictive performances of generalist species by taking into account the co-occurrences patterns through the region, which could be possible using our precise sampled data.

When looking at species richness of coprophagous beetles obtained by cumulating models for single species in the study region, the global trend is a diminution of the number of species with increasing altitude (Figure 7). This result is also mainly true for the richness of other taxa in the same region (Dubuis et al., 2011; Pradervand et al., 2013; Reymond et al., 2013; Pellissier et al., 2013; Scherrer et al., 2019; Seppey et al., 2020), for which the climatic predictors and especially temperature were also of great importance. However, it is important to notice that, for the dung beetles studied here, the strength of the decrease in species

richness depends on the nesting behavior: the paracoprids (Figure 7B) and the Hydrophilidae (Figure 7D) show a sharp decrease while the endocoprid a smoother one. This latter group forms the biggest part of the dung beetle diversity at high altitude where almost no paracoprids and Hydrophilidae are found (Figure 6B and 6E). This is consistent with other studies (Lobo et al. 2007) and is explained by the fact that endocoprid beetles are expected to be more cold tolerant since they need the dung patches to remain moist for the entire development of their larval stage and are outcompeted in warmer climates by paracoprids, which avoid the endocoprid to use dung by burying it (Hanski, 2016).

Our field sampling designed in a random stratified manner permitted to be representative of the environment of the study area and likely allowed us to find a high number of dung beetles species. From a faunistical point of view, our study brings precious new records for coprophagous beetles, an under sampled taxon in comparison to other insect groups such as orthopteras or butterflies, and even more compared with vertebrates (Troudet et al., 2017. Indeed, the data sampled in our study represents now 17.9% (N=1120) of all precise occurrences existing for the 46 dung beetle species in Switzerland (N=6258). We also found that an important proportion of the coprophagous beetle species of Switzerland is found in the Vaud Alps (41.6%). These data represent a key source of knowledge for ecologically and economically important taxa, which had never been studied in the Vaud Alps region, contrary to many other groups of organisms, reinforcing the status of biodiversity hotspot of this study region in the European Alps (Lassen and Savoia, 2005).

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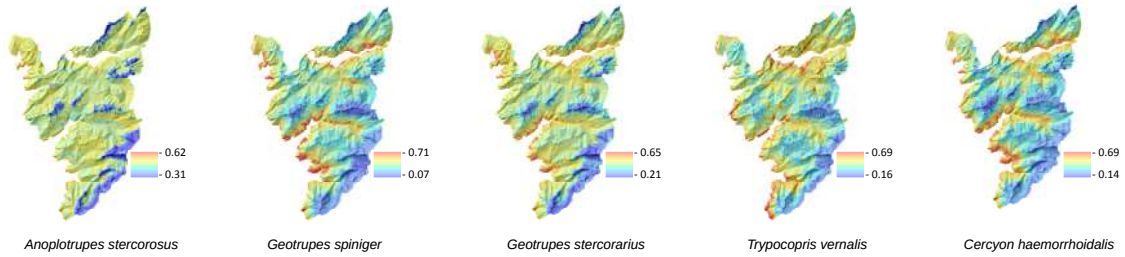
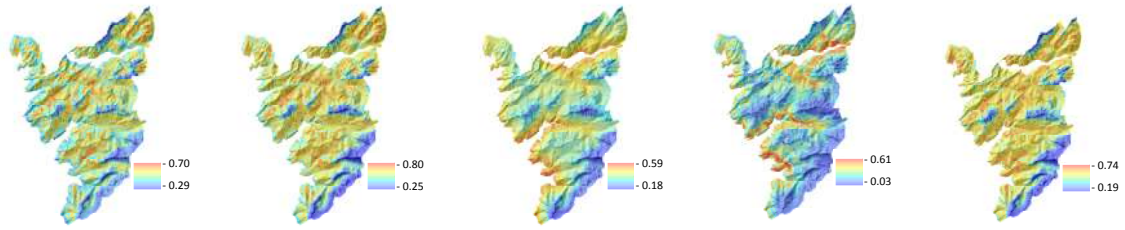
698 **Supplementary material**

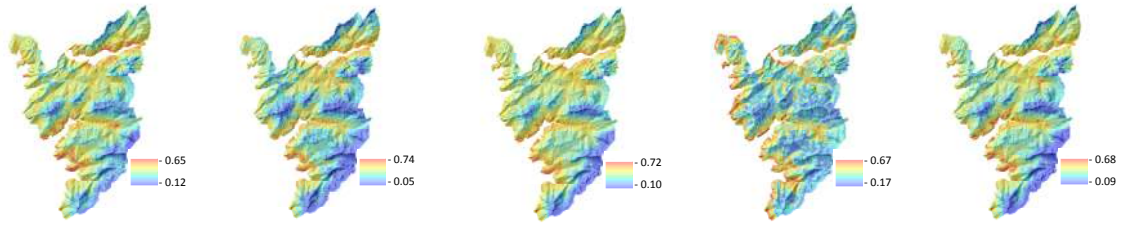
699



Anoplotrupes stercorosus *Geotrupes spiniger* *Geotrupes stercorarius* *Trypocopris vernalis* *Cercyon haemorrhoidalis*



Cercyon impressus *Cercyon lateralis* *Cercyon obsoletus* *Cercyon melanocephalus* *Cercyon pygmaeus*



Cercyon quisquilius *Cryptopleurum crenatum* *Cryptopleurum minutum* *Megasternum concinnum* *Sphaeridium bipustulatum*

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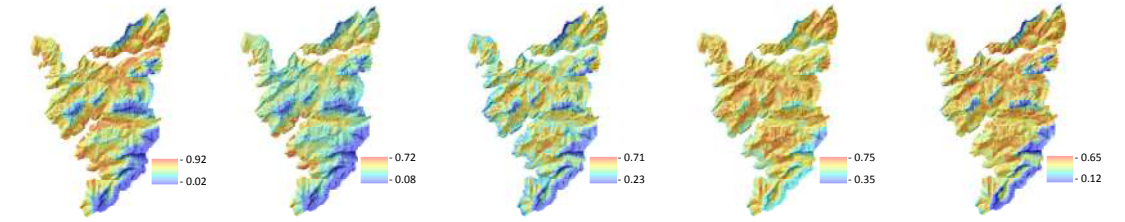
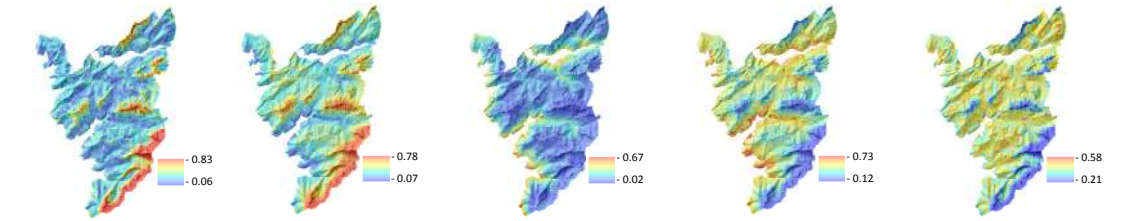
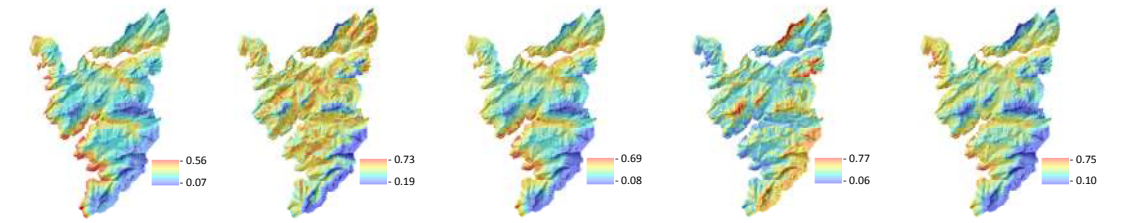


Sphaeridium lunatum *Sphaeridium marginatum* *Sphaeridium scarabaeoides* *Acrossus depressus* *Acrossus rufipes*



Agoliinus satyrus *Amidorus obscurus* *Ammoecius brevis* *Aphodius fimetarius* aggr. *Bodilopsis rufa*



Calamosternus granarius *Colobopterus erraticus* *Esymus pusillus* *Euheptaulacus carinatus* *Nimbus contaminatus*

701

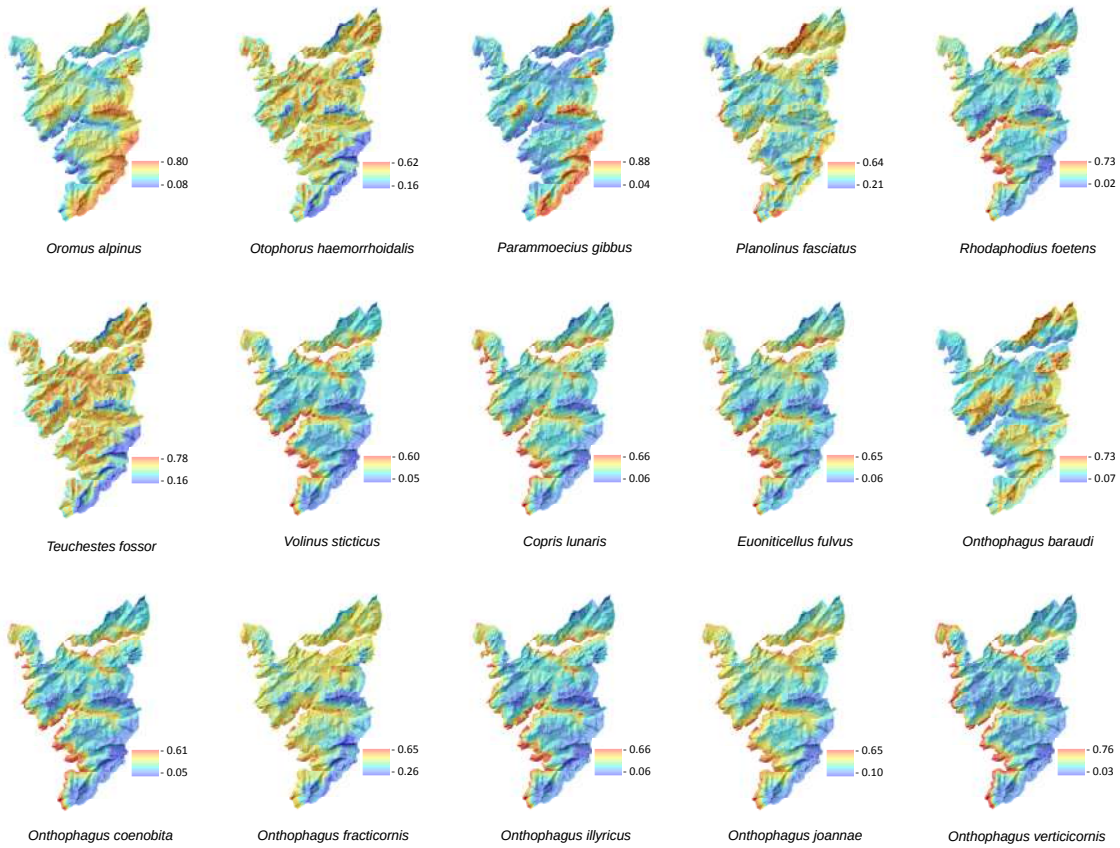


Figure S1. Map of all the 45 species for which a model was run at the Swiss scale. Red represent areas with high presence probability while blue the areas with low presence probability of the species.

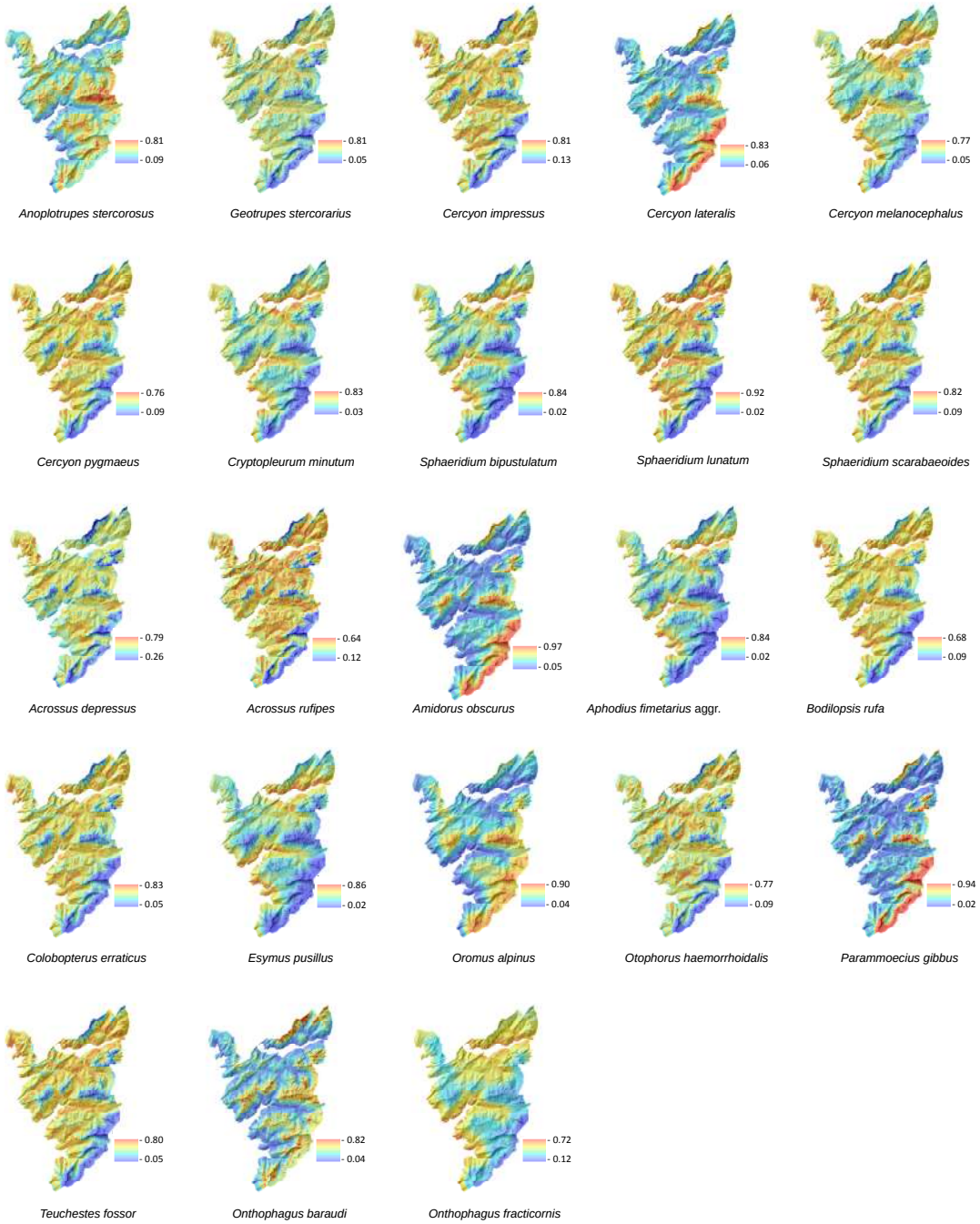
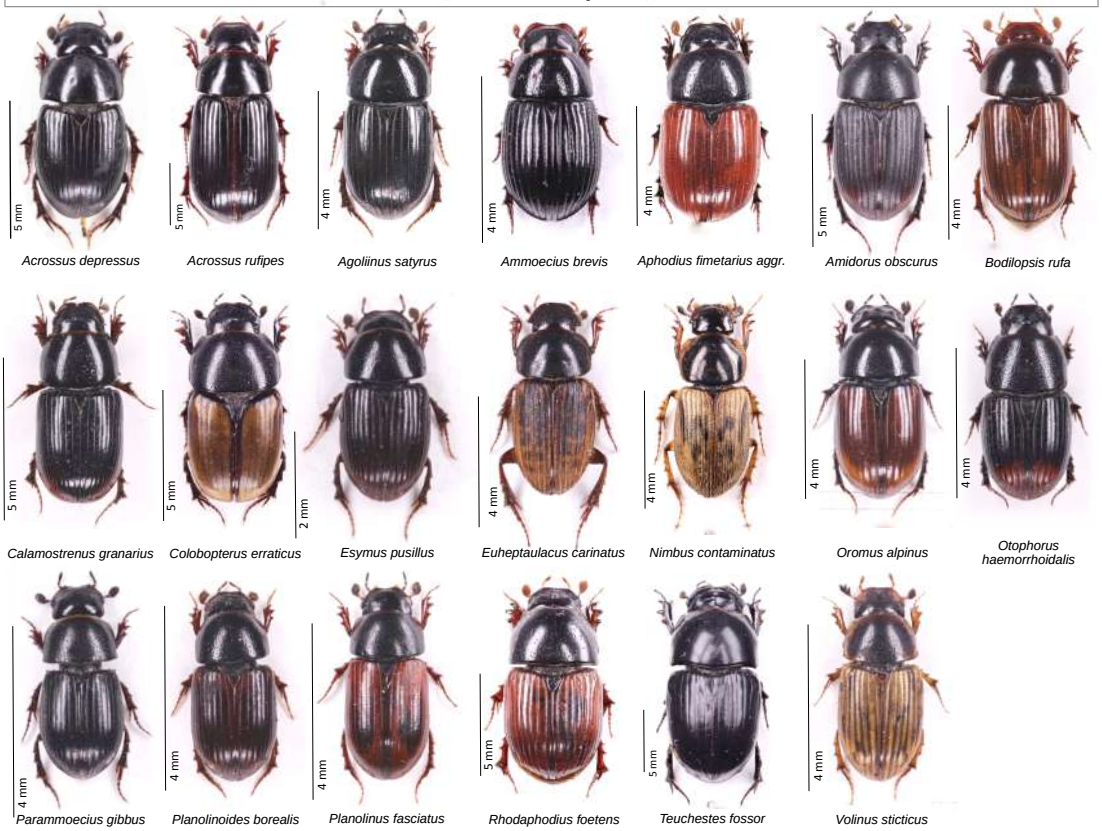


Figure S2. Map of the 23 species for which a model was run at the Regional scale. Red represent areas with high presence probability while blue the areas with low presence probability of the species.

Scarabaeidae, Aphodiinae



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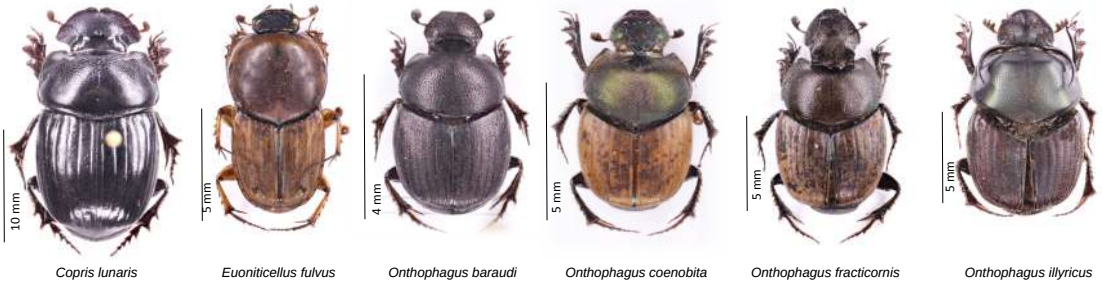
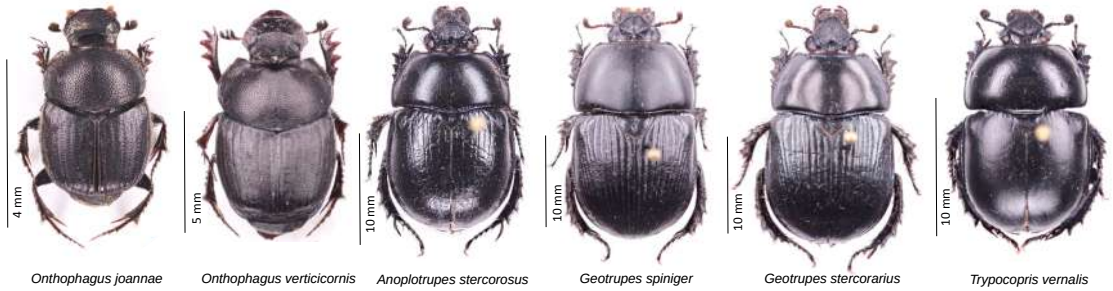
Scarabaeidae, Scarabaeinae



Scarabaeidae, Scarabaeinae | **Geotrupidae**



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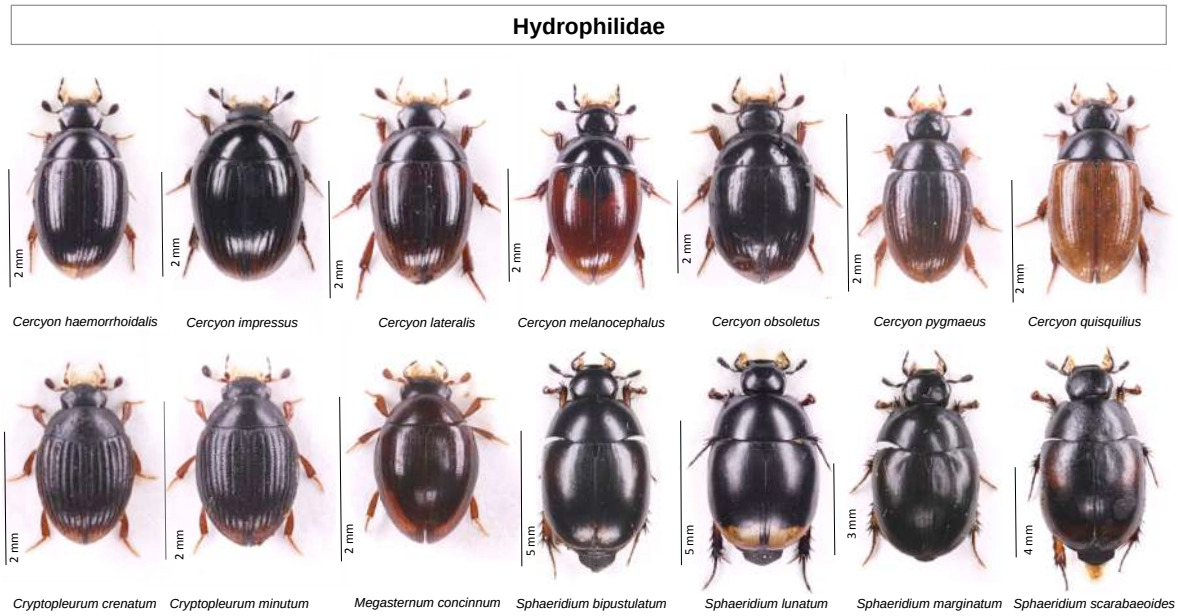

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716 **Figure S3.** Illustration of all the dung beetle species found in the study region. Illustration:
717 Vivien Cosandey.

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