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

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Abstract

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

Location The Western Alps of Switzerland.

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

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

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

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

Introduction

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

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

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

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

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

1. Adding information on the land cover as well as plant community composition should improve the fit and predictive power of SDMs solely based on topo-climatic predictors.

2. The relative importance of topo-climatic, land cover and biotic variables should be related to species biological traits. In particular, biotic and land cover factors should be important for

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

Material & Methods

Study area

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

Field sampling

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

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

Environmental variables

To model the distribution of butterfly species, we used several predictors from three categories. First we used three climatic variables: Degree-days (DDEG) affect both imago and caterpillar through physiological tolerance to freezing or cold temperature, influencing the survival of caterpillars (Fischer *et al.* 2003); this sum of monthly average temperatures was calculated following Zimmermann and Kienast (1999). Solar radiations (SRAD), retained as one of the best factor explaining butterfly distributions by Turner *et al.* (1987) and Bradford *et al.* (2003), was calculated using Kumar's approach (Kumar *et al.* 1997) and considers both direct and diffuse components of global solar radiation. A moisture index (MIND) was also calculated as the difference between precipitation and evapotranspiration. Moisture is an important factor to be considered for the egg survival. Indeed, beyond a certain threshold, eggs cannot counter desiccation, which brings larvae death (Merrill *et al.* 2008). We calculated three additional variables considered as biotic because they relate to the plant composition to which butterfly are trophically related: plant species richness, taken from the vegetation inventory and calculated with the count of inventoried species in each sampling plot. The pH has been extrapolated from the Landolt values of those plant species present in the $4m^2$ plot (Landolt 1977). Landolt values represent a characterization of the ecological conditions needed by the plant and include indexes of moisture, temperature, light, nutrients, reaction (acidity) and continentality. We used the reaction index, weighted by species abundances to calculate the mean pH value on each plot. The same method was applied to calculate a mean nutrient value for each plot (N). Finally two landscape variables were calculated from the land cover data: the proportion of forest, calculated with a 500m window around the plot (PROPFOR), showing the heterogeneity of the environment; and an indication of forest hedges that influence the diversity of open area species at fine scale (Schneider *et al.* 2001). We also calculated the Shannon diversity index (DIV) with a 500m moving window around the plot using the Fragstat software (McGarigal *et al.* 2002). Due to the size of the plots and the mobility of the species, we used a 100m resolution for all these variables.

Species modeling

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

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

Testing the importance of biotic and land cover predictors in SDMs

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

Assessing the role of species traits

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

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

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

Results

Species modeling

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

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

Importance of biotic and land cover predictors in SDMs

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

Role of species traits

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

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

Discussion

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

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

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

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

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

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

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

Conclusions

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

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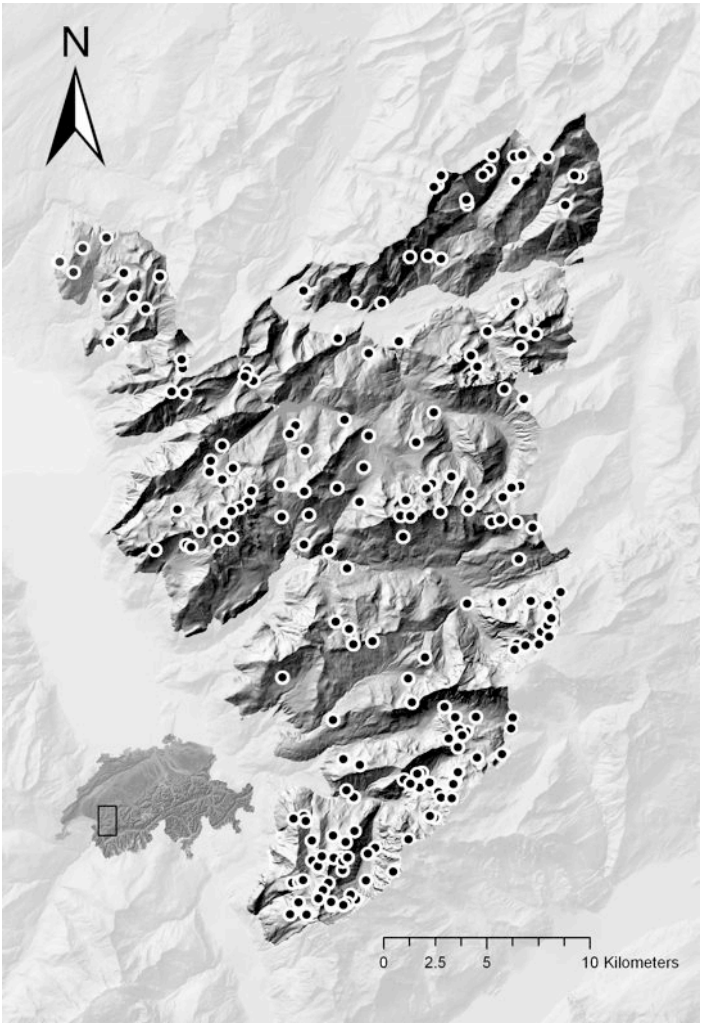
Figures

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



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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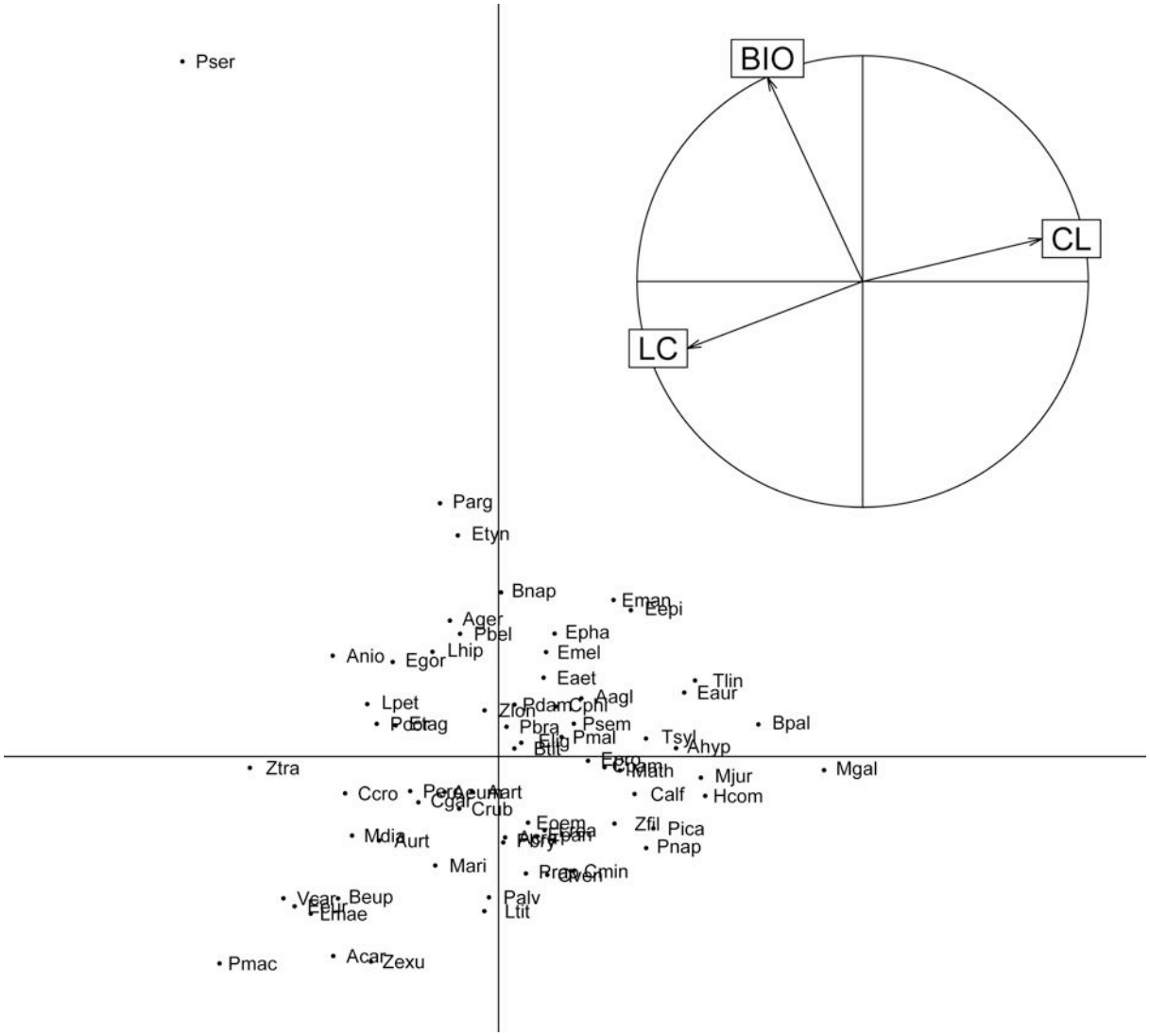

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***Figure 3**: Principal component analysis on the species traits, namely trophic specialization (TS), habitat specialization (HS) and dispersal capacity (DC) with correlation circle of these variables. The arrows indicate species with numerous host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

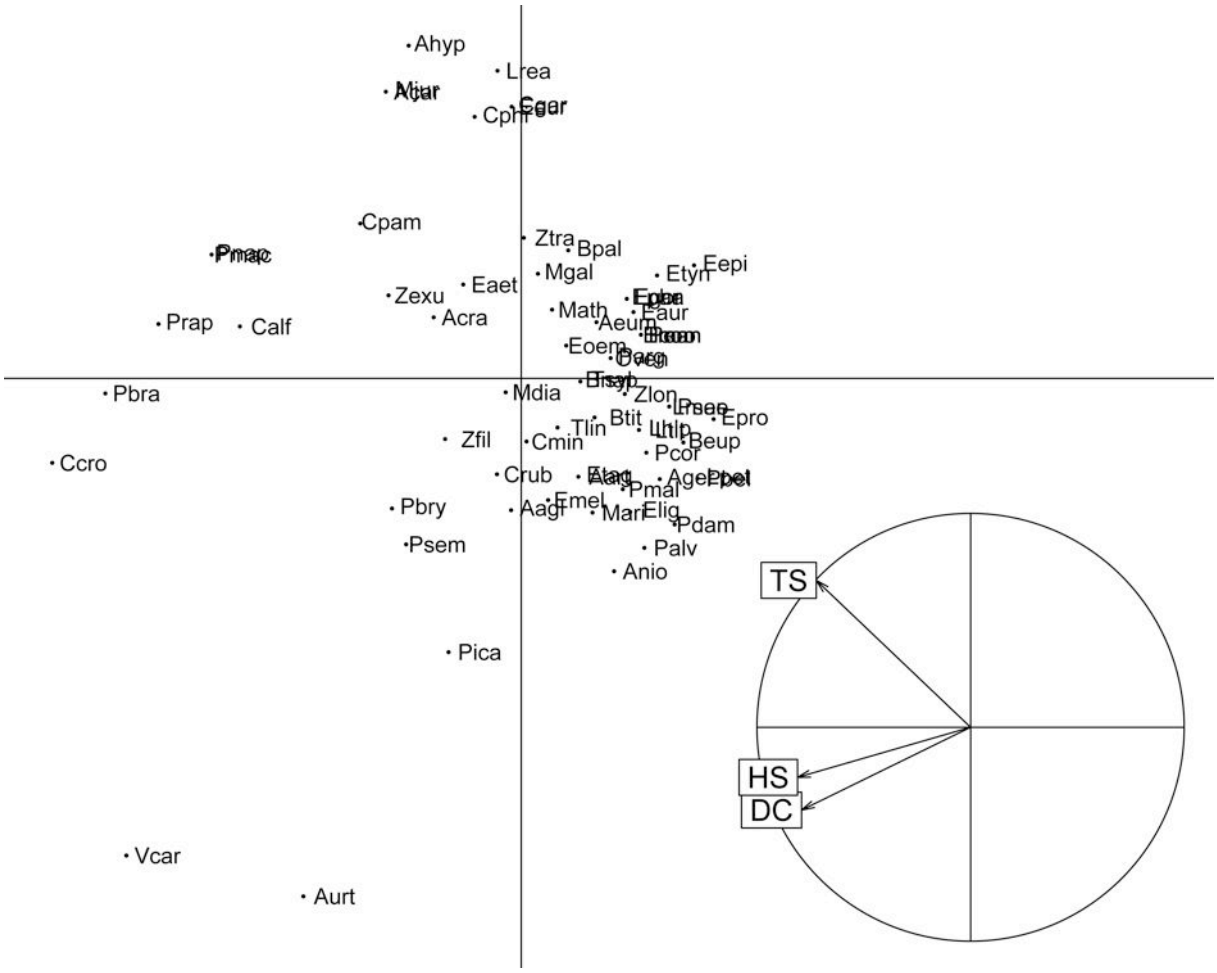
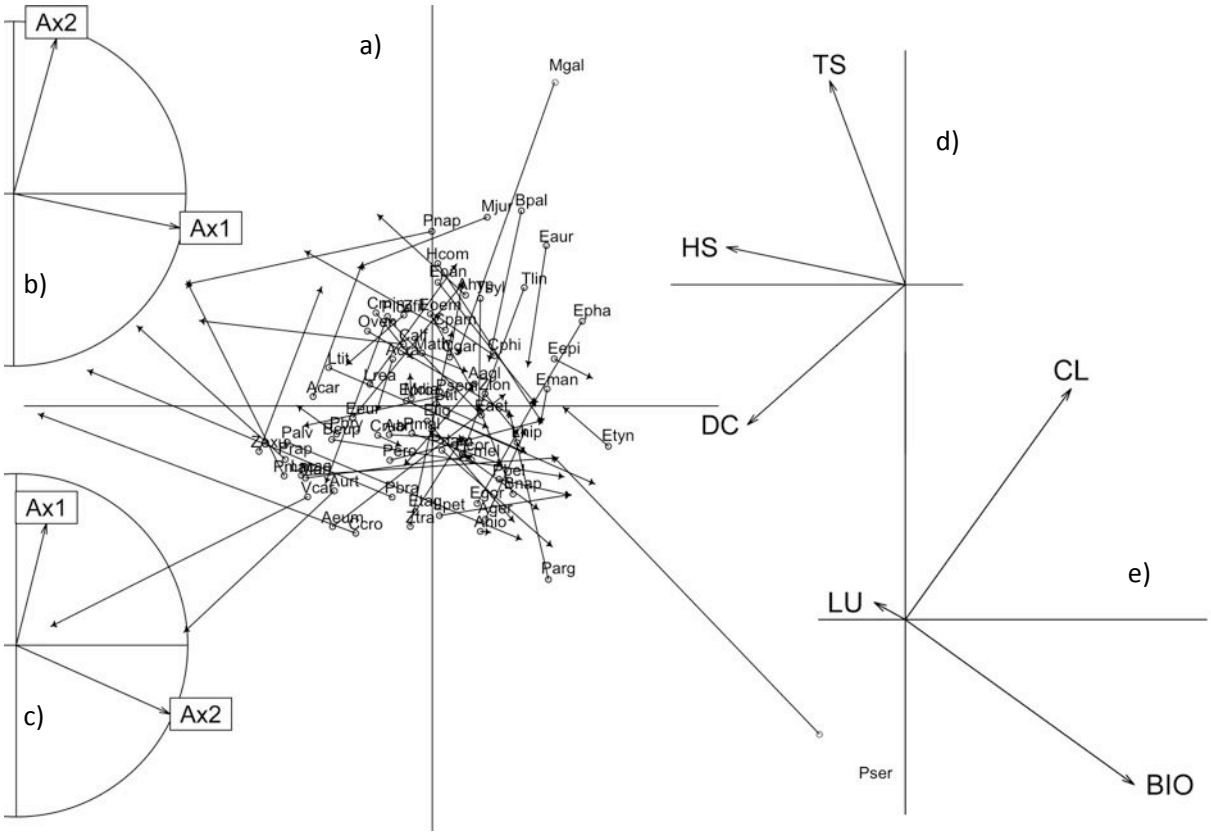


***Figure 4**: Co-inertia analysis on the PCAs. a) Co-inertia analysis; b) Inertia of the X axis from the PCAs, Ax1 represents the PCA on the modeling variables, Ax2 represents the PCA on the traits ; c) Inertia of the Y axis of the two PCAs, Ax1 represents the modeling variables and Ax2 the traits; d) Inertia of the species traits; the arrows indicate the species with more variance explained by the LC, CL or BIO variables; e) Inertia of the variables; the arrows indicate species with numerous host plants for TS, several habitats for HS and a great dispersal for DC.*



Tables

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 the biotic variables (b). Tot. R^2 and AUC represents the total fit and AUC of the models for the three factors, R^2 represents the partitioned variance 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 (%)*
Boloria euphrosyne	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
Polyommatus coridon	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
Papilio machaon	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
Lasiommata maera	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
Zygaena transalpina	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
Vanessa cardui	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
Polyommatus eros	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 (%)*
Pieris brassicae	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
Adscita geryon	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
Polyommatus coridon	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
Pyrgus serratulae	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
Polyommatus eros	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
Colias crocea	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
Vanessa cardui	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 (*Alnus viridis*)
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

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.

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
Coenonmypha 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 gardetta	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	Etyn	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
Euphydrias 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

Zygaena exulans	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
Zygaena filipendulae	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
Zygaena lonicerae	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
Zygaena transalpina	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

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