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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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39 Abstract

40 Dung beetles depend on mammal droppings as unique trophic resource and are thus 41 considered key ecosystem services providers. Since our knowledge of dung beetles 42 distribution and ecology is still limited, we chose to investigate it with Species Distribution 43 Modeling (SDM), which allows quantifying the species-environment interactions (i.e. their 44 niche) and predict the species' presence probability. We sampled coprophagous beetles in 45 the Vaud Alps and calibrated for each species a regional SDM with our data and another one 46 with all occurrences for Switzerland. In both cases, the best predictors were temperature and 47 rock cover proportion, while a soil characteristic was important in the regional models and 48 precipitations in the Swiss models. The model performances were influenced by the 49 altitudinal range where the species occur but not by other species characteristics like their 50 size or nesting behavior (laying eggs inside or below the excrements). We also showed that 51 species richness decreased with altitude but that the species nesting in the dung represented 52 a higher proportion of dung beetles at high altitude. Overall this study brought new data and 53 insights for an ecologically important group of species, which is still poorly studied in 54 Switzerland.

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56 Résumé

57 Les bousiers dépendent exclusivement des excréments de mammifères pour se nourrir et 58 fournissent donc des services écosystémiques essentiels. La connaissance de la répartition 59 et de l'écologie des bousiers étant encore limitée, nous avons choisi de nous y intéresser en 60 utilisant des Modèles de Distribution d'Espèces (Species Distribution Models - SDM) qui 61 permettent de quantifier les besoins environnementaux des espèces (leurs niches) et de 62 prédire leur répartition géographique. Nous avons échantillonné des bousiers dans les Alpes 63 vaudoises et avons calibré pour chaque espèce un SDM régional avec nos données et un 64 second en utilisant toutes les données disponibles au niveau suisse. Dans les deux modèles, 65 les meilleures prédicteurs incluaient la température et la proportion de couverture rocheuse, tandis qu'une des caractéristiques du sol (∂^{13} C) et les précipitations étaient importantes 66 67 respectivement pour les modèles des Alpes vaudoises et les modèles suisses. Les 68 performances des modèles étaient influencées par l'amplitude altitudinale occupée par les 69 espèces alors que d'autres caractéristiques spécifiques telles que la taille ou le mode de 70 nidification (ponte des œufs dans les excréments ou en dessous) n'avaient aucun effet. 71 Nous démontrons également que la richesse spécifique des coléoptères coprophages 72 décroit avec l'altitude mais que les espèces pondant leurs œufs dans les excréments étaient 73 proportionnellement plus nombreuses en altitude. Dans cette étude, nous apportons de 74 nouvelles données et connaissance écologiques sur des taxa peu étudiés en Suisse bien 75 qu'écologiquement important.

77 Keywords

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

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81 Introduction

82 Coprophagous beetles are part of a specialized entomofauna feeding on the droppings of 83 mammals (Hanski, 2016). Some species have coprophagous adult and predaceous larvae, 84 which are chasing fly larvae from dung patches (Hydrophilidae, Sphaeridinae), while other 85 have coprophagous adults and larvae. In this latter case, some species lay their eggs directly 86 in the dung (endocoprids: Scarabaeidae, Aphodiinae) and other dig simple wells or 87 sophisticated network of tunnels and rooms where they stock dung and lay their eggs 88 (paracoprids: Geotrupidae and Scarabaeidae Scarabeinae) to avoid the harsh intra- and 89 inter-specific competition to exploit dung patches before they dry (Hanski, 2016). By feeding 90 and burying excrements, dung beetles are essential for dung decomposition (Gittings et al., 91 1994) and avoid the accumulation of excrements. Considered as key "Ecosystem Service 92 Providers" (Nichols et al., 2008), dung beetles prevent the loss of 4.8% of the pasture 93 surface per year in England (Beynon et al., 2012b) and allow sparing between 380 million 94 (Losey and Vaughan 2006) and 2 billion (Fincher 1981) of USD in the USA and at least 367 95 million pounds in the UK (Beynon et al. 2015). In addition, dung beetles represent locally an 96 important a part of the food for insectivorous animals such as birds (in particular corvids) 97 (Lumaret and Stiernet, 1990) or mammals (e.g. greater horseshoe bat (Rhinolophus 98 ferrumequinum)) (Beynon et al., 2015). The economic and ecological importance of dung 99 beetles coupled with the possibility to characterize the whole species assemblages found at 100 a given location (dung patch) in a given time point (Finn and Giller 2000; Hanski 2016) 101 makes them an adequate group to study biogeography (Lumaret 1979) and animal 102 communities (Hanski and Koskela, 1977). In Europe, the species assemblages of dung 103 beetle and their relative abundance were already characterized (Lumaret and Stiernet, 1989; 104 Errouissi et al., 2004; Lumaret and Stiernet, 1984; Negro, 2011) and the importance of 105 climatic and edaphic factors have been shown by the study of the species richness of the 106 dung beetles assemblages at a coarse level (Hortal et al., 2001; Lobo and Martin-Piera, 107 2002; Lumaret and Jay-Robert, 2002). However, ecological needs and fine geographic 108 distribution of individual dung beetle species remains an understudied topic.

109 The study of the realized environmental niche of species, adaptation to local conditions and 110 interspecific interactions (Hutchinson, 1957) allows a better understanding of the distribution 111 of species (see Niche-Geography duality: Colwell and Rangel 2009), which is crucial to 112 overcome Wallacean (knowledge about the geographical distribution of species) and 113 Hutchinsonian (knowledge about the tolerance of species to abiotic factors) shortfalls 114 concerning biodiversity (Hortal et al., 2015). The development of statistical models to quantify 115 the niche and derive geographic predictions, the Species Distribution Models (SDM; also 116 called 'habitat suitability' or 'ecological niche' models; see Franklin, 2010; Peterson et al., 117 2011; Guisan et al., 2017), have brought powerful tools to better understand, compare and 118 quantify the relationship between organism and environment (i.e. their environmental niche) 119 but also to predict their distribution in space and time (Guisan and Thuiller, 2005; Guisan and 120 Zimmermann, 2000), which can bring essential knowledge about the ecology of understudied 121 taxonomical groups like arthropods (Hochkirch et al., 2020). SDMs have been used to study 122 various groups of insects (Pradervand et al., 2014; D'Amen et al., 2015; Pellissier et al., 123 2012; Descombes et al., 2016; Mata et al., 2017) but there are few examples of individually 124 modeled dung beetle species (Chefaoui et al., 2005; Lobo, 2010).

125 The aim of this study is to bring a better understanding of the factors influencing the 126 distribution of individual dung beetle species in temperate mountain environments using an 127 SDM approach, which was never done before to our knowledge. To do so, we sampled dung 128 beetles throughout the Western Swiss Alps of the Vaud state in a random stratified manner 129 with the aim of assessing which dung beetle species are present and obtaining a sufficient 130 number of accurate species data to quantify species-environment relationships in SDMs. We 131 additionally obtained all the occurrences available in Switzerland for the beetle families of 132 interest (Hydrophilidae, Geotrupidae and Scarabaeidae) from the Swiss national database 133 (infofauna-CSCF). This allowed us to compare fine-scale models calibrated in the study 134 region using our precisely sampled data and larger-scale models calibrated at the Swiss 135 level with the infofauna data. We expected the latter to reduce the risk, while calibrating the 136 SDMs, of truncating the species' environmental niches, if not covering the complete extent of 137 the species' geographic distributions and environmental requirements, as could expectedly 138 be observed in the smaller extent (Chevalier et al., (In Review); Pearson et al., 2004; Thuiller 139 et al., 2004; Hannemann et al., 2016; Guisan et al., 2017; El-Gabbas and Dormann 2018; G. 140 Mateo et al., 2019). Here, we particularly focused on the climatic, land-use and edaphic 141 factors as environmental predictors of the species' presence. In addition, we investigated the 142 effects of species characteristics such as the altitudinal amplitude where the species are 143 found, the nesting behavior and the species' size on the SDMs performances. We also 144 interested us to the species richness of dung beetles patterns and the proportion of 145 endocoprids compared to the other dung beetles throughout the study region.

147 Material & Methods

148 Study area

149 The study was conducted in Western Switzerland, in the alpine region of the Canton de 150 Vaud, which goes from Vevey to Bex and to Rougemont (Figure 1). It spans a wide altitudinal 151 gradient, from 372 to 3051 meters above sea level. Since the lower part of the region is 152 dedicated to crop fields and the slopes of the mountain basis are covered by forests, we only 153 considered the upper part of the area, starting from an altitude of 1000 meters above sea 154 level (Figure 1), where pastures grazed by domestic livestock (principally cows an sheeps) 155 and alpine grasslands inhabited by big wild herbivores, like Alpine chamois (Rupicapra 156 rupicapra), Alpine ibex (Capra ibex) and Red deers (Cervus elaphus) occur. The study region 157 is of particular interest for interdisciplinary research as it constitutes a priority region for 158 research (http://rechalp.unil.ch; Reynard et al., 2020; von Däniken et al., 2014) and is also a 159 priority region for biodiversity conservation (Lassen and Savoia, 2005)



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

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164 Sampling & beetle data acquisition

165 From the 31 of May to the 12 September 2020, we collected dung beetles in 132 sampling 166 plots (Figure 1) of 20 meters radius located in a random stratified manner (Guisan and Hirzel, 167 2002) in open habitats (excluding the forests and built areas). We stratified the study region 168 in 10 strata according to altitude (every 300 meters until, from 1000 to 2500 meters) and the 169 yearly sum of solar radiations (two levels: lower and higher than the mean radiation observed 170 in the study area). In order to perform a monitoring that represents the environment of the 171 study area, we sampled a number of random points in each stratum proportional to its size. 172 Since it is the first time such sampling is done for this beetle group, it should ensure

173 optimizing the number of species to be found (according to the species-area relationship; 174 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 175 176 the point locations in the initial design, but their position was slightly shifted (maximum 200 177 meters, staying in the same strata) when the initial point was falling in places that had not 178 been recently pastured by domestic or wild herbivores. In each sampling plot, 20 minutes 179 were dedicated to the manual search of beetles inside of the dung using a little shovel with 180 the goal to catch the maximum number of species. The sampled individuals were stored in 181 Scheerpelz solution (55% water, 30% EtOH 96%, acetic acid 10%, acetic ether 5%). We 182 identified the collected beetles with the help of a binocular and based on identification keys 183 found in the specialized literature (Baraud, 1992; Fikáček, 2006; Klausnitzer, 2011; Vorst, 184 2009). The species were recorded as present or absent in each sampling plot but the 185 individuals were not counted because our sampling was not thought to reflect the abundance 186 of these insects. We classified the Scarabaeidae and Geotrupidae species according to their 187 nesting behaviour in 'endocoprids' (laying eggs in the dung), 'paracoprids' (laying eggs in 188 dung buried under the excrement) with the help of the specialized literature (Hanski, 2016; 189 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.

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195 Environmental data

196 To depict the species' niche and to fit our models, we used as predictors (see Table 1): (i) 197 land-use variables originating either from the Swiss Federal Office of Statistics (2004) -198 alpine pastures, lowland pastures, cultivation, human infrastructures (at a 50 meters 199 resolution) - or from the Swiss Federal Office of Topography (Topographic Landscape Model 200 3D catalogue, 2012); - humid habitats, forest edges, rock and bare soil covers (25 meters 201 resolution); and ii) climatic variables (at a 25 meters resolution) calculated from the 202 bioclimatic data of Switzerland (Hijmans et al., 2005; Broennimann, 2018) - mean 203 temperature of the warmest quarter of the year (Bio10), precipitation in the wettest year 204 quarter (Bio16), and precipitation in the driest year quarter (Bio17). Elevation was not 205 included as predictor, as it is not a causal variable for species (Guisan et al. 2017) and is 206 driving many other variables already included as predictors (e.g. temperature). To take into 207 account the movement of the dung beetles and the precision of the data at the Swiss level, 208 we ran, for each variable focal window (Bellamy et al., 2013; Scherrer et al., 2019), which 209 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 tocalibrate 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 ∂^{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).

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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.

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

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224 Statistical analyses

225 All the statistical analyses were performed with R Studio version 1.0.153. (R core team, 226 2017). The models were built using the biomod2 (Thuiller et al., 2009) and ecospat package 227 (Di Cola et al., 2017). Among the techniques available to fit Species Distribution Model 228 (SDM) (Elith et al., 2006; Guisan and al., 2017), we choose to use a particular approach 229 developed for small sample sizes: Ensemble of Small Models (ESMs; Lomba et al. 2010; 230 Breiner et al., 2015, 2018), a technique fitting many small (here bivariate) models and 231 averaging them in a weighted way within a single Ensemble model. This approach avoids 232 overfitting of the models and is thus very useful in the case of species with few occurrences 233 in a dataset (Breiner et al., 2015; Lomba et al., 2010), as was our case here. Using this 234 modeling approach, we calibrated two models for the dung beetle species found in the Vaud 235 Alps. First, and only for species found at least 15 times in the study area (Scherrer, et al., 236 2019), we calibrated a "Regional model" using presence-absence based on our accurately 237 sampled species data and all predictors (climatic, land use, edaphic and radiance; see Table 238 1). Secondly, for all the species found at least once in the study region and at least 15 times 239 in Switzerland, we calibrated a "Swiss model" using all occurrences available in Switzerland 240 (from infofauna-CSCF and our sampled data) with climatic and land-use variables as 241 predictors (see Table 1). We added to the "Swiss models" a same number of background 242 points (also called 'pseudo-absences') as the number of presences and iterated the models 243 many times.

244 We calibrated our 68 models (Regional and Swiss models) using only two techniques since 245 the addition of several modeling techniques has a low impact on the guality of the ESMs 246 predictions (Breiner et al., 2015). We choose to use Generalized Linear Models (GLM) and 247 Generalized Additive Models (GAM), to represent both parametric (GLM) and semi-248 parametric (i.e. more data-driven; GAM) modeling approaches. Hundred runs were 249 conducted with 70% of the dataset used for model calibration and 30% for model validation. 250 The GLM and GAM models were separately merged in two Ensemble models (ESM-GLM 251 and ESM-GAM) with the single bivariate runs weighted according to their AUC scores. 252 Finally, these two single-technique ESMs were included in a final Ensemble model (final 253 ESM), weighted by their respective SomersD score. All the final models were projected over 254 the study region. We evaluated the guality of our models, with a maximization of their True 255 Skill Statistic score (TSS; Allouche et al., 2006; maxTSS; Guisan et al., 2017). The relative 256 importance's of each variable in the models were also extracted using the 257 ecospat.ESM.VarContrib function of the ecospat package, which sums separately the 258 weights of the bivariate models including each variable and compares them to the sum of all 259 the bivariate models.

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261 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 nonnesting 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 Ime4 (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.

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272 Species richness patterns of dung beetles

273 We wanted to obtain the expected species richness patterns of dung beetles in the study 274 region, which can be approximated by summing the probabilities of presence of species 275 (Dubuis et al., 2011). In order to include the highest number of potential species, we summed 276 the maps of presence probabilities of the Swiss models ESMs to get a map of the global 277 species richness. We also summed the presence probabilities for the species with the same 278 nesting behavior (endocoprids, paracoprids or non nesting Hydrophilidae) to obtain 279 predictions of species richness per group. Finally, we investigated the proportion of the 280 coprophagous entomofauna represented by the endocoprids.

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282 Results

283 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).

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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	Р
Geotrupidae	Geotrupinae	Geotrupes spiniger (Marsham, 1802)	(9)	124	Р
Geotrupidae	Geotrupinae	Geotrupes stercorarius (Linnaeus, 1758)	17	76	Р
Geotrupidae	Geotrupinae	<i>Trypocopris vernalis</i> (Linnaeus, 1758)	(2)	72	Р
Hydrophilidae	Sphaeridiinae	Cercyon haemorrhoidalis (Fabricius, 1775)	(8)	82	Н
Hydrophilidae	Sphaeridiinae	Cercyon impressus (Sturm, 1807)	88	115	Н
Hydrophilidae	Sphaeridiinae	Cercyon lateralis (Marsham, 1802)	70	203	Н
Hydrophilidae	Sphaeridiinae	Cercyon melanocephalus (Linnaeus, 1758)	23	82	Н
Hydrophilidae	Sphaeridiinae	Cercyon obsoletus (Gyllenhall, 1808)	(4)	17	Н
Hydrophilidae	Sphaeridiinae	Cercyon pygmaeus (Illiger, 1801)	46	69	Н
Hydrophilidae	Sphaeridiinae	Cercyon quisquilius (Linnaeus, 1761)	(7)	162	Н
Hydrophilidae	Sphaeridiinae	Cryptopleurum crenatum (Kugelann, 1794)	(8)	17	Н

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

296 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 304 soils (Rock) and precipitation during the driest quarter of the year (Bio17) (Figure 3). The

305 human infrastructure, wet habitats and cultivation had the lowest impact (Figure 3).

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Figure 2. Results of the Ensemble of Small Models (ESMs) calibrated at the Swiss scale 309 presented for each of the 45 species treated with the max True Skills Statistics (maxTSS) 310 ordered by median. The boxplots are colored according to the nesting behavior of the 311 species (E - Endocoprids, P - Paracoprids, H - Hydrophilidae [predatory larvae, no 312 nesting]). All the model projections are presented in Figure S1 and all the species are 313 illustrated in Figure S3.



Predictors

315 Figure 3. Relative importance of the variables used as predictors in the 45 Ensemble of 316 Small Models (ESMs) calibrated at the Swiss scale presented in increasing order of 317 importance. The climatic conditions are Bio 10 (temperature of the warmest quarter of year), 318 Bio 16 (precipitation in the wettest year guarter) and Bio17 (precipitation of the driest guarter 319 of the year). For the full descriptions of the predictors, see Table 1.

320

321 Vaud Alps model (Regional)

322 On the 46 species recorded in the study area, 23 had at least 15 occurrences and were 323 therefore used to build ESMs. The regional models showed a high heterogeneity in their 324 performances (worst model: Acrossus rufipes, median maxTSS = 0.40, best: Parammoecius 325 gibbus, median maxTSS = 0.85) (Figure 4). We present all the maps in the supplementary 326 material (Figure S2). At the level of the study region, the variable with the highest 327 contribution in the models were the proportion of rock and bare soil cover (Rock), the carbon 328 isotope composition of the soil (∂^{13} C) the mean temperature of the warmest guarter of year 329 (Bio10) (Figure 5), while the cultivation proportion, the human infrastructure and the solar 330 radiation had the lowest contribution (Figure 5).

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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.

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350 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%.

366 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.

380

381 **Discussion**

382 We investigated the influence of various factors on the distributions of coprophagous beetle 383 species in the Western Swiss Alps using correlative species distribution modeling (SDM) 384 approaches based on quantifying habitat suitability (Guisan et al. 2017). Given the high 385 number of species with small number of occurrences, we used a particular approach recently 386 developed for small sample sizes: ensemble of small models (ESMs; Lomba et al., 2010; 387 Breiner et al., 2015, 2018). In our models, the predictors with the greatest importance always 388 included climatic variables (Figure 3; Figure 5), like in many SDM studies (Pradervand et al., 389 2013; Scherrer et al., 2019), demonstrating once more the importance of those limiting 390 factors. Interestingly, in both models (i.e. Swiss and Regional) the proportion of rock and 391 bare soil cover (Rock) was an important predictor (Figure 3B, Figure 5B), which could be due

392 to a higher proportion of unvegetated surfaces at higher altitudes, where the species are also 393 better modeled, artificially increasing the influence of species inhabiting these areas in the 394 results. Another possibility could be that more species are expected in pastures of high 395 ecological value (i.e. with a high overall biodiversity), which are grasslands with 396 discontinuous vegetation cover due to low fertilization rate (Delarze et al., 2015). In addition, 397 the superficial cover by rocks could be an indirect way of quantifying the heterogeneity of the 398 landscape around the occurrence points. For instance, Negro et al. (2011) suggested that 399 habitat heterogeneity, especially the presence of natural forested areas next to pastures, 400 plays an important role in increasing dung beetle species richness. Forest edges brought an 401 important contribution as predictor in our models even if this predictor was not in the top ones 402 (Figure 3B; Figure 5B). In contrast, some variables had little influence in our models. These 403 are often land cover or land use variables with small cover in Switzerland (e.g. wet habitats) 404 or in the study region (e.g. cultivations) but it is difficult to know if it is the low frequency of 405 these variables over the landscape that induces their smaller influence in the models or if 406 they really do not have an influence on species distributions.

407 Our ESMs had very variable predictive performances as measured by the maximized TSS 408 (see Guisan et al., 2017), with values ranging from 0.27 to 0.93 for the Swiss models (Figure 409 2) and from 0.40 to 0.85 for the regional models (Figure 4). We tried to explain the variability 410 of our model performances with species characteristics and found that species present over 411 a wide altitudinal range had weaker models compared to the species occurring in a narrower 412 altitudinal amplitude (Figure 6A). Our results are in line with those of Guisan and Hofer 413 (2003) and Grenouillet et al. (2011), who showed that the distributions of generalist species 414 are more difficult to predict. These results are also consistent with those of Tessarolo et al. 415 (2021), who found that niche marginality has a major influence on the models' quality for 416 dung beetles in Spain. On the other hand, we found no influence of the nesting behavior 417 (Figure 6B) nor the size of the species (Figure 6C) on the maxTSS of the models meaning 418 that these biological traits seems not being relevant to explain the models quality. However, 419 further analyses could be performed to try to improve the predictive performances of 420 generalist species by taking into account the co-occurrences patterns through the region, 421 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

429 richness depends on the nesting behavior: the paracoprids (Figure 7B) and the 430 Hydrophilidae (Figure 7D) show a sharp decrease while the endocoprid a smoother one. This 431 latter group forms the biggest part of the dung beetle diversity at high altitude where almost 432 no paracoprids and Hydrophilidae are found (Figure 6B and 6E). This is consistent with other 433 studies (Lobo et al. 2007) and is explained by the fact that endocoprid beetles are expected 434 to be more cold tolerant since they need the dung patches to remain moist for the entire 435 development of their larval stage and are outcompeted in warmer climates by paracoprids, 436 which avoid the endocoprid to use dung by burying it (Hanski, 2016).

- 437 Our field sampling designed in a random stratified manner permitted to be representative of 438 the environment of the study area and likely allowed us to find a high number of dung beetles 439 species. From a faunistical point of view, our study brings precious new records for 440 coprophagous beetles, an under sampled taxon in comparison to other insect groups such 441 as orthopteras or butterflies, and even more compared with vertebrates (Troudet et al., 2017. 442 Indeed, the data sampled in our study represents now 17.9% (N=1120) of all precise 443 occurrences existing for the 46 dung beetle species in Switzerland (N=6258). We also found 444 that an important proportion of the coprophagous beetle species of Switzerland is found in 445 the Vaud Alps (41.6%). These data represent a key source of knowledge for ecologically and 446 economically important taxa, which had never been studied in the Vaud Alps region, contrary 447 to many other groups of organisms, reinforcing the status of biodiversity hotspot of this study
- region in the European Alps (Lassen and Savoia, 2005).
- 449

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698 Supplementary material





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



709Teuchestes fossorOnthophagus baraudiOnthophagus fracticornis710Figure S2. Map of the 23 species for which a model was run at the Regional scale. Red

- 711 represent areas with high presence probability while blue the areas with low presence
- 712 probability of the species.













Copris lunaris

Euoniticellus fulvus

Onthophagus baraudi

Onthophagus coenobita Onthophagus fracticornis

Geotrupidae

Onthophagus illyricus

Scarabaeidae, Scarabaeinae









Geotrupes spiniger

m

Geotrupes stercorarius



Trypocopris vernalis

714



- **Figure S3.** Illustration of all the dung beetle species found in the study region. Illustration:
- 717 Vivien Cosandey.
- 718