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Unequal before the laws of nature: importance of environmental variables in butterfly distributions vary according to functional traits

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Jean-Nicolas Pradervand

Directeur : Pr. Antoine Guisan

Superviseurs : Pr. Antoine Guisan, Pr. Daniel Cherix, Loïc Pellisier

Expert (s) : Dr, Mary, Wisz

Département d'écologie et d'évolution

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Jean-Nicolas Pradervand^{1*}, Loïc Pellissier¹, Anne Dubuis¹, Julien Pottier¹, Luigi Maiorano¹, Daniel Cherix^{1,2}, Antoine Guisan^{1,3}

1 Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland; 2 Museum of Zoology, Palais de Rumine, Place de la Riponne 6, CH-1014 Lausanne, Switzerland; 3 Faculty of Geosciences and Environment, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland

*Corresponding author: Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland; Fax +41 21 692 42 65; E-mail: Jean-Nicolas.Pradervand@unil.ch

Abstract

1

2 **Aim** In the light of global changes, environmental drivers determining species distributions need to
3 be understood to protect remaining natural ecosystems or create artificial new sites for conservation
4 purpose. The importance of environmental drivers, whether biotic or abiotic, can vary according to
5 the species characteristics. In this study, we investigated the importance of several drivers of
6 butterfly distribution and if this is related to species functional characteristics.

7 **Location** The Western Alps of Switzerland.

8 **Methods** We compared species distribution models (SDM) of 68 of the most frequent butterfly
9 species monitored in the area modeled using a set of climatic, land cover, or vegetation-derived
10 variable. We calculated the fit and predictive power of the models with climatic drivers only
11 compared models with climatic and land cover or vegetation derived variable. Using a variance
12 partitioning approach, we assessed the relative importance of each of the three groups of drivers and
13 related it to three ecological traits (namely dispersal capacity, trophic specialization and habitat
14 specialization) using a co-inertia analysis.

15 **Results** The improvement of the fit and predictive power of the SDMs when adding land cover or
16 vegetation-derived variables vary unequally across species. The relative importance of the three
17 groups of variables is related to the species traits. The distributions of habitat specialist or trophic
18 specialist species were more explained by vegetation-derived variables than those of the more
19 generalist species. The importance of climatic variables in the models was higher for species
20 displaying lower dispersal abilities.

21 **Main conclusions** Our study shows the importance of using appropriate modeling variables in SDMs
22 highlighted by the important differences in the accuracy of species models depending the different
23 variables. All distributions should not be modeled with similar variables, but their choice of should
24 depend on species characteristics to achieve accurate predictions of species distribution under global
25 change.

26 **Keywords** Species distribution modeling; ecological traits; biotic factors; abiotic factors; butterfly;
27 mountain.

28

28 **Introduction**

29

30 Understanding the drivers whether abiotic or biotic determining species range is a
31 fundamental question in both ecology and biogeography and has gained much interest recently in
32 the light of global changes. In particular, human imprint on natural ecosystems causes biodiversity
33 erosion and knowledge on biodiversity pattern can help protect the remaining natural ecosystems or
34 create artificial site to optimize conservation (Sala et al. 2000). Climatic but also biotic and habitat
35 variables are considered important drivers of species range (Randin et al. 2009; Pellissier et al. 2010).
36 However, the relative importance of these drivers can vary according to the species characteristics.
37 For instance, competitively dominant or generalist species can occupy the entire abiotic environment
38 that is favorable, while low competitive species or specialized species will occupy only a subset of the
39 climatic niche (Pellissier et al. 2010). Several studies showed that such functional traits can affect
40 habitat suitability and species distributions (Thuiller *et al.* 2010; Hanspach *et al.* 2010). Accounting for
41 biotic drivers, namely variables directly related to living organisms, in complement to climatic ones
42 can bring more precise information on local environmental conditions, sometimes totally
43 independent from the climatic conditions (Meier et al. 2010). Similarly, while some species have no
44 specific habitat requirements, others thrive only in particular habitats (Garcia-Barros & Romo Benito
45 2010) and accounting for this information can increase the ability to predict species range. As a
46 consequence, the importance of biotic and habitat in complement to climatic variables might depend
47 on species traits and this should be considered when investigating the species distributions. Yet, few
48 studies investigated the importance of abiotic and biotic components in determining species range
49 and how this is related to traits.

50 Butterflies are highly variables as regard to their functional traits that in turn can affect their
51 distributions. Indeed, there is a wide variation range, for example, with high dispersal species
52 migrating towards South in autumn and strict habitat specialists, closely linked to small areas, or
53 polyphagous species feeding on dozen of host plants and monophagous species, dependant on single
54 host plants. (Kuusaari *et al.* 2007; McPherson & Jetz 2007; Pöyry *et al.* 2008; Stefanescu *et al.* 2010).
55 Pöyry et al. (2008) showed that species traits have an important impact on the reliability of the
56 bioclimatic models with some species groups more accurately modeled than others (see also
57 McPherson & Jetz 2007). This high functional variability as regard to their ecological traits makes
58 them good test species. Moreover, they are considered an excellent bioindicator of ecosystem health
59 and understanding the drivers of distribution of this group can be useful to protect more cryptic
60 organisms. Also, butterflies respond very quickly to both climate change (Bradford et al. 2003, Currie
61 *et al.* 2004, Parmesan 2006; Wilson *et al.* 2007) and habitat change (Kuussaari *et al.* 2007). Several

62 studies have demonstrated rapid altitudinal or poleward shifts in butterfly populations to counter
63 the raise of temperature due to global warming (Parmesan *et al.* 1999, Walther *et al.* 2002;
64 Parmesan *et al.* 2003; Malcolm *et al.* 2002). However, the ability to track climate change was also
65 shown to depend on species traits with mobile species often living in more available habitats, i.e. like
66 forest hedges instead of dry grasslands and showing more important shifts towards North than
67 specialized species sometimes strongly related to rare environments (Parmesan *et al.* 1999; Pöyry *et*
68 *al.* 2009). The important differences in the species' response to climate change show the differences
69 between the species' adaptability. Thus, it is necessary to consider species characteristics when
70 predicting responses to environmental changes.

71 The use of climatic drivers dominates as predictors of butterfly's distributions and a few
72 models use biotic interactions (Guisan & Thuiller 2005). Hence, Gutiérrez *et al.* (2010) found that
73 climatic variables were the most important variables when modeling species distributions in
74 mountain meadows, even at fine resolutions, while the effect of other variables, like land cover were
75 very limited. In opposition, Bergman *et al.* (2004) found a significant effect of the landscape
76 structures on butterfly assemblages, especially near deciduous forest and semi-natural grasslands
77 with trees and bush cover. Moreover, human pressure on natural habitats can have a strong impact
78 on species distributions, through the land use (Stefanescu *et al.* 2010). Hence, land cover changes
79 destructing species habitat has been cited as one of the major causes of species extinction (Dirzo &
80 Raven 2003). However, biotic variables can also be important drivers of butterfly distributions
81 through the host plant or vegetation diversity, but also through other biotic interactions like, for
82 some species, the host insect (Araujo & Luoto 2007; Schweiger *et al.* 2008; Jiménez-Valverde *et al.*
83 2008, Wharton & Kriticos 2004; Garcia-Barros & Romo Benito 2010).

84 The aim of this study is to investigate the drivers of distribution of the butterfly fauna in a
85 mountainous region of the western Alps of Switzerland and also if this distribution is related to
86 species functional characteristics. We compared the distribution models of 68 of the most frequent
87 species when modeled with climatic, climatic and land cover, or climatic and biotic variables and we
88 calculated the variance explained by each variables for all the species. We related the importance of
89 the three categories of variable to three functional traits using a co-inertia analysis on two principal
90 component analysis tables calculated on the traits and on the variables. We expected the following:

- 91 1. Adding information on the land cover as well as plant community composition should
92 improve the fit and predictive power of SDMs solely based on topo-climatic predictors.
- 93 2. The relative importance of topo-climatic, land cover and biotic variables should be related to
94 species biological traits. In particular, biotic and land cover factors should be important for

95 specialist species like trophic specialists and habitat specialists, whereas climate variables
96 should be more important for highly mobile and generalist species.

97 **Material & Methods**

98

99 **Study area**

100 The study area is located in the western Alps of Switzerland, in the Canton de Vaud and is
101 ranging from 1000m elevation to 3120m, on the top of *Diablerets* chain (Fig. 1). Along the altitudinal
102 gradient, a turnover of several vegetation belts can be found. The mountain belt composed of mixed
103 forests of European beech (*Fagus sylvatica*) and Silver fir (*Abies alba*) is gradually replaced by the
104 subalpine belt, a coniferous forest principally composed of Norway spruce (*Picea abies*). at higher
105 elevation, the alpine belt with heath, meadow, and grassland vegetation dominates (e.g. *Nardus*
106 *stricta*, *Carex sempervirens*) and finally is replaced by the nival belt composed of scattered patches of
107 vegetation dominated by cold tolerant taxa like *Saxifraga aizoides* or *Cerastium latifolium*. The
108 influence of land use is important in this mountain region where almost all pastures and meadows
109 are or have been exploited. However, the strongest impact happens in open areas at lower altitudes
110 where land use is particularly intense, with fertilized arable lands and grasslands used for silage
111 dominated by nitrophile species like *Arrhenatherum elatius* or *Trifolium sp.* while at intermediate
112 elevations, fertilized pastures or meadows for the cattle can be found. In less intensively managed
113 parcels grasslands are more diversified with dominance of *Bromus erectus*. Above the treeline, the
114 impact is restricted to summer grazing in low productive pastures dominated by *Poa alpina*, *Nardus*
115 *stricta* and *Sesleria caerulea*.

116 **Field sampling**

117 We selected plots of non-forest vegetation following a random stratified sampling based on
118 altitude, slope and aspect. During the summers 2009 and 2010, we sampled 192 plots between June
119 1 and September 15 during optimal flight periods for butterflies, meaning a minimum of 18°C (13°C
120 for high elevations), low wind, a minimum of 80% of cloudless, and between 10:00 and 17:00 (see
121 Pollard and Yates 1993). To ensure the catching of every species, independently of their phenology,
122 each plot was visited every three weeks. For each plot, a 2,500m² area was delimited, corresponding
123 to a 50 by 50 meters plot. We randomly walked this area during 45 minutes, captured butterflies
124 with a net, identified them on the field and then released them. At the center of each plot, we
125 conducted a 2 by 2 meters exhaustive vegetation inventory. Species cover was estimated in 10
126 classes following Vittoz & Guisan (2007): <0.1%, 0.1-0.5%, 0.5-1%, 1-3%, 3-5%, 5-15%, 15-25%, 25-
127 50%, 50-75% and >75% and a total of 562 plant species have been inventoried. We found 131
128 butterfly species, including skippers (*Hesperiidae*) and burnet moth (*Zygaenidae*). For further analysis

129 we used only species with a minimum of 20 occurrences to avoid statistical errors due to the
130 important number of predictors used in the models.

131 **Environmental variables**

132 To model the distribution of butterfly species, we used several predictors from three
133 categories. First we used three climatic variables: Degree-days (DDEG) affect both imago and
134 caterpillar through physiological tolerance to freezing or cold temperature, influencing the survival of
135 caterpillars (Fischer *et al.* 2003); this sum of monthly average temperatures was calculated following
136 Zimmermann and Kienast (1999). Solar radiations (SRAD), retained as one of the best factor
137 explaining butterfly distributions by Turner *et al.* (1987) and Bradford *et al.* (2003), was calculated
138 using Kumar's approach (Kumar *et al.* 1997) and considers both direct and diffuse components of
139 global solar radiation. A moisture index (MIND) was also calculated as the difference between
140 precipitation and evapotranspiration. Moisture is an important factor to be considered for the egg
141 survival. Indeed, beyond a certain threshold, eggs cannot counter desiccation, which brings larvae
142 death (Merrill *et al.* 2008). We calculated three additional variables considered as biotic because they
143 relate to the plant composition to which butterfly are trophically related: plant species richness,
144 taken from the vegetation inventory and calculated with the count of inventoried species in each
145 sampling plot. The pH has been extrapolated from the Landolt values of those plant species present
146 in the 4m² plot (Landolt 1977). Landolt values represent a characterization of the ecological
147 conditions needed by the plant and include indexes of moisture, temperature, light, nutrients,
148 reaction (acidity) and continentality. We used the reaction index, weighted by species abundances to
149 calculate the mean pH value on each plot. The same method was applied to calculate a mean
150 nutrient value for each plot (N). Finally two landscape variables were calculated from the land cover
151 data: the proportion of forest, calculated with a 500m window around the plot (PROPFOR), showing
152 the heterogeneity of the environment; and an indication of forest hedges that influence the diversity
153 of open area species at fine scale (Schneider *et al.* 2001). We also calculated the Shannon diversity
154 index (DIV) with a 500m moving window around the plot using the Fragstat software (McGarigal *et*
155 *al.* 2002). Due to the size of the plots and the mobility of the species, we used a 100m resolution for
156 all these variables.

157 **Species modeling**

158 We modeled each species distributions using Generalized Linear Models (GLM) (Mc Cullagh &
159 Nelder, 1989) with second order polynomials (i.e. quadratic terms) with a binomial distribution and a
160 logistic link function. We used GLMs because of the biological explanation that can be more easily
161 drawn from them. Indeed, comparing factors among species is easier with the parameters and
162 response curves supplied by the GLM than with many other modeling techniques, consequently

163 more difficult to interpret in an ecological way. In this study we modeled the distributions of 68
164 butterfly species with climatic predictors (DDEG, SRAD and MIND) and then included sequentially
165 land cover predictors (PROPFOR and SHADIV), biotic predictors (pH, N and DIV), or both. GLMs were
166 implemented in the R environment (R Development Core Team 2010). In order to evaluate SDMs, we
167 run a 10-fold cross-validation and measured the predictive power using the area under the receiver
168 operating characteristics (ROC) curve (AUC, Fielding and Bell, 1997). We also compared the model fit
169 estimated with the adjusted geometric mean squared improvement R^2 (Cox and Snell 1989;
170 Nagelkerke 1991). It is rescaled to a maximum of 1 and adjusted to the number of observations and
171 predictors in the model (Guisan & Zimmermann 2000).

172 **Testing the importance of biotic and land cover predictors in SDMs**

173 We used a variance partitioning approach based on partial regression analysis to separate
174 the variance allocated to each factor. This approach enables variance partitioning into four fractions
175 (Brocard *et al.* 1992; see Randin *et al.* 2009 for a similar implementation). A total of seven GLMs were
176 run for each species to catch the variance explained by each factor: 1) pure climatic (CL), 2) pure land
177 cover (LU), 3) pure biotic (BIO), 4) shared climatic and land cover (CL+LU), 5) shared climatic and
178 biotic (CL + BIO), 6) shared land cover and biotic (LU + BIO), 7) shared climatic, land cover and biotic
179 (CL + LU + BIO).

180 **Assessing the role of species traits**

181 To evaluate the influence of the different factors, we sorted the species depending on three
182 species biological traits, namely the trophic specialization (TS), the habitat specialization (HS) and the
183 dispersal capacity (DC). We calculated the two first traits (the foraging capacity and the habitat
184 specialization) from a summary of the different biological characteristics of Swiss butterfly species
185 principally taken LSPN (1987). The habitat specialization corresponds to the number of typical
186 biotope where the species can be found and is ranging from 1 to 13 (cf. table 2). The trophic
187 specialization is an index containing the sum of the species' host plants. The dispersal capacity was
188 taken from Bink *et al.* (1992) and updated to cover the 68 species. The dispersal capacity follows a 9
189 groups classification from 1 (Very sedentary) to 9 (Highly mobile). These different traits have been
190 used to classify the butterfly species into several groups to have a better understanding of the
191 importance of biotic and/or land cover variables on each group.

192 To investigate the relationships between the traits, the variables and the species, we
193 performed a principal component analysis on each of the two datasets (traits and variables) and
194 matched these PCAs using a co-inertia analysis (COIA) (Dolédec *et al.* 1996). This multivariate analysis
195 couples two tables defining axes that will explain the highest possible variance for each of the two
196 datasets. Hence we could match the two different PCA tables previously analyzed and find a co-

197 structure (Dray *et al.* 2003). A Monte-Carlo test, with 100'000 random permutations, has then been
198 applied on this co-structure for testing its validity.

199 **Results**

200 **Species modeling**

201 When the land cover variables were added, the mean AUC increased ((+ 14.1% in fit; +1.0% in
202 the AUC) but remained nevertheless relatively low and varied a lot depending on the species. The
203 improvement was particularly high for several species like *Zygaena transalpina* (+ 76.4% in fit;
204 +12.2% in the AUC) *Vanessa cardui* (+ 87.6% in fit; +14.4% in the AUC) and *Polyommatus eros* (+
205 77.1% in fit; +17.5% in the AUC). However, the predictive power of the models of other species
206 decreased, for example *Pieris rapae* (+ 3.1% in fit; -8% in the AUC), *Boloria napae*(+ 0.5% in fit; -5% in
207 the AUC) or *Erebia aethiops* (+ 1.7% in fit; -3% in the AUC).

209 Overall, when the biotic variables were added, the fit increased, but the predictive power of
210 the models decreased (+ 6.9% in fit; -0.2% in the AUC). Nevertheless, the models of some species
211 were particularly improved, for example *Polyommatus eros* (-6.0% in fit; +5.1% in the AUC) or *Colias*
212 *crocea* (+ 51.2% in fit; +7.1% in the AUC), and *Vanessa cardui* (+ 67.4% in fit; +14.3% in the AUC),
213 whereas the predictive power of the model of some other species decreased like for *Erebia tyndarus*
214 (+ 1.6% in fit; -7.0% in the AUC), *Pyrgus alveus* (+ 0.2% in fit; -6.7% in the AUC) or *Papilio machaon* (+
215 7.9% in fit; -6.1% in the AUC).

216 **Importance of biotic and land cover predictors in SDMs**

217 The principal component analysis (PCA) performed on the variance of the three variables
218 (Fig. 2) discriminated between the biotic, land cover and climate variables, with the two latter being
219 strongly opposed. In the second PCA on the traits (Fig. 3), the species were irregularly distributed,
220 indeed although a good sorting by the three traits, an important group remains clumped with a low
221 discrimination of DC and HS traits while the other group was well spread across the PCA, with a good
222 discrimination by these two traits. The patch of grouped species principally included specialist
223 species, strongly bound to a certain type of environment, often trophic specialists while the other
224 species being more mobile species, potentially found in several habitats. Moreover, those two traits
225 were closely related.

226 **Role of species traits**

227 The co-inertia analysis (Fig 4a) performed with the two PCA was significant in a Monte-Carlo
228 permutation test ($p=0.0057$, 100'000 permutations) and clearly indicated a good discrimination of
229 the land cover variance compared to climate or biotic variance for some widely distributed species.
230 But the land cover variance was however low and almost opposed to the effect of climate. The co-

231 inertia axis were explaining an important part of the variance of the two PCA tables with respectively
232 64.1% and 84.3% for the X axis (Fig. 4b) and 95.6% and 97.7% for the Y axis (Fig 4c). The global
233 structure of the two tables was rather conserved by the co-inertia analysis and indicated a co-
234 structure between the species traits and the explained variance of the models. The co-inertia
235 analysis was then interpreted using the two factor maps (Fig. 4d & Fig. 4e). The first pattern coming
236 out revealed a strong negative relation between dispersal capacity (DC) and climate factors. The
237 second pattern reflected habitat specialization (HS), also negatively related to biotic factors. The
238 trophic specialization (TS) was related in equal part to climate and biotic factors. We could also infirm
239 the low inertia of the land cover in this analysis due to the very limited relationship between the
240 traits and the land cover variables.

241 **Discussion**

242

243 Species displaying distinct functional characteristics are unlikely to respond identically to
244 environmental factors (Pöyry *et al.* 2008). We showed that including land cover and biotic variables
245 in the climatic SDMs of butterflies improved their fit and predictive power in accordance with our
246 first expectation, but unequally across species. Also, the importance of the three groups of variables
247 in the models was dependant on species trait: the distribution of the species which are specialized in
248 term of habitat and host plants was more explained by biotic factors than those of the more
249 generalist species. Moreover, the importance of climatic variables in the models was higher for
250 species displaying lower dispersal abilities. On the other hand, the improvement brought by land
251 cover factors, despite improving some models, was not related to any species traits. Considering the
252 ecological characteristics of the species can thus provide an important insight on the variables to
253 include in SDMs to explain butterfly species distribution.

254 According to MacArthur (1972), climatic factors are the main drivers of species range limit
255 under stressful conditions, while biotic interactions are more important determinants towards less
256 stressful conditions. The caterpillars of generalist species can feed on a wide range of host plants
257 while some specialists just have a few, or even a single (Kuussaari *et al.* 2007). Also, specialization on
258 a restricted range of plants allows maximizing their efficiency towards competitors and favoring this
259 strategy in order to improve feeding efficiency on plant with singular chemistry. However, this
260 remains advantageous as long as the plant can be easily found and might be reduced in perturbed or
261 harsh environments (Jaenike 1990). This kind of trophic specialization generally occurs on species
262 rich and stable environments (Moldenke 1975), principally at low or mid-elevations (Futuyma &
263 Moreno 1988; Moldenke 1975). Hence, the trophic relationship between caterpillars and their host

264 plant is very strong and likely to have a direct effect on butterfly distributions, because specialized
265 species depend on the occurrence of a restricted range of host plants where to lay their eggs (Merrill
266 *et al.* 2008). For those species, higher plant species richness relates to a higher probability of finding
267 the suitable host plant, while acidity and nitrogen relate to the composition of the plant community.
268 At lower altitude, land use is particularly intense and causes strong heterogeneity in particular as
269 regard to plant species richness (Stevens *et al.* 2004, Randin *et al.* 2009, Dubuis *et al.* 2010).
270 Unaccounting for this important variation in land use affecting butterfly trophic interactions with
271 plants, the distribution of trophically specialized species might not be entirely captured in SDMs.

272 While the global impact of adding biotic factors is limited, we showed, as expected, the
273 strong importance of biotic factors on SDMs of trophically specialized species. These results are in
274 accordance with McPherson & Jetz (2007) or Hernandez *et al.* (2006) who showed differences in the
275 reliability of SDMs depending on species traits. Indeed, there is a clear trend in the modeling
276 accuracy of some species, principally specialists, sorted with biological traits. Hence, the strong
277 relationship between the trophic specialization, the butterflies' habitats and the biotic factors can be
278 linked, like in Pöyry *et al.* (2007), to more sedentary and trophic specialist species showing models
279 with more variance explained by the biotic factors than generalist species. Moreover, from these,
280 several are nitrogen-free grasslands species (mainly habitat, trophic specialist or both), supporting
281 the study of McPherson *et al.* (2007) who pointed accuracy of the models to depend on dispersal,
282 habitat specialization and trophic specialization.

283 In opposition, despite improving the fit and predictive power of some models, the
284 importance of land cover was not related to the functional traits considered. Habitat and landscape
285 diversity is particularly important for maintaining biodiversity (Schneider *et al.* 2001). Indeed highly
286 diversified environments are often richer in species composition than homogeneous environments
287 (Weibull *et al.* 2000) because it allows a higher number of species with specialized habitat to occur.
288 As a consequence, we expected that models of habitat specialists should be improved by this factor.
289 However, despite the low global improvement for most species brought by the land cover predictors,
290 as observed in Guitérrez Illán *et al.* (2010) or Jonason *et al.* (2010), some particular species models
291 were strongly improved. Nevertheless, the importance of land cover in the SDMs was not related to
292 any species traits not even to habitat specialization. Hence, land cover variables improved both
293 habitat specialists and habitat generalists, which could explain the absence of trend. But, this
294 absence might also be due the landscape variables, possibly too general, thus affecting all species.
295 However, as expected, models of habitat specialist like *Polyommatus eros* found in rocky pastures or
296 *Lasiommata maera* more present on grasslands with forest edges and rocks are improved when the
297 land cover variables are added. Indeed diversified areas relate to areas less homogenized by

298 agriculture where such particular habitat can still be found. Hence, the importance of land cover was
299 high for several migratory or globally distributed species able to thrive in multiple habitats like
300 *Vanessa cardui* or *Papilio machaon*. In their study of butterfly species richness in agricultural
301 landscape, Kuussaari *et al.* (2007) noticed great diversity richness for forest margins and small and
302 various patchy landscapes, whereas bigger patches were generally less diversified due to several
303 factors like greater wind exposure (Krauss *et al.* 2003, Schneider *et al.* 2001). In such context, the
304 influence of land cover variables takes all its sense, indicating the richness of the landscape and thus
305 potentially species rich areas. Moreover, the proportion of forest induces variations in the probability
306 of the presence of the species, with several species having more occupancy probabilities depending
307 on the surrounding proportion of forests or with mobile species more present in landscapes with a
308 low amount of forest (Bergmann *et al.* 2004). Besides, a threshold value of habitat loss should exist
309 below which the species cannot survive. (Fahrig 2001)

310 Climate variables are recognized as one of the main driver of butterfly distribution (Turner *et al.*
311 1987; Bradford *et al.* 2003; Guitérrez Illán *et al.* 2010), and many studies only based their SDMs on
312 climatic variables. However, we showed that the importance of climatic variables in SDMs was higher
313 for species with low dispersal abilities. Indeed, Pöyry *et al.* (2008), noticed a decrease in the accuracy
314 of the models for highly mobility species whereas Menendez *et al.* (2007) showed that the
315 importance of these variables for generalist species outclassed the biotic or land cover variables.
316 These patterns are not opposite and can be explained in different ways. First the highly mobile
317 species will be distributed more stochastically and will however not exceed their climatic tolerances
318 at the larvae level, nor at the imago level (Stefanescu *et al.* 2010; Parmesan *et al.* 2003; Larsen & Lee
319 1993). Consequently, they will stay closer to their climatic niche. Even if high dispersers are able to
320 face harsh climatic conditions for short periods (like *Danaus* species in Larsen & Lee, 1993), they
321 should overnight in refuges at lower elevations to avoid freezing. Climatic variables should
322 consequently remain efficient to predict them, at least in resting sites. Furthermore, the
323 performance is lower for trophic specialists than for generalists showing the limited importance of
324 climatic variables for specialist species. This is related to their climatic niche but also limited by biotic
325 factors (Merrill *et al.* 2008) like the host plant, or biotic interaction with other species like those in
326 the *Maculinea* genus, needing ants from the *Myrmica* genus during their development (LSPN 1987).
327 However, climate stays an important predictor for biotope specialized species closely linked to
328 climatic conditions, like dry grasslands or wetlands.

329 The main limitation of our approach might be that instead of using directly the occurrence of
330 the host plant as a biotic factor, we do not model host plant distribution to compare the butterfly
331 and plant models like Schweiger *et al.* (2008) or Merrill *et al.* (2008). This method, efficient for

332 specialist species, has however to be cautiously handled due to the climatic interactions both on the
333 host plant and the butterfly, and the consistency of the data. Several species are well documented
334 with regards to their host plant, but it is frequent to face incomplete data. However, the higher the
335 plant richness, the higher the chance to find the host plant on the plot. Consequently the plant
336 richness (DIVEG) represents the host plant, but with the advantage to be a general variable not
337 species dependant.

338 These assumptions are even reinforced in a global changes context, where species
339 distributions are more likely to be dependant on their biological characteristics. For example, more
340 tolerant species or species with greater dispersion rates polewards could be favored. Indeed the
341 ecology of the species (i.e. migratory or sedentary, specialist or generalist) can have a strong
342 influence on the models and their accuracy. For sedentary species, good predictors can however
343 decrease the power of migratory species models in trying to fit the distributions with factors
344 unrelated to the species (Luoto *et al.* 2005). These changes, already important at low elevations are
345 even stronger on mountain environments such as the Alps (Theurillat & Guisan, 2001). Up there, the
346 arable surfaces, already less considerable than in the lowland, are often totally exploited generalizing
347 the human impact on the whole area. In addition, the species present at high elevations are already
348 on the limit of their altitudinal distribution range and cannot cope with the rise in temperature by
349 altitudinal migration.

350 **Conclusions**

351 In this study we presented three different traits having a significant importance in shaping
352 butterfly distributions. We demonstrated that adding biotic or land cover factors can improve models
353 for several specialist species (and some generalists) but also that models for some other species
354 could loose predictive power. The co-inertia analysis helps us here to point at interesting trend that
355 should be taken into account when modeling species distribution. The clear split between specialists
356 and generalists, as much for the habitat specialization than the trophic specialization, is a typical
357 example of these. These important variations have to be taken into account when modeling
358 communities or groups of species. All the distributions should not be modeled with similar variables,
359 but the choice of them should depend on species traits to match as much as possible the ecological
360 preferences of groups or species.

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362
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366 **Bibliography**

367

368 Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under
369 climate change. *Global Ecology and Biogeography* 16:743-753.

370 Bergman KO et al. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography*
371 27:619-628.

372 Bink FA (1992) *Ecologische Atlas van de Dagvlinders van Noordwest-Europa*, Schuyt & Co, Haarlem. 512pp.

373 Borcard D, Legendre P, Drapeau P (2010) Partialling out the Spatial Component of Ecological Variation
374 *Ecology* 73 :1045-1055

375 Bradford A, Hawkins B, Porter EE (2003) Does herbivore diversity depend on plant diversity? The case of
376 California butterflies. *The American naturalist* 161:40-9.

377 Cox DR, Snell EJ (1989), *Analysis of Binary Data* (2nd Ed.), London: Chapman & Hall

378 Currie DJ et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in
379 taxonomic richness. *Ecology*:1121-1134.

380 Dirzo R, Raven PH (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*
381 28:137-167.

382 Dolédec S, Chessel D, ter Braak CJF, Champely S (1996), Matching species traits to environmental variables : a
383 new three-table ordination method. *Environmental and Ecological statistics* 3 :143-166

384 Dray S, Chessel D, Thioulouse J (2003) Co-inertia analysis and the linkage of ecological data tables. *Ecology*
385 84:3078-3089.

386 Fahrig L (2001) How much habitat is enough? *Biological Conservation* 100:65-74.

387 Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation
388 presence/absence models. *Environmental Conservation* 24:38-49.

389 Fischer K, Brakefield PM, Zwaan BJ (2003) Plasticity in Butterfly Egg Size: Why Larger Offspring At Lower
390 Temperatures? *Ecology* 84:3138-3147.

391 Fleishman E, Austin GT, Weiss AD (1998) an Empirical Test of Rapoport'S Rule: Elevational Gradients in
392 Montane Butterfly Communities. *Ecology* 79:2482-2493.

393 Futuyma DJ, Moreno G (1988) The Evolution of Ecological Specialization. *Annual Review of Ecology and*
394 *Systematics* 19:207-233.

395 Garcia-Barros E, Romo Benito H (2010) The relationship between geographic range size and life history traits:
396 is biogeographic history uncovered? A test using the Iberian butterflies. *Ecography* 33:392-401.

397 Gutiérrez-Illán J, Gutiérrez D, Wilson RJ (2010) Fine-scale determinants of butterfly species richness and
398 composition in a mountain region. *Journal of Biogeography* 37:1706-1720.

399 Guisan A & Thuiller W (2005) Predicting species distribution: offering more than simple habitat models.
400 *Ecology Letters* 8:993-1009.

401 Guisan A & Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*
402 135:147 - 186.

403 Hanspach J, Kühn I, Pompe S, Klotz S (2010) Predictive performance of plant species distribution models
404 depends on species traits. *Perspectives in Plant Ecology, Evolution and Systematics* 12:219-225.

405 Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics
406 on performance of different species distribution modeling methods. *Ecography* 5:773-785.

407 Jaenike J (1990) Host Specialization in Phytophagous Insects. *Annual Review of Ecology and Systematics*
408 21:243-273.

409 Jiménez-valverde A, Gómez JF, Lobo JM, Baselga A, Hortal J (2008) Challenging species distribution models :
410 the case of *Maculinea nausithous* in the Iberian Peninsula. 2450:200-210.

411 Jonason D, Milberg P, Bergman K-O (2010) Monitoring of butterflies within a landscape context in south-
412 eastern Sweden. *Journal for Nature Conservation* 18:22-33.

413 Krauss J, Steffan-dewenter I, Tscharnke T (2003) How does landscape context contribute to effects of habitat
414 fragmentation on diversity and population density of butterflies? *Diversity*:889-900.

415 Kumar L, Skidmore AK, Knowles E. (1997) Modeling topographic variation in solar radiation in a GIS
416 environment. *International Journal of Geographic Information Science*, 11:475-497.

417 Kuussaari M, Heliola J, Luoto M, Poyry J (2007) Determinants of local species richness of diurnal Lepidoptera
418 in boreal agricultural landscapes. *Agriculture, Ecosystems & Environment* 122:366-376.

419 Kuussaari M, Heliölä J, Pöyry J, Saarinen K (2007) Contrasting trends of butterfly species preferring semi-
420 natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation*
421 11:351-366.

422 Körner C (2009) Global Statistics of “Mountain” and “Alpine” Research. *Mountain Research and Development*
423 29:97-102.

424 Kühn I, Bierman SM, Durka W, Klotz S (2006) Relating geographical variation in pollination types to
425 environmental and spatial factors using novel statistical methods. *The New phytologist* 172:127-39.

426 Landolt E (1977) *Ökologische Zeigerwerte zur Schweizer Flora. Veroff. Geobot. Inst. Rubel* 64. 208pp.

427 Larsen K, Lee E (1994) Cold Tolerance Including Rapid Cold-hardening and Inoculative Freezing of Fall Migrant
428 Monarch Butterflies in Ohio. *J. Insect Physiol* 40:859-864.

429 Luoto M, Pöyry J, Heikkinen RK, Saarinen K (2005) Uncertainty of bioclimate envelope models based on the
430 geographical distribution of species. *Global Ecology and Biogeography*:575-584.

431 LSPN (1987) *Les papillons de jour et leur biotopes : espèces, dangers qui les menacent, protection. Ligue suisse*
432 *pour la Protection de la Nature, Bâle*. 512pp.

433 Malcolm JR (2002) Estimated migration rates under scenarios of global climate change. *Journal of*
434 *Biogeography* 7:137-849.

435 McArthur RH (1972) *Geographical Ecology. Harper & Row, New York*. 265pp.

436 McCullagh P, Nelder J (1989) *Generalized linear models. 2nd. Ed. Monography on statistics and applied*
437 *probabilities* 37. New York (NY). Chapman & Hall/CRC

438 McGariral K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS : Spatial pattern analysis program for
439 categorical maps. *Comp Software prog Univ. Mass. Amhast*.

440 McPherson J, Jetz W (2007) Effects of species? ecology on the accuracy of distribution models. *Ecography*
441 30:135-151.

442 Meier ES et al. (2010) Biotic and abiotic variables show little redundancy in explaining tree species
443 distributions. *Ecography*:no-no.

444 Menéndez R et al. (2007) Direct and indirect effects of climate and habitat factors on butterfly diversity.
445 *Ecology* 88:605-11.

446 Merrill RM et al. (2008) Combined effects of climate and biotic interactions on the elevational range of a
447 phytophagous insect. *The Journal of animal ecology* 77:145-55.

448 Moldenke AR (2011) International Association for Ecology Niche Specialization and Species Diversity along a
449 California Transect. *Ecology* 21:219-242.

450 Nagelkerke NJD (1991) A Note on a General Definition of the Coefficient of Determination. *Biometrika* 78:691.

451 Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of*
452 *Ecology, Evolution, and Systematics* 37:637-669.

453 Parmesan C et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional
454 warming. *Nature* 399:579-583.

455 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems.
456 *Nature*:37-42.

457 Pellissier L et al. (2010) Species distribution models reveal apparent competitive and facilitative effects of a
458 dominant species on the distribution of tundra plants. *Ecography*.

459 Pollard E, Yates T. J (1993) Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London

460 Pöyry J, Luoto M, Heikkinen RK, Kuussaari M, Saarinen K (2009) Species traits explain recent range shifts of
461 Finnish butterflies. *Global Change Biology* 15:732-743.

462 Pöyry J, Luoto M, Heikkinen RK, Saarinen K (2008) Species traits are associated with the quality of bioclimatic
463 models. *Global Ecology and Biogeography* 17:403-414.

464 Randin CF et al. (2009) Climate change and plant distribution: local models predict high-elevation persistence.
465 *Global Change Biology* 15:1557-1569.

466 Sala OE (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287:1770-1774.

467 Schneider C, Fry GLA (2001) The influence of landscape grain size on butterfly diversity in grasslands. *Journal*
468 *of Insect Conservation*:163-171.

469 Schweiger O, Settele J, Kudrna O, Klotz S, Kühn I (2008) Climate change can cause spatial mismatch of
470 trophically interacting species. *America* 89:3472-3479.

471 Stefanescu C, Carnicer J, Peñuelas J (2010) Determinants of species richness in generalist and specialist
472 Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography*.

473 Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of nitrogen deposition on the species richness of
474 grasslands. *Science. New York (N.Y.)* 303:1876-9.

475 Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in European alps : A Review.
476 *Climatic Change*:77-109.

477 Thuiller W, Albert CH, Dubuis A, Randin C, Guisan A (2010) Variation in habitat suitability does not always
478 relate to variation in species' plant functional traits. *Biology letters* 6:120-3.

479 Turner JRG, Gatehouse CM, Corey C a (1987) Does Solar Energy Control Organic Diversity? Butterflies, Moths
480 and the British Climate. *Oikos* 48:195.

481 Vittoz, P and Guisan A (2007). How reliable is the monitoring of permanent vegetation plots? A test with
482 multiple observers. *Journal of Vegetation Science* 18:413-422.

483 Walther GR et al. (2010) Ecological responses to recent climate change. *Nature* 416:389-395.

484 Wharton TN, Kriticos DJ (2004) The fundamental and realized niche of the Monterey Pine aphid, *Essigella*
485 *californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia.
486 *Diversity and Distributions* 10:253-262.

487 Weibull AC, Bengtsson J, Nohlgren E (2010) Diversity of Butterflies in the Agricultural Landscape : the role of
488 farming system and landscape heterogeneity. *Ecography* 23:743-750.

489 Wilson RJ, Gutiérrez D, Gutiérrez J, Monserrat VJ (2007) An elevational shift in butterfly species richness and
490 composition accompanying recent climate change. *Global Change Biology* 13:1873-1887.

491 Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus
492 community approach. *Journal of Vegetation Science* 10:469-482.

493

493 **Figures**

494

495 **Figure 1:** *Sampled plots of the area. Western Alps of Switzerland*

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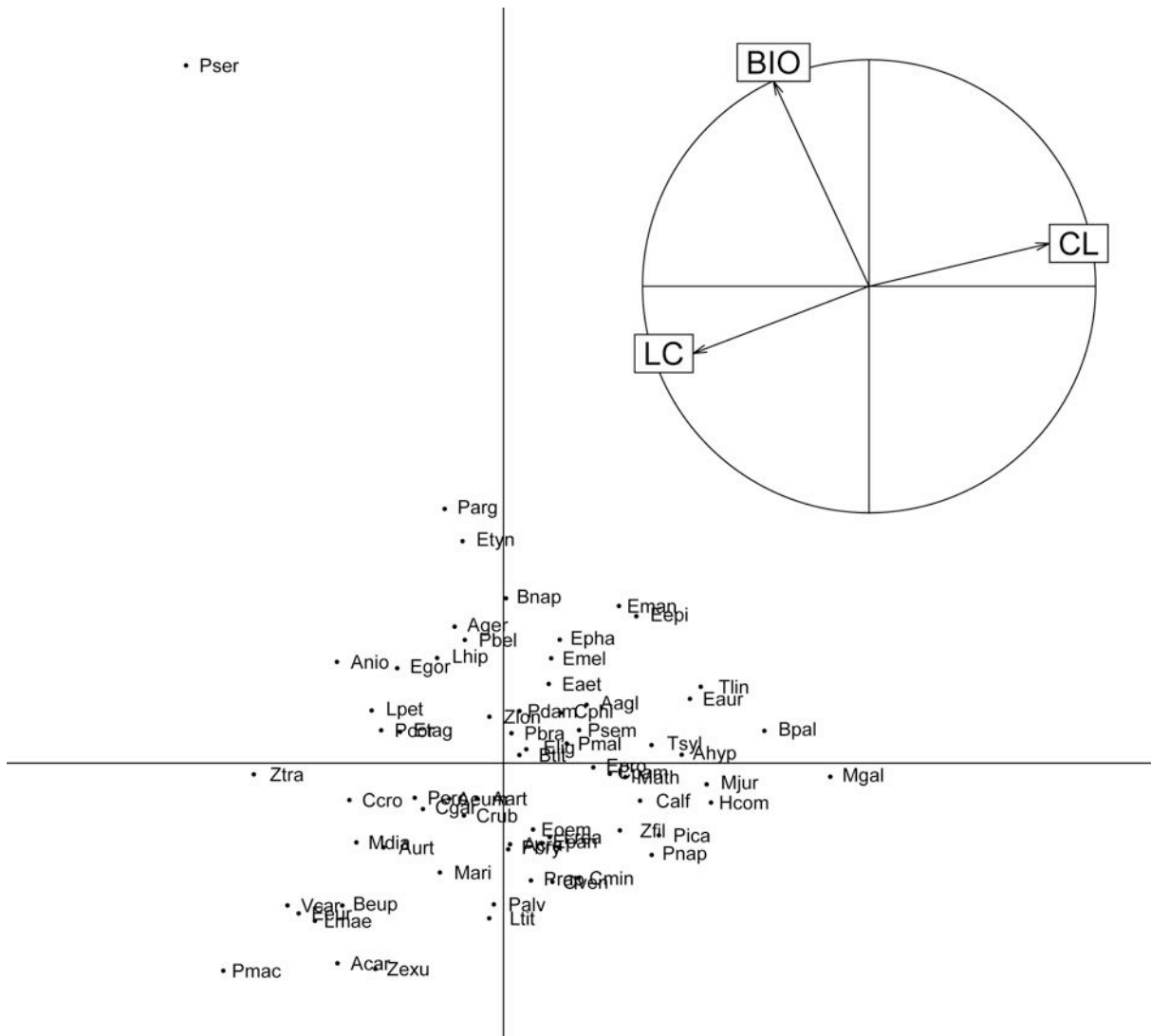


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498 **Figure 2:** Principal component analysis on the variance partitioning of climatic (CL), biotic (BIO) and
 499 land use (LU) variables with the correlation circle of these variables. The arrows indicate the species
 500 with more variance explained by the LC, CL or BIO variables.

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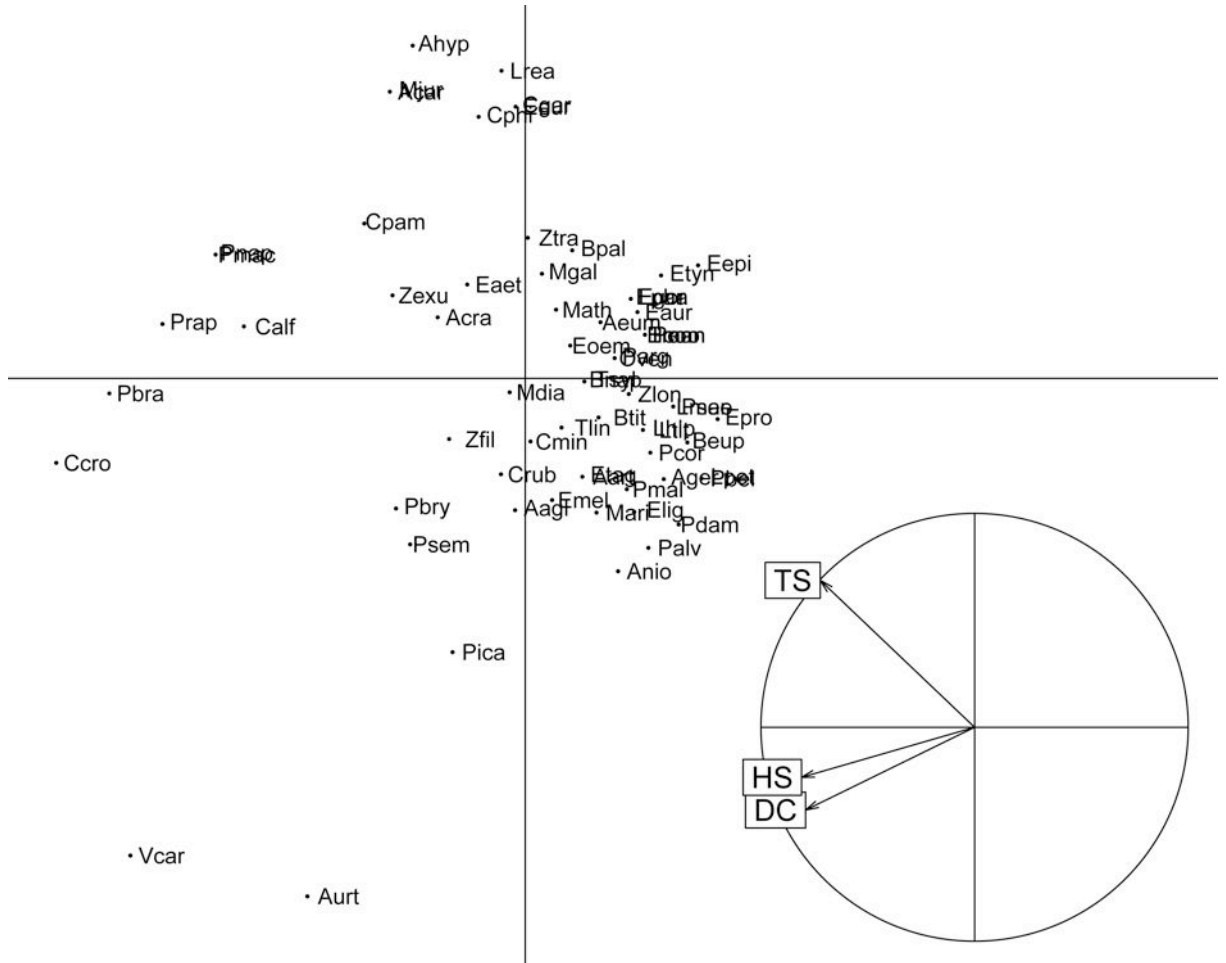


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503 **Figure 3:** Principal component analysis on the species traits, namely trophic specialization (TS),
 504 habitat specialization (HS) and dispersal capacity (DC) with correlation circle of these variables. The
 505 arrows indicate species with numerous host plants for TS, several habitats for HS and a great
 506 dispersal for DC.

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517 **Tables**

518

519 **Table 1:** Summary of the results for the 7 species most improved in their AUC values by the land use variables (a), and 7 species most improved by
 520 the biotic variables (b). Tot. R² and AUC represents the total fit and AUC of the models for the three factors, R² represents the partitioned variance
 521 for the biotic, land use, climatic, shared and unexplained factors.

a) Species	R ² BIO	R ² LU	R ² CL	R ² Sh.	R ² Un.	Tot. R ² TC	Tot. R ² LC	Tot. R ² BIO	R ² Imp. LU (%)	R ² Imp. LO (%)	AUC TC	AUC TCLC	AUC TCBIO	AUC Imp. LC (%)	AUC Imp. BIO (%)
<i>Boloria euphrosyne</i>	0.022	0.076	0.089	0.047	0.652	0.245	0.293	0.257	19.469	4.888	0.709	0.751	0.728	5.924	2.680
<i>Polyommatus coridon</i>	0.061	0.063	0.143	0.034	0.682	0.180	0.265	0.198	47.420	10.340	0.699	0.744	0.721	6.438	3.147
<i>Papilio machaon</i>	0.020	0.106	0.042	0.098	0.722	0.141	0.229	0.152	62.507	7.880	0.652	0.697	0.612	6.902	-6.135
<i>Lasiommata maera</i>	0.020	0.074	0.049	0.022	0.798	0.102	0.177	0.093	73.429	-9.366	0.620	0.693	0.633	11.774	2.097
<i>Zygaena transalpina</i>	0.065	0.085	0.068	0.025	0.710	0.129	0.228	0.126	76.423	-2.868	0.648	0.727	0.659	12.191	1.698
<i>Vanessa cardui</i>	0.027	0.078	0.038	-0.022	0.825	0.065	0.122	0.109	87.759	67.397	0.568	0.65	0.649	14.437	14.261
<i>Polyommatus eros</i>	0.038	0.046	0.102	-0.001	0.811	0.088	0.156	0.083	77.145	-5.990	0.582	0.684	0.612	17.526	5.155
b) Species	R ² BIO	R ² LU	R ² CL	R ² Sh.	R ² Un.	Tot. R ² TC	Tot. R ² LC	Tot. R ² BIO	R ² Imp. LU (%)	R ² Imp. LO (%)	AUC TC	AUC TCLC	AUC TCBIO	AUC Imp. LC (%)	AUC Imp. BIO (%)
<i>Pieris brassicae</i>	0.039	-0.011	0.076	0.046	0.796	0.160	0.169	0.172	5.791	7.948	0.655	0.641	0.675	-2.14	3.053
<i>Adscita geryon</i>	0.074	0.018	0.107	-0.012	0.721	0.194	0.204	0.260	5.475	34.511	0.711	0.728	0.733	2.39	3.094
<i>Polyommatus coridon</i>	0.061	0.063	0.143	0.034	0.682	0.180	0.265	0.198	47.420	10.340	0.699	0.744	0.721	6.44	3.147
<i>Pyrgus serratulae</i>	0.246	0.051	0.116	0.014	0.475	0.227	0.258	0.277	13.629	22.054	0.739	0.751	0.764	1.62	3.383
<i>Polyommatus eros</i>	0.038	0.046	0.102	-0.001	0.811	0.088	0.156	0.083	77.145	-5.990	0.582	0.684	0.612	17.53	5.155
<i>Colias crocea</i>	0.044	0.046	0.035	-0.001	0.757	0.127	0.182	0.192	43.238	51.177	0.700	0.733	0.750	4.71	7.143
<i>Vanessa cardui</i>	0.027	0.078	0.038	-0.022	0.825	0.065	0.122	0.109	87.759	67.397	0.568	0.650	0.649	14.44	14.217

521

521 **Table 2:** Summary of the different classes for the habitat specialists

Environment	Definition
Nitrogen free grasslands/pastures	Grasslands without regular addition of fertilizers
Fertilized grasslands/pastures	Grasslands with regular addition of fertilizers
Dry grasslands	Grasslands with a low water budget (often on southern slopes) and a low nutrient level
Xerothermophile grasslands	Category of grasslands very dry and a with a poor nutrient level
Wetlands	Grasslands or pastures with a high water budget, wet most part of the year
Tall herbs	High vegetation, transition between forest and wetland
Bogs	Wetlands with accumulation of acid peat
Schrubs	Schrubs areas, like for the green alder (<i>Alnus viridis</i>)
Forest edges	Limits of forests
Forest	Any forest areas
Crops	Cultivated meadows
Garden and nursery	Anthropomorphic green areas
Anthropomorphic environments	Like roads borders, railways tracks, gravel pit
Fallen rocks	Any Fallen rock or boulder areas
River banks	Any river banks

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Supplementary material

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Table 3: List of the species with their abbreviations and the variance partitioning. Tot. R^2 and AUC represents the total fit and AUC of the models for the three variables (CL, LU, BIO), R^2 represents the partitioned variance for the biotic (BIO), land use (LU), climatic (CL), shared and unexplained factors.

526

Species	Abbr.	R^2 BIO	R^2 LU	R^2 CL	R^2 Sh.	R^2 Un.	Tot. R^2 TC	Tot. R^2 LC	Tot. R^2 BIO	R^2 Imp. LU (%)	R^2 Imp. LO (%)	AUC TC	AUC TCLC	AUC TCBIO	AUC Imp. LC (%)	AUC Imp. BIO (%)
Adscita geryon	Ager	0.0742	0.0177	0.107	-0.0118	0.721	0.194	0.204	0.260	5.475	34.511	0.711	0.728	0.733	2.391	3.094
Aglais urticae	Aurt	0.0285	0.0458	0.054	0.009	0.826	0.117	0.112	0.111	-4.645	-5.836	0.642	0.619	0.632	-3.583	-1.558
Anthocharis cardamines	Acar	0.0096	0.0900	0.110	0.060	0.561	0.330	0.407	0.339	23.276	2.507	0.786	0.81	0.777	3.053	-1.145
Aphantopus hyperantus	Ahyp	0.0186	0.0022	0.250	0.097	0.347	0.634	0.632	0.656	-0.307	3.398	0.911	0.898	0.91	-1.427	-0.110
Aporia crataegi	Acra	0.0172	0.0421	0.172	0.063	0.546	0.385	0.377	0.418	-2.148	8.696	0.807	0.792	0.818	-1.859	1.363
Argynnis aglaja	Aagl	0.0412	0.0103	0.194	0.093	0.537	0.417	0.422	0.423	1.060	1.260	0.805	0.809	0.813	0.497	0.994
Argynnis niobe	Anio	0.0815	0.0564	0.098	0.010	0.715	0.144	0.168	0.165	16.642	14.478	0.661	0.656	0.645	-0.756	-2.421
Aricia (eumedionia) eumedon	Aeum	0.0298	0.0111	0.027	0.058	0.816	0.120	0.154	0.143	27.940	18.482	0.668	0.671	0.645	0.449	-3.443
Aricia artaxerxes	Aart	0.0304	0.0313	0.118	0.031	0.771	0.151	0.195	0.151	29.615	0.054	0.674	0.691	0.642	2.522	-4.748
Boloria euphrosyne	Beup	0.0218	0.0761	0.089	0.047	0.652	0.245	0.293	0.257	19.469	4.888	0.709	0.751	0.728	5.924	2.680
Boloria napaea	Bnap	0.0753	0.0079	0.138	0.044	0.646	0.276	0.278	0.271	0.485	-1.840	0.775	0.731	0.748	-5.677	-3.484
Boloria pales	Bpal	0.0169	-0.0004	0.335	0.094	0.322	0.664	0.662	0.679	-0.243	2.293	0.911	0.9	0.922	-1.207	1.207
Boloria titania	Btit	0.0369	0.0270	0.162	0.122	0.499	0.435	0.436	0.463	0.148	6.406	0.827	0.816	0.838	-1.330	1.330
Callophrys rubi	Crub	0.0278	0.0352	0.112	0.00712	0.727	0.186	0.235	0.203	26.738	9.082	0.736	0.752	0.747	2.174	1.495
Coenonympha pamphilus	Cpam	0.0224	0.0168	0.217	0.101	0.448	0.508	0.526	0.527	3.586	3.760	0.877	0.876	0.878	-0.114	0.114
Coenonympha gartetta	Cgar	0.0391	0.0765	0.203	0.0521	0.462	0.412	0.495	0.423	20.174	2.703	0.813	0.844	0.805	3.813	-0.984
Colias alfacariensis/hyale	Calf	0.0104	-0.0158	0.186	0.0101	0.816	0.186	0.182	0.197	-1.848	6.033	0.726	0.725	0.742	-0.138	2.204
Colias crocea	Ccro	0.0437	0.0463	0.035	0.00065	0.757	0.127	0.182	0.192	43.238	51.177	0.7	0.733	0.75	4.714	7.143
Colias phicomone	Cphi	0.0442	0.0289	0.224	0.0391	0.466	0.449	0.484	0.445	7.804	-0.949	0.817	0.817	0.816	0.000	-0.122
Cupido minimus	Cmin	0.0007	0.0305	0.195	0.0572	0.638	0.330	0.347	0.325	5.409	-1.478	0.766	0.783	0.752	2.219	-1.828
Erebia aethiops	Eaet	0.0506	0.0148	0.176	0.0528	0.640	0.292	0.297	0.296	1.736	1.510	0.744	0.717	0.73	-3.629	-1.882
Erebia epiphron	Eepi	0.0582	0.0031	0.250	0.0333	0.512	0.397	0.419	0.418	5.708	5.391	0.826	0.832	0.838	0.726	1.453
Erebia euryale	Eeur	0.0272	0.0993	0.115	0.00902	0.635	0.245	0.257	0.239	4.920	-2.240	0.759	0.745	0.739	-1.845	-2.635
Erebia gorge	Egor	0.0725	0.0429	0.115	0.286	0.229	0.586	0.701	0.696	19.720	18.838	0.937	0.956	0.941	2.028	0.427
Erebia ligea	Elig	0.0366	0.0190	0.146	0.0419	0.507	0.441	0.444	0.448	0.747	1.560	0.832	0.842	0.845	1.202	1.563
Erebia manto	Eman	0.0619	-0.00589	0.226	0.0477	0.589	0.352	0.355	0.375	0.778	6.532	0.784	0.785	0.793	0.128	1.148
Erebia melampus	Emel	0.0548	-0.0113	0.140	0.0418	0.671	0.284	0.280	0.283	-1.358	-0.283	0.771	0.748	0.749	-2.983	-2.853
Erebia oeme	Eoem	0.0199	0.0489	0.222	0.0657	0.604	0.333	0.349	0.336	4.675	0.639	0.747	0.75	0.733	0.402	-1.874
Erebia pandrose	Epan	0.0165	0.0555	0.248	0.0587	0.455	0.466	0.507	0.461	8.600	-1.238	0.847	0.868	0.842	2.479	-0.590

Erebia pharte	Epha	0.0650	0.0432	0.291	0.00087	0.519	0.367	0.383	0.409	4.495	11.617	0.811	0.801	0.817	-1.233	0.740
Erebia pronoe	Epro	0.0231	-0.0032	0.149	0.0337	0.716	0.233	0.267	0.260	14.769	11.745	0.78	0.767	0.757	-1.667	-2.949
Erebia tyndarus	Etynd	0.0987	0.0418	0.219	0.0273	0.499	0.348	0.384	0.354	10.264	1.593	0.827	0.824	0.769	-0.363	-7.013
Erynnis tages	Etag	0.0551	0.0368	0.079	0.0333	0.734	0.175	0.208	0.181	19.349	3.839	0.673	0.683	0.671	1.486	-0.297
Euphydryas aurinia	Eaur	0.0343	0.0175	0.324	0.0265	0.574	0.376	0.388	0.367	3.216	-2.351	0.795	0.799	0.79	0.503	-0.629
Hesperia comma	Hcom	0.0035	-0.0015	0.258	0.0380	0.545	0.450	0.455	0.460	1.090	2.167	0.858	0.846	0.864	-1.399	0.699
Lasiommata maera	Lmae	0.0201	0.0739	0.0492	0.0221	0.798	0.102	0.177	0.093	73.429	-9.366	0.62	0.693	0.633	11.774	2.097
Lasiommata petropolitana	Lpet	0.0646	0.0469	0.089	0.00785	0.742	0.148	0.201	0.182	35.864	22.834	0.672	0.702	0.685	4.464	1.935
Leptidea sinapis/reali	Lrea	0.0121	0.0192	0.143	0.0708	0.569	0.384	0.404	0.394	5.263	2.566	0.819	0.824	0.815	0.611	-0.488
Lycaena hippothoe	Lhip	0.0722	0.0484	0.177	0.0114	0.499	0.371	0.389	0.380	4.885	2.462	0.821	0.84	0.813	2.314	-0.974
Lycaena tityrus	Ltit	0.0006	0.0444	0.135	0.0444	0.752	0.214	0.250	0.208	16.857	-2.573	0.748	0.736	0.709	-1.604	-5.214
Maculinea arion	Mari	0.0144	0.0281	0.0473	0.0387	0.807	0.137	0.149	0.162	8.490	17.689	0.669	0.66	0.675	-1.345	0.897
Maniola jurtina	Mjur	0.0111	0.0175	0.314	0.0994	0.326	0.634	0.650	0.650	2.538	2.407	0.927	0.927	0.913	0.000	-1.510
Melanargia galathea	Mgal	0.0018	0.0182	0.445	0.0478	0.388	0.592	0.598	0.596	0.922	0.569	0.893	0.886	0.892	-0.784	-0.112
Melitaea diamina	Mdia	0.0382	0.0867	0.157	0.0664	0.544	0.349	0.353	0.357	1.178	2.283	0.782	0.766	0.772	-2.046	-1.279
Mellicta athalia	Math	0.0183	0.0034	0.189	0.0723	0.552	0.419	0.422	0.427	0.637	2.007	0.841	0.838	0.844	-0.357	0.357
Ochlodes venatus	Oven	0.00264	0.0342	0.179	0.0114	0.574	0.367	0.397	0.384	8.311	4.716	0.839	0.853	0.83	1.669	-1.073
Papilo machaon	Pmac	0.0204	0.1062	0.042	0.0975	0.722	0.141	0.229	0.152	62.507	7.880	0.652	0.697	0.612	6.902	-6.135
Pieris brassicae	Pbra	0.0393	-0.0111	0.076	0.0457	0.796	0.160	0.169	0.172	5.791	7.948	0.655	0.641	0.675	-2.137	3.053
Pieris bryoniae	Pbry	0.0126	0.0179	0.092	0.0233	0.774	0.181	0.208	0.203	15.020	12.009	0.681	0.704	0.688	3.377	1.028
Pieris napi	Pnap	-0.00223	0.0309	0.278	0.00942	0.654	0.312	0.326	0.314	4.394	0.578	0.769	0.76	0.759	-1.170	-1.300
Pieris rapae	Prap	-0.0147	-0.0073	0.049	0.00359	0.973	0.037	0.039	0.039	3.142	4.376	0.573	0.526	0.548	-8.202	-4.363
Plebejus argus	Parg	0.103	0.0057	0.097	-0.0195	0.749	0.147	0.144	0.185	-2.242	25.595	0.667	0.656	0.647	-1.649	-2.999
Polyommatus (Cyaniris) semiargus	Psem	0.0352	0.0086	0.173	0.0770	0.613	0.349	0.347	0.349	-0.547	0.079	0.772	0.773	0.781	0.130	1.166
Polyommatus (Lysandra) bellargus	Pbel	0.0711	0.0266	0.142	0.00438	0.692	0.193	0.239	0.226	24.034	17.538	0.731	0.729	0.742	-0.274	1.505
Polyommatus (Lysandra) coridon	Pcor	0.0610	0.0630	0.143	0.0335	0.682	0.180	0.265	0.198	47.420	10.340	0.699	0.744	0.721	6.438	3.147
Polyommatus damon	Pdam	0.0461	0.0133	0.133	0.00328	0.776	0.157	0.187	0.176	19.208	12.401	0.699	0.724	0.704	3.577	0.715
Polyommatus eros	Pero	0.0383	0.0460	0.102	0.00131	0.811	0.088	0.156	0.083	77.145	-5.990	0.582	0.684	0.612	17.526	5.155
Polyommatus icarus	Pica	-0.00163	0.000887	0.197	0.0559	0.642	0.354	0.352	0.362	-0.620	2.084	0.801	0.804	0.808	0.375	0.874
Pyrgus alveus	Palv	0.000728	0.0187	0.062	0.0146	0.882	0.095	0.119	0.095	26.019	0.237	0.626	0.64	0.584	2.236	-6.709
Pyrgus malvae	Pmal	0.0316	-0.0116	0.129	0.0261	0.785	0.199	0.188	0.194	-5.547	-2.237	0.709	0.69	0.682	-2.680	-3.808
Pyrgus serratulae	Pser	0.2464	0.0511	0.116	0.0142	0.475	0.227	0.258	0.277	13.629	22.054	0.739	0.751	0.764	1.624	3.383
Thymelicus lineola	Tlin	0.0339	-0.0018	0.284	0.120	0.349	0.618	0.614	0.624	-0.582	0.982	0.892	0.883	0.888	-1.009	-0.448
Thymelicus sylvestris	Tsyl	0.0254	0.0127	0.255	0.0969	0.400	0.551	0.559	0.588	1.340	6.650	0.905	0.905	0.906	0.000	0.110
Vanessa cardui	Vcar	0.0271	0.0776	0.038	-0.0220	0.825	0.065	0.122	0.109	87.759	67.397	0.568	0.65	0.649	14.437	14.261

<i>Zygaena exulans</i>	Zexu	-0.0029	0.0576	0.044	0.142	0.634	0.302	0.351	0.307	16.226	1.475	0.825	0.828	0.808	0.364	-2.061
<i>Zygaena filipendulae</i>	Zfil	0.00699	0.0161	0.207	0.0386	0.719	0.240	0.258	0.260	7.346	8.199	0.751	0.735	0.748	-2.130	-0.399
<i>Zygaena lonicerae</i>	Zlon	0.0517	0.0428	0.194	0.0100	0.577	0.317	0.334	0.341	5.263	7.298	0.822	0.798	0.789	-2.920	-4.015
<i>Zygaena transalpina</i>	Ztra	0.0646	0.0851	0.068	0.0246	0.710	0.129	0.228	0.126	76.423	-2.868	0.648	0.727	0.659	12.191	1.698
