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DETERMINANTS OF ALPINE BUTTERFLY DIVERSITY VARY ACCORDING TO THEIR ECOLOGICAL TRAIT

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Determinants of Alpine Butterfly Diversity Vary According to their Ecological Traits

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Abstract

Aim

This study investigates the relations between butterfly species richness patterns, environmental variables and ecological traits. We aim at establishing how the diet, the habitat requirements and the dispersal ability influence the relative importance of butterfly diversity drivers. We also used different species distribution modeling approaches in order to ensure the accuracy of the results.

Location

Butterfly species richness was modeled based on data collected in the western Swiss Alps.

Methods

We assessed butterfly species richness on 192 plots located in a typical alpine environment. We split the inventoried species in different classes for each of the three ecological traits we investigated; the caterpillar diet (i.e. the number of host plant on which they feed

themselves), the imago habitat requirement (i.e. the number of different habitat in which they live in) and their dispersal ability. Then, we studied how a set of seven environmental predictors – comprising two topoclimatic variables (degree-day and solar radiation), two landscape variables (the proportion of forest and the habitat diversity), two pedologic variables (nitrogen soil content and soil acidity) and one biotic variable (the plant richness) – influence the species richness of those classes. Afterward, we applied a repeated randomization procedure to four species distribution modeling approaches (generalized linear model, generalized additive model, generalized boosted model and random forest) in order to determine the relative influence of each of the seven environmental variables on butterfly species richness.

Results

Relative influence of environmental predictor on butterfly species richness display clear differences whether we consider specialized species (i.e. species whose larva feed themselves on a limited numbers of host plants or that are restricted to a few different habitats or else that are characterized by low dispersal ability) or generalist ones. Topoclimatic variables are the most important determinants of butterfly species richness when considering generalist species. Habitat diversity, plant richness and to a lesser extent soil acidity are at least as much important as topoclimatic predictors for specialized species. Moreover, the four modeling approaches provided outputs that are consistent with each other, thus ensuring the result accuracy.

50 **Main conclusions**

While climate variables appear to be the strongest drivers affecting trends in generalist
52 butterfly species richness, local landscape predictors such as plant richness and habitat diversity are at least as much important when considering patterns of specialist butterfly
54 species richness. This highlights the importance of taking into account differences in ecological traits that exist among taxa when modelling species distribution, at least for
56 specialized species. Two alarming issues thus result from our observations. First, it is likely that current climate change is strongly affecting butterfly species distribution in alpine
58 ecosystem. And second, specialized species, which are already the most threatened ones, also undergo the pressure of present habitat homogenisation of and land-use changes.

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Keywords

62 Species distribution modeling, species richness, diet, dispersal ability, habitat requirements, generalized linear models (GLMs), generalized additive models (GAMs), generalized boosted
64 models (GBMs), random forests (RFs), generalist and specialist species.

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Introduction

Global changes are recognised to negatively affect biodiversity (Walther *et al.*, 2002); species distribution and abundance are highly sensitive to climate change (Thuiller *et al.*, 2005) and habitat degradation (Donald *et al.*, 2001; Hewison *et al.*, 2001). Species are not equal in the face of those changes and recent investigations demonstrate that pronounced differences between taxonomical groups exist which is due to differences in ecological traits (Henle *et al.*, 2004; Syphard & Franklin, 2009). For example, Williams et al. (2010) observed that social bee species were more affected by isolation from natural habitat and pesticides than solitary species while habitat specialists of a given taxa suffer more from habitat degradation than generalists (plants: Fischer & Stocklin, 1997; butterflies: Warren *et al.*, 2001; mammals: Fisher *et al.*, 2003; carabid beetle : Kotze & O'hara, 2003; birds: Julliard *et al.*, 2004). Therefore, in order to have a better understanding of global change impacts on species distribution and diversity, studying how taxa are distributed along environmental gradients require considering the ecological traits of species. Yet, few studies relate the importance of variables in explaining species distribution or diversity to ecological traits (Menendez *et al.*, 2007; Stefanescu *et al.*, 2010).

Butterflies display a large variety of ecological properties as regard to the diet, habitat requirements or dispersal ability. For example and as it is also the case in numerous other groups of herbivorous invertebrates, caterpillars have developed a large range of trophic specialisation levels during evolution ranging from strictly monophagous to polyphagous. And adult habitat requirements are linked with larval diet since habitat determines the composition of the vegetal community. Moreover, species that are specialized to a restricted numbers of different habitats generally show a sedentary

behaviour, whether more generalist species display higher dispersal ability in order to pass from one habitat type to another. Butterflies thus provide a very useful model to highlight if important differences between species relate to their environmental niche.

Major drivers of butterfly diversity and abundance have been identified and it is established that climatic factors such as temperature, degree-day, rainfall or solar radiation strongly influence both butterfly diversity (Turner *et al.*, 1987; Parmesan *et al.*, 1999; Luoto *et al.*, 2006; Illan *et al.*, 2010; Stefanescu *et al.*, 2010) and abundance (Pollard, 1988; Roy *et al.*, 2001). To a smaller extent, soil acidity (Erhardt, 1985; Van Swaay, 2002) and especially plant diversity (Hawkins & Porter, 2003) have also been identified has main predictors of butterfly species richness. This observation is mainly explained by the previously mentioned trophic relation that exists between butterfly larva and their host plant species. Therefore, habitat homogenisation, in decreasing plant diversity, negatively affects butterfly diversity (Illan *et al.*, 2010; Stefanescu *et al.*, 2010). Such a negative effect has also been demonstrated to result from increase of human induced disturbances such as intensive farming techniques which decrease at the same time plant richness and larva survival probability (Erhardt, 1985; Dover, 1996).

Differences in ecological traits are related to the influence of environmental drivers on butterfly diversity. In particular, in Britain lowland areas climate predictors had strong effect on habitat generalist butterflies whereas host-plant richness and habitat diversity are more influential for specialist species (Menendez *et al.*, 2007). This observation could be explain when knowing that specialist species are defined either as species whose larvae feed on a limited number of host-plant species or whose imagos are found in a restricted number of different habitats. Studying Mediterranean Basin butterfly fauna, Stefanescu et al. (2010) showed that the main threats to specialist species, which are mostly restricted to mountain

regions, are climate warming and habitat loss caused by the abandonment of exploitation in marginal areas, whereas generalist species are predominantly threatened by increase in aridity and agricultural intensification in lowland regions.

In this study, we investigated patterns of butterfly species richness in the western Swiss Alps, using both local topoclimatic and landscape structure data, coupled with data about diet, dispersal ability and habitat requirement of the species. Since using different statistical approaches might provide different results (Marmion *et al.*, 2009), we used four different predictive modelling techniques. The aims are (i) to establish how ecological traits influence the relative importance of butterfly species richness drivers and (ii) to compare diverse statistical approaches that are widely used in species richness modelling in order to test for their consistency and ensure a good predictive power.

Material and methods

Study area

The study area is located in the Western Swiss Alps (Figure 1) and stretch over an altitudinal gradient ranging from 1000 to 3210 m a.s.l. Along this gradient, four vegetation belts characteristic of the northern Alps can be found; at the bottom the mountainous belt is dominated by mixed forest (*Fagus sylvatica*, European beech, and *Abies alba*, silver fir), followed by the subalpine belt characterized by coniferous forest (Picea abies, Norway spruce), then the alpine belt with herbaceous vegetation (e.g. *Sesleria caerula*, *Nardus stricta*), and finally at the top the nival belt covered with sparse vegetation constituted by typical high altitude plant species (e.g. *Saxifraga oppositifolia*, purple mountain saxifrage). In addition, human influence on the major part of this area is pronounced which strongly

affects plant communities. Anthropogenic pressure is particularly important at lower altitude where nearly all the open areas are exploited as fertilised grasslands for cattle farming. At higher elevation, such activities are made less beneficial from an economic point of view by topographic and climatic factors (e.g. steep slopes), explaining the fact that some natural grassland still exist. In this area, underlying geological material is mainly calcareous and the climate is considered as temperate (Bouët, 1973).

Field sampling

We selected sampling plots following a balanced stratified sampling design based on altitude, slope and aspect (Hirzel & Guisan, 2002) and considering only open and non-woody areas. During summers 2005, 2009 and 2010, we visited a total of 192 plots. According to recommendations done by Pollard and Yates (1993), we realised sampling only in nice weather conditions (low wind, sunny and high temperature) and when butterfly activity is important, that is between 10:00 and 17:00. We visited each plot every three weeks between June 1 and September 15. Butterfly species richness was assessed through a sampling method that consisted in collecting during 45 minutes with a net all the butterflies (Papilionidae, Hesperiidae and Zygaenidae) occurring in a square of 2,500 m^2 and then identifying them in the field. We observed 131 different species (Table S1). Moreover, we carried out an exhaustive vegetation inventory covering a 4 m^2 surface out at the centre of each plot, resulting in the identification of a total of 780 plant species, and thus providing for each plot a plant richness value (PLRI).

With the intention of highlighting that differences in diet, habitat requirements and dispersal ability result in variations among the influence of main butterfly diversity drivers, we split the inventoried species into different classes for each one of these ecological traits (Table S2). Concerning caterpillar diet, we classified the species into two classes according to

164 the number of host plants present in the study area used by the caterpillars; specialist species for one to three host plant(s) (n=61 species) and generalist species for more than 166 three (n=70). Regarding to habitat requirements, we built three classes depending on the number of different habitats in which imago could be found (we classified habitats in dry 168 grasslands, nitrogen free grasslands, fertilized grasslands, peat bogs, wetlands, swamps, boulders, anthropogenic meadows, forest edges, forests, gardens and croops, and river 170 banks); specialist species for those restricted to one or two different habitats (n=58), intermediate for those found in up to four habitats (n=42) and generalists for species 172 associated with more than four habitats (n=31) (Table S2). These data relative to diet and habitat requirements were collected from the monograph of the butterflies of Switzerland 174 (Lspn, 1987). For dispersal ability, we developed two classes according to Bink (1992); the first one put together classes one to three established by Bink (1992) and thus comprises 176 sedentary species with low dispersal ability (n=84), the second one put together the six left-out classes and hence characterized mobile species with higher dispersal aptitude (n=47). 178 Thereafter, we will use the terms specialist or specialized species to speak about species whose larva feed themselves on a limited numbers of host plants (i.e. diet specialists) or that 180 are restricted to a few different habitats (i.e. habitat specialists) or else that are characterized by low dispersal ability, and the term generalist for species with larger host 182 plant number, lower habitat requirements or higher dispersal aptitude.

184 **Environmental predictors**

In order to study the pattern of butterfly species richness through the study area, we 186 selected on the basis of butterfly ecology a set of seven environmental variables that comprises two topoclimatic, two landscape and two pedologic predictors (in addition to

plant richness previously mentioned). The temperature has been shown to strongly affect butterfly distribution (Luoto *et al.*, 2006), essentially because it is tightly linked with the ability of the caterpillar to emerge as an imago and to the physiological tolerances to freezing. This parameter was here taken into account through the degree-day (DDEG) which were calculated on the basis of monthly average temperatures following Zimmermann and Kienast (1999). Turner et al. (1987) proposed solar radiation as the main driver of butterfly richness. We calculated this variable using Kumar's approach (Kumar *et al.*, 1997). The positive relationship between spatial environmental heterogeneity and species richness is currently a widely accepted concept that has notably been highlighted in arthropods by Hendrickx et al. (2007). Consequently, we included two landscape predictors, the proportion of forest (PROPFOR) and the Shannon habitat diversity (HABDI), both derived from land cover data provided by the Swiss Federal Office of Statistics (OFS). These variables were calculated at a resolution of 100 m using the software FRAGSTAT (Mcgarigal & Marks, 2000) using a mobile window (a 500 m side square in the case of habitat diversity and a circle of 250 m radius for the proportion of forest). Finally, we included two pedologic predictors derived from "Landolt ecological values" (Lauber & Wagner, 2007); an index of soil nitrogen content (N) and an index of soil acidity (PH). For each sampled plot, both indexes were calculated as the mean "nutritive substance value N", respectively the mean "reaction value R", of the plant species inventoried.

Modelling approaches

Each species distribution modelling approaches introduce a variability in the results. In order to reduce uncertainty of predictions and to avoid an artefact due to the method, we used four modelling techniques; generalized linear models GLMs (Mccullagh & Nelder,

1989), generalized additive models GAMs (Hastie & Tibshirani, 1990), generalized boosted models GBMs (Ridgeway, 1999) and random forests RFs (Breiman, 2001). We used a Poisson distribution in the case of GLMs and GAMs, a maximum of 3000 trees allowing a Poisson distribution for the GBMs and a maximum of 3000 trees for the construction of RFs. In order to test the prediction accuracy, we applied to each model a repeated (100 times) data splitting procedure similar to the one described by Dubuis et al. (Dubuis *et al.*, in review) and that consists in splitting the original dataset into two 70%-30% partitions, using the 70% partition for fitting the models and the 30% left-out for independently evaluating them. Then, for each split-sample repetition and for each model, we calculated a Spearman correlation between observed and predicted species richness on the evaluation data set (i.e. predictive power of the model). We also evaluated reliability of GLMs and GAMs by calculating the adjusted deviance (i.e. explanatory power of the model).

With the purpose of characterising variable contribution in model predictions, we applied to each predictor within each model an iterated (100 times) randomisation procedure (Thuiller *et al.*, 2009). This procedure uses Pearson correlation between the standard predictions and predictions where the variable under investigation has been randomly permutated in order to assess the influence of this variable. Thus, a high correlation value suggests that the variable in question is of little importance for the predictive power of the model, whether a weaker correlation coefficient indicates the opposite.

Results

Concerning the influence of the investigated predictors on the butterfly species richness (Figure 2), both topoclimatic predictors clearly appear to be the most important ones when considering all the species without ecological trait partitioning. Thus, DDEG and SRAD standed out from the other predictors, when considering diet generalist species only, or species with low habitat requirements only, or else species with high dispersal ability. Moreover, no clear difference exists between species with low and with intermediate habitat requirements. However, a different pattern appears for the other classes. Relatively to habitat specialist species, biotic predictor PLRI and landscape predictor HABDI have more influence on species richness than DDEG and SRAD. Even if it isn't so obvious, similar results are obtained for diet specialized species and for the ones with low dispersal ability. To a lesser extent, PH also seems to contribute to richness of specialized species whether it is not affecting generalist species. Finally, in all cases, variables PROPFOR and N only have a very weak influence on species richness.

The explanatory and predictive power of the models were good and with high correlations between observed and predicted species richness (Table 1) whether we use adjusted deviance ($R^2 \in [0.278 ; 0.638]$) or data splitting procedure ($R^2 \in [0.422 ; 0.698]$). In addition to this and relatively to dispersal and habitat traits, significantly better predictions are done for species with high dispersal ability (0.737±0.008) and low (0.657±0.022) or intermediate (0.689±0.011) habitat requirements than for the ones characterized by short dispersal aptitude (0.499±0.014) or high habitat requirements (0.463±0.053). On the other hand, no similar difference is observed between diet specialist and diet generalist species. With reference to prediction accuracy, none of the four tested

models stand out from the others. All four models are consistent with each other in the influence estimations they gave to the different predictors, even if RFs and GLMs generally provide the highest value (Table S1).

Discussion

At this day, most of the study that investigated butterfly species richness patterns didn't take into consideration differences in ecological traits existing between species. Here, we examine how the influence of different environmental predictors of butterfly species richness varies when taking into account those differences. With this purpose, we collected data in an area of the Western Swiss Alps and applied to them four different commonly used species distribution modelling approaches in order to ensure the accuracy of the results. In accordance with what has been established by previous studies, we found that DDEG and SRAD are the most powerful descriptors of butterfly diversity when considering all species irrespective of their ecological traits. However, local predictors such as PLRI and HABDI have strong influence on richness of specialized species. Moreover, those observations were consistent across statistical methods and thus highly reliable.

In northern areas, climatic predictors linked with the input of solar energy constitute the most restrictive variables to diversity of many groups of organisms (Currie, 1991), butterfly included (Turner *et al.*, 1987; Hawkins & Porter, 2003; Luoto *et al.*, 2006). We showed that when considering all species irrespective of their ecological traits, DDEG and SRAD are the most powerful predictors of butterfly richness. These findings are consistent with those earlier works. Indeed, in mountain regions, climate applies pressure on organisms in two distinct ways (Hawkins *et al.*, 2003); it constrains species richness directly through

physiological requirements of organisms (e. g. butterfly larvae cannot grow under a given threshold), and indirectly in affecting resource availability via a trophic cascade.

Siemann et al. demonstrated that arthropods diversity and plant richness are strongly correlated (1998a; 1998b), and Kumar et al. (2009) established that spatial heterogeneity greatly influences patterns in butterfly species richness. On this subject, divergences among the influence of plant richness and habitat heterogeneity exist between the most recent publications on butterfly species diversity. For example, Menénendez et al. (2007) concluded that species richness of habitat specialist depend on the diversity of environments/resources available to them whereas Illán (2010) demonstrated that species richness is more closely related to topoclimate than to land cover. In addition to this, Stefanescu et al. firstly found that the number of plant communities was not related to butterfly species richness (2004) and then that plant communities was positively associated with butterfly species richness but was a relatively poor predictor variable (2010). Here, we provide strong evidence that predictors such as PLRI and HABDI clearly affect butterfly richness of specialized species. Evidently, ecological trait data allowing identifying specialist species as well as local scale predictors for habitat and plant diversity are required to detect such relations. Thus it appears that, relative to predictor variable scale, vegetation data determining the number of plant communities (Stefanescu *et al.*, 2004; 2010) and land cover data (Illan *et al.*, 2010) are not sufficiently specific. Finally, the fact that we also detect a strong influence of HABDI and PLRI on species richness of butterfly characterized by low dispersal ability can be explained by the link existing between those species and the habitat specialist ones. Actually, they are generally the same, given that habitat specialist species are sedentary. Thereby, ecological trait approach seems to be of great interest in butterfly species distribution modelling, at

least when it concerns specialist species (either this term refers to habitat or to diet requirements).

Contrary to what has been proposed by Stefanescu et al. (2004; 2010), we found evidence for a weak but significant influence of PH on butterfly richness of specialized species. This is interpretable by the fact that composition of vegetal community changes with soil acidity. In particular, soil acidification results in a decrease of the group number of host plants that are highly favourable to most butterfly larva such as Fabaceae or Poaceae. On the other hand, nitrogen soil content, a predictor that was to our knowledge till yet not investigated, appeared to be a poor predictor of butterfly richness. This can seems counterintuitive at first sight, but can easily be explained by the fact that even if N is related to plant community composition, plant diversity is nevertheless globally independent of this variable.

Forest edges constitute a full-fledged environment which is greatly favourable to some butterfly species. Specifically, a forest edge effect positively affecting butterfly species richness and decreasing with distance to this structure has been observed in different regions of the globe (Asia: Ohwaki *et al.*, 2007; Africa: Bossart & Opuni-Frimpong, 2009; Europe: Marini *et al.*, 2009). However, no similar effect was observed in our study and the predictor PROPFOR appears to be in all cases a poor predictor of trends in species richness. This probably account for the fact that the study area is limited to a mountainous zone with no sampling plot located under 1000 m a.s.l. Thus, the vast majority of inventoried species are typical alpine species which are mostly devoid of woody structures.

Relatively to model predictive power, we found that predictions are done with less confidence when concerning habitat specialists or low dispersal species in comparison of habitat generalists or species with higher dispersal aptitude. This observation can be

explained by the fact that it is supersensitive species for which the predictors we used are not sufficient to explain the whole variability that characterized their distribution. Thus, even if we take into account local predictors such as PLRI and HABDI, we guess that other variables that we don't know affect their distribution and are required to adequately model it. However, we highlighted the fact that the four species distribution modelling we used provided here results that are consistent with one another, leading to homogeneous patterns. Nonetheless, variability between those approaches remains, almost certainly due to the mathematical differences that distinguish them (e.g. the fact that GLMs and GAMs are based on polynomial regressions whether GBMs and RFs issued from decision tree principle). Several recent studies emphasize that errors and uncertainties represent a problems for habitat predictive modelling (Elith *et al.*, 2002; Barry & Elith, 2006; Heikkinen *et al.*, 2006). Thus, our results are congruent with conclusions expressed by Marmion et al. (2009) who recommend a multi-method approach in species distribution modelling in order to ensure the predictions and avoid results that would be significant due to method artefact.

In conclusion, our results show that, while climate variables appear to be the strongest drivers affecting trends in generalist butterfly species richness, local landscape predictors such as plant richness and habitat diversity are at least as much important when considering patterns of specialist butterfly species richness. The importance of climate variables for both generalist and specialist species is of prior concern in the current context of climate change. It allows us to predict a rapid evolution of butterfly range limits in response to global warming, as it has still been shown by Parmesan et al. (1999) and Hill et al. (2001; 2002). Moreover, the influence of plant richness and habitat diversity highlights the importance of taking into account differences in ecological traits that exist among taxa when modelling species distribution of specialized species. This is in addition supported by

two distinct observations. First, the fact that unfortunately the most endangered species currently often belongs to species specialist (Poyry *et al.*, 2009). And second, the fact that those species that are of prior concern for conservation are also the one for which species distribution modelling is the less accurate and the hardest to predict with confidence. This conclusion thus underlines the crying need for developing suitable predictors of specialized species distribution.

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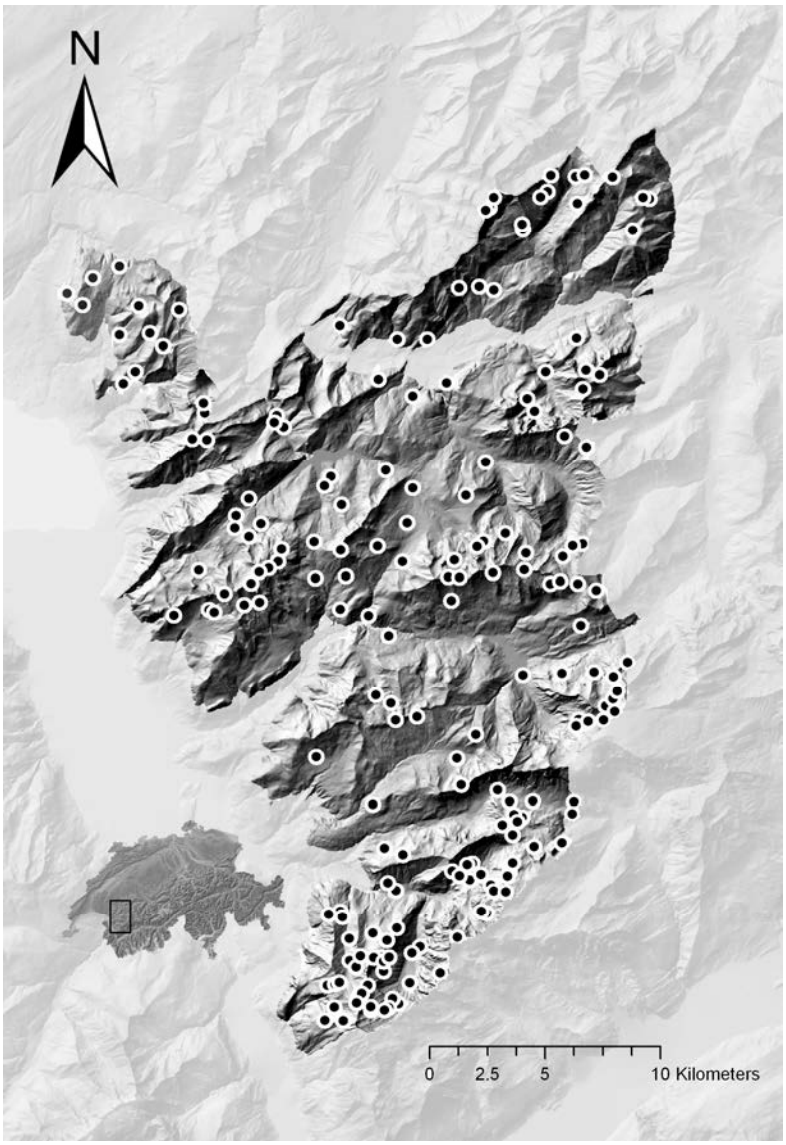
516 Figures

518 **Figure 1:** Study area situated in the western Swiss Alps. The black dots represent the location of the butterfly plots sampled following a balanced stratified sampling.

520



522 **Figure 2:** Influence of different environmental predictors – degree-day (DDEG), solar radiation (SRAD), proportion of forest (PROPFOR), plant richness (PLRI), habitat diversity 524 (HABDI), nitrogen soil content (N) and soil acidity (PH) – on butterfly species richness according to diverse ecological trait classifications.

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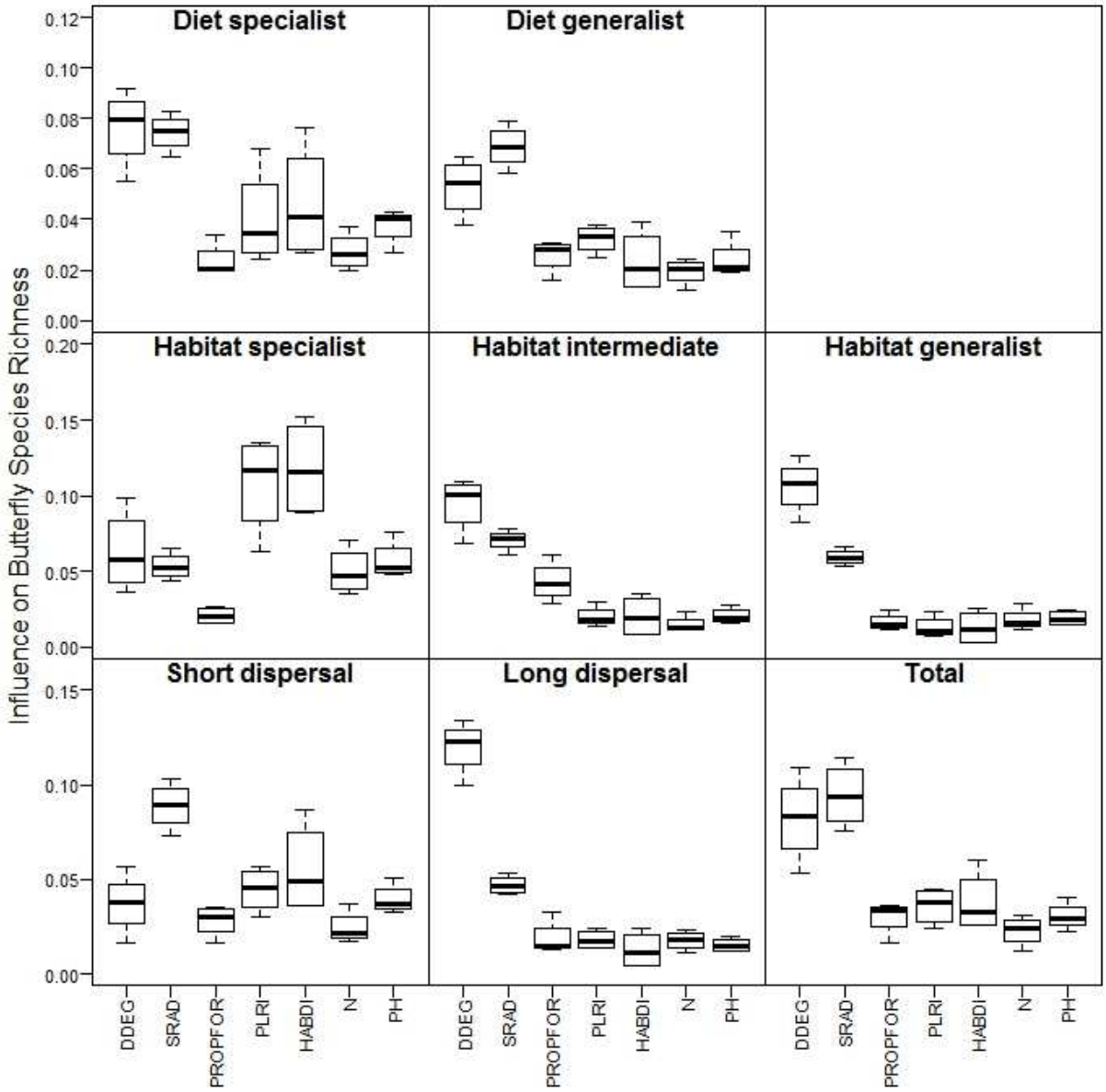

528 Table

530 **Table 1:** Predictive power (i.e. adjusted deviance) and explanatory power (i.e. data splitting procedure) values for four different species richness models according to the diverse
532 ecological traits investigated.

Ecological trait classe		Statistical method	GLM	GAM	GBM	RF	Average
Diet	**specialist**	**Ajusted deviance**	0.452	0.515			
		Data splitting procedure	0.613	0.565	0.607	0.630	0.604 ± 0.028
	generalist	**Ajusted deviance**	0.426	0.477			
		Data splitting procedure	0.571	0.570	0.564	0.608	0.578 ± 0.020
Dispersal	**short**	**Ajusted deviance**	0.359	0.414			
		Data splitting procedure	0.503	0.498	0.481	0.514	0.499 ± 0.014
	long	**Ajusted deviance**	0.597	0.638			
		Data splitting procedure	0.731	0.739	0.730	0.748	0.737 ± 0.008
Habitat	**specialist**	**Ajusted deviance**	0.278	0.347			
		Data splitting procedure	0.440	0.422	0.450	0.540	0.463 ± 0.053
	intermediate	**Ajusted deviance**	0.531	0.564			
		Data splitting procedure	0.697	0.698	0.674	0.690	0.689 ± 0.011
	generalist	**Ajusted deviance**	0.512	0.570			
		Data splitting procedure	0.638	0.649	0.653	0.689	0.657 ± 0.022
Total		**Ajusted deviance**	0.474	0.523			
		Data splitting procedure	0.607	0.414	0.588	0.617	0.557 ± 0.096

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538 Supplementary materials

540 **Table S1:** Results of the environmental predictor influence on butterfly species richness for the four species distribution modeling approaches investigated and following diverse
542 ecological trait classifications.

Ecological trait classes		Predictors	GLM	GAM	GBM	RF	Average
Diet	Specialist	DDEG	0.092	0.078	0.055	0.082	0.077 ± 0.016
		SRAD	0.083	0.074	0.065	0.076	0.074 ± 0.007
		PROPFOR	0.019	0.021	0.020	0.034	0.024 ± 0.007
		PLRI	0.039	0.024	0.030	0.068	0.040 ± 0.020
		HABIV	0.030	0.027	0.052	0.077	0.046 ± 0.023
		N	0.028	0.024	0.019	0.037	0.027 ± 0.007
		PH	0.043	0.041	0.027	0.039	0.037 ± 0.007
	Generalist	DDEG	0.065	0.051	0.038	0.058	0.053 ± 0.012
		SRAD	0.079	0.071	0.058	0.067	0.069 ± 0.009
		PROPFOR	0.030	0.027	0.016	0.030	0.026 ± 0.007
		PLRI	0.038	0.031	0.025	0.035	0.032 ± 0.006
		HABIV	0.013	0.014	0.028	0.039	0.023 ± 0.012
		N	0.022	0.020	0.012	0.024	0.019 ± 0.005
		PH	0.021	0.019	0.021	0.035	0.024 ± 0.007
Habitat requirements	Specialist	DDEG	0.048	0.036	0.068	0.098	0.063 ± 0.027
		SRAD	0.050	0.044	0.055	0.065	0.054 ± 0.009
		PROPFOR	0.017	0.023	0.016	0.027	0.021 ± 0.005
		PLRI	0.135	0.104	0.063	0.130	0.108 ± 0.033
		HABIV	0.091	0.089	0.139	0.152	0.118 ± 0.033
		N	0.053	0.035	0.041	0.071	0.050 ± 0.016
		PH	0.048	0.050	0.056	0.076	0.057 ± 0.013
	Intermediate	DDEG	0.109	0.096	0.069	0.105	0.095 ± 0.018
		SRAD	0.078	0.072	0.061	0.072	0.071 ± 0.007
		PROPFOR	0.044	0.038	0.029	0.061	0.043 ± 0.013
		PLRI	0.018	0.013	0.018	0.030	0.020 ± 0.007
		HABIV	0.008	0.009	0.029	0.035	0.020 ± 0.014
		N	0.012	0.013	0.011	0.023	0.015 ± 0.006
		PH	0.020	0.018	0.016	0.028	0.020 ± 0.005
	Generalist	DDEG	0.126	0.106	0.083	0.110	0.106 ± 0.018
		SRAD	0.067	0.058	0.053	0.060	0.059 ± 0.006
		PROPFOR	0.016	0.014	0.012	0.025	0.017 ± 0.005
		PLRI	0.010	0.007	0.012	0.024	0.013 ± 0.007
		HABIV	0.003	0.004	0.020	0.025	0.013 ± 0.011
		N	0.012	0.016	0.016	0.029	0.018 ± 0.007
		PH	0.015	0.015	0.022	0.025	0.019 ± 0.005

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Dispersal ability	Short	DDEG	0.057	0.037	0.016	0.039	0.037 ± 0.016
		SRAD	0.103	0.093	0.073	0.086	0.089 ± 0.013
		PROPFOR	0.035	0.033	0.016	0.028	0.028 ± 0.008
		PLRI	0.051	0.041	0.030	0.057	0.045 ± 0.012
		HABIV	0.036	0.037	0.062	0.087	0.055 ± 0.024
		N	0.023	0.021	0.017	0.037	0.024 ± 0.009
	Long	PH	0.037	0.038	0.033	0.051	0.040 ± 0.008
		DDEG	0.134	0.124	0.100	0.122	0.120 ± 0.014
		SRAD	0.048	0.042	0.044	0.053	0.047 ± 0.005
		PROPFOR	0.013	0.015	0.014	0.032	0.019 ± 0.009
		PLRI	0.020	0.014	0.014	0.024	0.018 ± 0.005
		HABIV	0.004	0.004	0.017	0.024	0.012 ± 0.010
		N	0.019	0.016	0.011	0.024	0.018 ± 0.005
Total		PH	0.012	0.012	0.017	0.020	0.015 ± 0.004
		DDEG	0.082	0.065	0.040	0.060	0.062 ± 0.017
		SRAD	0.086	0.076	0.057	0.064	0.071 ± 0.013
		PROPFOR	0.026	0.024	0.012	0.027	0.023 ± 0.007
		PLRI	0.033	0.024	0.018	0.033	0.027 ± 0.007
		HABIV	0.020	0.019	0.029	0.045	0.028 ± 0.012
		N	0.020	0.017	0.009	0.023	0.017 ± 0.006
		PH	0.022	0.022	0.017	0.031	0.023 ± 0.006

Table S2: Classification of the 131 butterfly species inventoried for the three investigated ecological traits, that is caterpillar diet ("s" stands for specialists, "g" for generalists), imago dispersal ability ("l" stands for low dispersal ability, "h" for high dispersal ability) and habitat requirements ("s" stands for specialists, "i" for intermediate and "g" for generalists).

Species	Diet	Dispersion ability	Habitat requirments
Argynnis adippe	g	h	i
Aricia agestis	s	h	s
Argynnis aglaja	g	h	g
Aricia artaxerxes	s	l	g

Anthocharis cardamines	g	h	i
Aporia crataegi	g	h	i
Aricia eumedon	g	l	i
Adscita geryon	s	l	g
Aphantopus hyperantus	g	l	g
Apatura iris	s	l	s
Argynnis niobe	s	h	i
Argynnis paphia	g	h	i
Adscita statices	g	l	s
Aglais urticae	s	h	g
Boloria aquilonaris	s	l	s
Brintesia circe	s	h	s
Brenthis daphne	g	l	i
Boloria dia	s	h	s
Boloria euphrosyne	s	l	s
Brenthis ino	g	l	s
Boloria napaea	g	l	i
Boloria pales	g	l	i
Boloria selene	g	l	i
Boloria titania	g	l	i
Everes alcetas	s	h	i
Colias alfacariensis	s	h	i
Celastrina argiolus	g	h	s
Colias crocea	g	h	g
Coenonympha gardetta	g	l	i
Colias hyale	g	h	g
Cupido minimus	g	l	g
Cupido osiris	s	l	s
Caterocephalus palaemon	s	l	i
Colias palaeno	s	h	s
Coenonympha pamphilus	g	l	g
Collias phicomone	g	h	s
Callophrys rubi	g	h	g
Erebia aethiops	g	l	g
Erebia alberganus	s	l	i
Euphydryas aurinia	g	l	i
Erebia cassioides	g	l	s
Euphydryas cynthias	s	h	i
Erebia epiphron	g	l	s
Erebia eriphyle	s	l	s
Erebia euryale	g	l	i
Erebia gorge	g	l	s
Erebia ligea	s	h	s
Erebia manto	g	l	s

Erebia medusa	s	l	g
Erebia melampus	s	l	g
Erebia meolans	g	l	s
Erebia mnestra	g	l	s
Erebia montana	g	l	s
Erebia oeme	g	l	i
Erebia pandrose	g	l	s
Erebia pharte	g	l	s
Erebia pluto	s	l	s
Erebia pronoe	s	l	s
Euchloe simplonia	s	h	s
Erynnis tages	s	l	g
Erebia tyndarus	g	l	s
Glauchopsyche alexis	s	l	s
Hesperia comma	g	l	s
Haemeris lucina	s	l	i
Inachis io	s	h	g
Issoria lathonia	s	h	s
Limentis camilla	s	l	s
Lycaena helle	s	l	i
Lyceana hippothoe	s	l	i
Lasiommata maera	s	l	s
Lasiommata megera	g	h	i
Lasiommata petropolitana	s	l	s
Lycaena phlaeas	s	h	i
Leptidea reali	g	l	i
Leptidea sinapis	g	h	i
Lyceana tityrus	s	l	i
Maculinea arion	s	l	g
Melitea athalia	g	l	i
Melitaea cinxia	g	l	i
Melitea diamina	g	l	g
Melanargia galathea	g	l	i
Maniola jurtina	g	h	i
Maculinea nausithous	s	l	s
Mellicta parthenoides	g	l	s
Maculinea rebeli	s	l	s
Nymphalis antiopa	g	h	g
Oeneis glacialis	g	h	s
Ochlodes venatus	g	l	i
Parage aegeria	g	h	s
Pyrgus alveus	s	h	s
Pyrgus andromedae	s	l	s
Parnassius apollo	s	l	s

Plebeius argus	g	l	i
Lysandra bellargus	s	l	s
Pieris brassicae	g	h	g
Pieris bryoniae	g	h	g
Pyrgus cacaliae	s	l	s
Polygonia c-album	g	h	g
Pontia callidice	g	h	i
Pyrgus carlinae	s	l	s
Lasandra coridon	s	h	s
Polyommatus damon	s	h	s
Plebicula dorylas	s	h	s
Polyommatus eros	g	l	s
Polyommatus escheri	s	l	s
Argiades glandon	s	l	s
Polyommatus icarus	s	h	g
Lycaeides idas	g	l	s
Papilio machaon	g	h	g
Pyrgus malvae	s	l	i
Pyrgus malvoides	s	l	s
Parnassius mnemosyne	s	l	s
Pieris napi	g	h	g
Albulina orbitulus	g	l	s
Parnassius phoebus	s	h	s
Pieris rapae	g	h	g
Cyaniris semiargus	g	h	g
Pyrgus serratulae	s	l	s
Polyommatus thersites	s	l	s
Spialia sertorius	s	l	i
Thymelicus lineola	g	h	i
Thymelicus sylvestris	g	l	i
Vanessa atalanta	s	h	g
Vanessa cardui	g	h	g
Zygaena exulans	g	l	g
Zygaena fausta	s	l	i
Zygaena filipendulae	g	l	g
Zygaena lonicerae	g	l	i
Zygaena loti	g	l	s
Zygaena purpuralis	s	l	g
Zygaena transalpina	g	l	i