Trophic interactions impact butterflies' future distribution under climate change

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Abstract

Continental-scale studies proved the importance of biotic interactions in species distribution models (SDMs) for future ranges predictions under climate change. Since most of the trophic interactions take place at a local scale, studies with coarse resolution are of limited relevance. Here, we investigate the effects of global warming (A1B scenario) on 10 high-altitude butterfly species specialized on up to 6 host plants with 2 different species distribution models (SDMs): a SDM using climatic variables only (climatic SDM) and the same SDM filtered with the distribution of butterflies' host plants (filtered SDM). In these models, we use very high resolution data (between 10m and 50m), accurate temperature data measured by thermologgers placed at the soil level and consider the different dispersal abilities of the plants. We predict the extinction of 60% to 90% of the butterflies by 2050. Projected habitat loss is significantly higher with the filtered SDM than with the climatic SDM. Thus, our high-resolution analysis indicates a clear overestimation of butterflies' future distribution under climate change by the climatic SDM. This suggests that trophic filters are important in SDMs used to predict future species habitat under climate change at a local scale.

Keywords: butterflies, host plants, global change, species distribution models, trophic interactions, Swiss Alps

Introduction

It is of common knowledge that climate plays a dominant role in species distribution through various gradients such as temperature or wetness and this can be directly used to define the actual habitat of a species: its climatic niche. The climatic niche is derived from the concept of ecological niche developed by Hutchinson (1957), who defines it as a multidimensional volume, where dimensions are the resources and the environmental conditions influencing the fitness of an organism. Hutchinson's ecological niche has two principal components, the fundamental and the realized niches. In our study, the climatic niche corresponds to Hutchinson's fundamental niche, which is the full range of environmental conditions, such as temperatures, rainfall or any other factor where an individual is able to survive and reproduce. Since global warming has a huge impact on those environmental variables, it is obvious that climate change will affect future species distribution. It has been shown that this phenomenon leads to a poleward latitudinal range shift and an upward altitudinal range shift (Parmesan and Yohe 2003). Particularly, studies that have been done on butterflies showed an elevational shift of 300 m for a period from 1967-2005 (Wilson et al. 2007; Merrill et al. 2008) and predicted a potential elevational shift of 650m in 2100 (Merrill et al. 2008). Although the effects of global warming are not deleterious for all species, leading to range expansion for some invasive or fast-adapting species, most of them will suffer range contraction and even extinction in the worst cases. Especially, because of the altitudinal shift, it has been shown that high-altitude species, unable to colonize higher, colder habitats, will suffer the most (Dirnböck, Essl, and Rabitsch 2011; Wilson et al. 2007). In order to assess the impact of climate change on each species, species distribution models (SDMs), also called bioclimatic envelope models, are frequently used. These relate a series of climatic variables to the current geographical distribution of species, in terms of presence/absence or abundance, in order to calculate the species' realized niches. These models have been developed to make projections of distributions under different scenarios of future climate change, making the assumption of niche conservatism (Pearman et al. 2008). But, one of the major issues with this type of models is that it does not take biotic interactions into account. Recent studies have already shown that climatic factors are not the only forces acting on species distribution, but biotic interactions, such as predators, competitors, parasites or insects' host plants play a major role as well (Pradervand et al. in prep.). Following a recent debate on whether these effects were visible at a macroecological scale, Araújo and Luoto (2007) have found a significant effect of biotic interactions on the explanatory and predictive power of bioclimatic envelope models. Moreover, Schweiger et al. (2008) proved the importance of biotic interactions when modelling butterflies' future distributions, showing that spatial mismatch between the butterfly and its host plant can occur because of global warming. Thus, models using climatic data only could lead to an overestimation of the potential future habitat of the species, as it has been shown by Preston et al. (2008).

Although previous authors have investigated the effect of climate change on butterflies using SDMs, their conclusions are of limited relevance, essentially because two factors are problematic. Firstly, these studies used coarse spatial resolution data (e.g. 50x100km, Heikkinen et al. 2009). Indeed, Randin et al. (2009) proved that the use of low resolution spatial data leads to an under-estimation of the future distribution of the species, especially in high-altitude areas, because it doesn't allow the capture of microclimatic conditions potentially corresponding to suitable refugia for species (Scherrer and Körner 2011). Secondly, authors used climatic data from meteorological stations, measuring the temperature 1.5-2m above the ground without taking into account solar radiations. Knowing that the growth rate of the caterpillars is correlated to the amount of solar radiations received, it is essential to measure temperature at the soil level rather than 2m above. In a recent study (Graae et al. 2011; Scherrer and Körner 2011) proved that the difference between temperature within-site measured by meteorological stations and those measured by thermologgers placed directly on the ground represented an altitudinal shift of 300m. Thus, for studies along altitudinal gradient, incorporation of microclimatic data is essential.

Our study combines very high-resolution data (10m, 50m) with accurate temperature data measured by thermologgers placed on the ground to assess whether predictions with models that take into account biotic interactions (i.e. distribution and dispersion of the host plants) are different from the projections made by simple climatic models for the distribution of 10 butterflies species in the western Alps of Switzerland. Considering aforementioned arguments, we expect to find an overestimation of the future distribution of the butterflies with the simple climatic models.

Material and methods

Study area

The study area is located in the western Alps of Switzerland in an area ranging from 1000 to 3210 meters a.s.l. (Fig.1). Various vegetation belts are observed along the elevational gradient of this calcareous region: the mountainous belt (800m - 1600m) is composed of mixed forest (dominated by *Fagus sylvatica and Abies alba)*; the subalpine belt (1600m – 2400m) consist of coniferous forests (dominated by *Picea abies*); the alpine belt located above the tree line (2400m – 3000m) includes heaths, meadows and pastures (e.g. *Sesleria caerula*, *Nardus stricta*); and finally, the nival belt (above 3000m) with sparse vegetation dominated by tolerant taxa of high altitudes (e.g. *Saxifraga oppositifolia, Cerastium latifolium*) (Aeschimann & Burdet 1989). The study area undergoes a long tradition of land use management. Forests are often interspersed with anthropogenic meadows and pastures from the bottom of the valley up to the lower alpine belt. In the montane belt, the land use is particularly intense with fertilised arable lands and pastures or meadows for the cattle. Thus, open areas are mainly managed grasslands dominated by *Poa sp.* and nitrophilous species (e.g. *Arrhenatherum elatius, Trifolium sp.).* Parcels that are less exploited present a greater diversity, with dominance of *Cynosurus cristatus*. At the subalpine belt, fertilised pastures and meadows are used for the cattle. The agriculture is less intensive and promotes more diversified meadows, dominated by *Cynosurus cristatus*, *Trisetum flavescens* and *Heracleum sphondylium.* In areas that are limited in access and economically non suitable, species-rich grasslands dominated by *Bromus erectus* are present (*Mesobromion*). The extent of these areas decreased significantly in the last decades due to human fertilisation. At the alpine belt, low productive pastures are used for summer grazing and are dominated by *Poa alpina*, *Sesleria caerulea*, or *Nardus stricta*.

Field sampling

Sampling sites were selected in open areas, following a balanced stratified random sampling design based on elevation, slope and aspect (Hirzel and Guisan 2002). Between 2006 and 2010, an exhaustive inventory of the vegetation was performed on a total of 912 sites of $4m^2$ in the study area. A total of 771 plant species were inventoried. In 2009 and 2010, butterflies were sampled on a subset of 192 of these sites selected with the same stratified design. The butterfly sampling was performed between the 1st of June and the 15th of September in optimal conditions for butterflies to fly (i.e., most activity between 10:00–17:00, low wind, less than 20% cloud cover, sunny, minimum 18°C for low elevation and minimum 13°C for high elevation) as recommended by Pollard and Yates (1993). To ensure the possibility of recording every species independently of its phenology, each plot was visited every three weeks (resulting in two to five visits per plot depending on the elevation). Each visit consisted of a random walk of 45min in a $2500m^2$ area (50m-50m) centred on the $4m^2$ vegetation plot, assuming that the vegetation plot are representative of the surrounding vegetation (Dubuis et al. 2011). Butterflies were collected with a net, identified in the field and then released. A total of 131 butterfly species were inventoried, including members of the Papilionoidea superfamily as well as Hesperiidae and Zygaenidae families. For the following analyses, we selected only butterflies' species that had at least one host plant with 20 occurrences in order to have a more reliable and detailed modelling of the plant distribution. For each butterfly species, host plants have been determined according to the checklist of Swiss butterfly species and their biotopes (Pro Natura, Ed. 1987). We discarded butterfly species observed in fewer than 20 sites and any species displaying high mobility, as their presences were unlikely to be related to local environmental conditions (i.e. *Aglais urticae*, *Vanessa atalanta*) (Pöyry et al. 2009). We retained the butterfly species that had good AUC (Area Under Curve) values (threshold > 0.7) in the four predicting models used. Finally, for further analyses, we selected 10 butterfly species of high altitude. Each of these butterfly species has between 1 and 6 host plant species (Table A).

Environmental variables

Temperature data were collected with thermologgers in 49 sites in open areas following a stratified sampling based on altitude and exposure. The thermologgers collected the temperature every hour from January 2006 to August 2006. To predict plants and butterflies distribution, we calculated the mean day temperature (between 10-17 h) and mean night temperature (between 0-5 h) for three periods in 2006 (January-February, March-May and June-August). Daily temperature have been calculated using the elevation and the solar radiations in a quadratic general linear model (GLM) (McCullagh & Nelder 1989) as night temperature only took elevation into account. The layers were adjusted for the 2006 anomalies in order to offset the temperature deviation between 2006 and the 1983-2010 average. Anomalies were calculated as the difference between the mean of monthly temperatures (day and night) for 2006 and 1983-2010. Temperatures data for 1983-2010 were collected from the Meteo Suisse IDAWEB (Federal Office of Meteorology and Climatology MeteoSwiss: https://gate.meteoswiss.ch/idaweb) for 8 stations located in and around the study area. Climatic variables were then extracted in a 10 m and 50 m resolution.

Global change scenario

In this study, we predicted the evolution of the species distribution for each 5 years steps from 2015 to 2100 under a western Switzerland A1B climate change scenario at daily resolution based on probabilistic method (CH2011 2011; Bosshard et al. 2011). The A1B climate change scenario is a scenario of rapid economic growth in a homogeneous and economically focused world, with an increase of 1.4 - 6.4 °C according to regions. A regression on the predictive mean values for the January-February, March-May and June-August periods of 2035, 2065 and 2085 confirmed the linearity of the scenario. We then calculated the predictive mean values for each 5 years from 2015 to 2100 for the January-February, March-May and June-August periods and extracted the climatic variables predictions for each 5 years step according to the 2006 anomalies.

Distribution modelling

Plants and butterflies distribution were modelled respectively at 10 m and 50 m resolution. We submitted each species to the global warming predictions for each 5 years step from 2015 to 2100 using four techniques implemented in the BIOMOD package (Thuiller et al. 2009) in R (R Development Core Team 2007). We used the settings for each algorithm presented in Thuiller et al. (2009): a generalised linear model (GLM) (McCullagh & Nelder 1989), a generalised additive model (GAM) (Hastie & Tibshirani, 1990), a gradient boosted model

(GBM) (Friedman, Hastie, & Tibshirani 2000; Ridgeway 1999) and a random forest model (Breiman 2001). These techniques are all considered appropriate statistical methods for fitting presence-absence SDMs (see Elith et al. 2006 for an evaluation of GLM, GAM and GBM). We applied an ensemble forecasting function on each butterfly species by averaging all single model projections, weighted by AUC (Araújo and New 2007). For the plants projections, the presence was considered when at least three of the models predicted the plant as present. We then considered the dispersal ability of each plant species in our SDM by using the MigClim package (Engler and Guisan 2009) in R. The dispersal ability was based on dispersal modes and plant traits according to Vittoz and Engler (Vittoz and Engler 2008). Plants SDMs were then aggregated in a 50 m resolution with a function that considers the maximum value. For each lapse rate, we built a mask for each butterfly species with its host plants distributions and used it as a filter to determine suitable habitats for the butterfly. A non-parametric paired test (Wilcoxon signed rank test) was then performed to see if there was a significant difference between the area predicted by the butterfly climatic model and the area predicted by the butterfly climatic model filtered with the host plants (filtered model) for 2015, 2030, 2050 and 2080.

Results

Environmental variables

The importance of the environmental variables in our models is not the same for the butterflies and for the plants (Fig.1). Concerning the models for the future distribution of butterflies, the most important variable is the nocturnal temperature for the months of January and February (median = 0.29). This factor is also part of the most influencing variables on the plant models (median = 0.33). However, the most important environmental factor is the diurnal temperature of the period from March to May in that case (median = 0.38).

Changes in butterflies distributions between 2015-2080

The models based only on the climatic conditions predict the loss of 10% of the species in 2015, 30% in 2030, 60% in 2050 and 70 % in 2080. According to these models, only *Boloria napaea*, *Cupido minimus* and *Meliatea diamina* will survive climate change by 2080. Models taking host plant interactions into account predict the loss of 10% of the species in 2015, 50% in 2030, 90% in 2050 and 100% in 2080. Thus, no butterfly will survive global warming by 2080 according to filtered SDMs.

A comparison was made between the areas for the butterflies predicted by the two different models (Fig. 2). The difference was significant both for 2015 (Wilcoxon signed rank test, P-value < 0.01, N = 10) and for 2030 (Wilcoxon signed rank test, P-value = 0.02, N = 10), but there was no significant variation for 2050 and 2080 (Wilcoxon signed rank test, P-value > 0.1, N = 10). Nevertheless, the values obtained for 2050 and 2080 can be explained by the fact that the predicted areas tend toward 0, especially with the filtered model.

For 2015 and 2030, we observe two different trends (Fig.3). When the butterfly distribution is limited by its host plant (Fig. 3, upper panel), the difference between butterfly climatic and filtered models is important. But, if the host plants of the butterfly are widespread (Fig. 3, lower panel), the butterfly climatic model is a good approximation of the butterfly filtered model.

Discussion

Our study indicates that SDMs based only on climatic variables (i.e. climatic models) are clearly overestimating butterflies' future habitat under climate change, compared to SDMs using host plant interactions (i.e. filtered models). The climatic models are a good approximation of the range of environmental conditions suitable for an individual. However, since species interact with each other, their actual distribution is also limited by biotic interaction, which takes into account not only climatic, but also biotic factors. Since filtered models take interactions with butterflies' host plants in consideration, they should then fit a more realistic actual and future distribution of butterflies than climatic models. Our results are a good example of the advantage and the relevance of using filtered models.

A recent study that has been done with coarse spatial resolution (e.g. 10'x10', Araújo and Luoto 2007) has proved the importance of biotic interactions, precisely butterfly – host plants interactions, in SDMs. However, the resolution they use is too coarse to detect potentially favourable microclimatic conditions, thus underestimating potential habitat both for butterflies and their host plants (Randin et al. 2009). Moreover, since an altitudinal shift of the plants under climate change is a commonly accepted phenomenon, including their dispersal in the filtered models is essential. Nevertheless, modelling dispersion for plants with little dispersal abilities is impossible with coarse spatial resolution. In our study, we use data with a very high spatial resolution (10m x 10m) that allows us to model plant dispersal and capture microclimatic conditions. The results obtained with our models are consistent with the results found by Araújo and Luoto (2007), confirming that, even at a local scale, models based only on climatic variables are clearly overestimating butterflies' potential future distribution.

The precision of actual temperature data is essential, when modelling future habitat under climate change (Graae et al. 2011). The thermologgers used in our study are a better way to measure temperature at the level where development of butterflies' caterpillars and chrysalis occurs, than meteorological stations measuring air temperature 2 m above soil level. Thus, our climatic models are more accurate than models using meteorological stations data, employed in previous studies. Based on our models, we have seen that climatic variables do not have the same importance (Fig. 2). The most important factor for butterflies is the nocturnal temperature of January and February. These temperatures are the coldest measured in our dataset. Knowing that during this period, most of the butterfly species studied hibernate in a caterpillar stage (except for *Pontia callidice*, chrysalis), low temperatures will impact their survival during the winter. The most important factors for the plants are the daily temperature of March and May and the nocturnal temperature of January and February. From an ecological point of view, the March and May period is important for plant growth, because plant need mild temperature for their development. As already mentioned, the January and February period shows the coldest temperatures measured in our dataset; moreover, it has a restrictive impact on the plants' development and survival, particularly because frost risks are higher.

Although our filtered model is more realistic to predict the future habitat of butterflies, other factors should be considered in order to increase the precision of predictions. We did not take into account the fact that butterflies could shift to novel host plants, as it has been shown by recent studies (Jahner et al. 2011; Singer et al. 2008). However, the alpine specialist species studied might not be able to use novel host plants, because the phytochemicals produced by other plants are not close enough from the chemicals, produced by their host plants, used to pick oviposition sites (Jahner et al. 2011). This phenomenon has more chance to happen for generalist butterflies that have a wider range of host plants and thus are more likely to find new plants with the same chemical properties. Nevertheless, it would be really difficult to test and predict this event. Other biotic interactions than just host-plant interactions could also be integrated in the models, such as inter-specific competition, in case of a rarefaction of the resources because of global warming. Another example would be butterflies, like the endangered lycaenid *Maculinea alcon*, that interact with ants (Habel et al. 2007). Models should then be filtered not only with the distribution of the host plants, but also with the distribution of the ants' species butterflies interact with. In addition, it has to be pointed out that we only used climatic variables and dispersal ability to model plant future distribution. For a more realistic model, we should use other biotic and abiotic factors. The type of soil available could have a major importance, as Richard observed that, on a moraine recently liberated by the ice at 1900m, the formation of suitable soil avoiding pioneer states needs at least 200 years (Richard et al. 1973). Soil formation in places where it does not yet exist at high altitude would even take much longer. Moreover, competition for the habitat between plant species in colonisation events should be considered. An improvement of our butterfly and plant climatic models could also be achieved using only the environmental variables that are the most important (Fig. 1). Thus, our models would not be forced to fit the distribution of the species with unimportant factors.

Finally, in our study, we modelled the future distribution of the butterflies under an A1B global change scenario. We have seen that for 2050, between 60% and 90% of the butterfly species are predicted to extinct with both climatic and filtered models. This scenario is one of the worst future scenarios, but it would be interesting to investigate this question applying less stringent projections (e.g. A2, B1, B2), as it has been done on mountain flora across Europe by Engler et al. (2011).

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Tables

Table 1: Studied butterflies and their presence belt, altitudinal range and host plants species. Data found in: Les papillons de jour et leurs biotopes, espèces, dangers qui les menacent, Protection. (Pro Natura 1987)

Butterfly species	**Presence belt**	**Altitudinal range**	**Host plants species**
Boloria napaea	Subalpine - Alpine	2200 - 3200 m	*Viola biflora*
Boloria pales	Subalpine - Alpine	1500 - 3000 m	*Plantago alpina* *Valeriana montana* *Viola calcarata*
Cupido minimus	Coline - Alpine	400 - 3000 m	*Anthyllis vulneraria sl*
Erebia gorge	Subalpine - Alpine	1600 - 3000 m	*Festuca ovina aggr* *Festuca pratensis sl* *Festuca quadriflora* *Festuca rubra aggr* *Festuca violacea aggr* *Poa minor*
Erebia pluto	Subalpine - Alpine	1600 - 3000 m	*Festuca quadriflora* *Poa minor*
Erebia pronoe	Subalpine	1200 -2400 m	*Festuca ovina aggr* *Festuca quadriflora*
Erebia tyndarus	Subalpine - Alpine	1200 - 2700 m	*Festuca ovina aggr* *Festuca pratensis sl* *Festuca quadriflora* *Festuca rubra aggr* *Festuca violacea aggr* *Nardus stricta*
Meliatea diamina	Coline - Subalpine	400 - 2400 m	*Valeriana montana*
Plebejus glandon	Subalpine - Alpine	1500 - 3000 m	*Androsace chamaejasme*
Pontia callidice	Subalpine - Alpine	1500 - 3500 m	*Pritzelago alpina sstr*

Figures

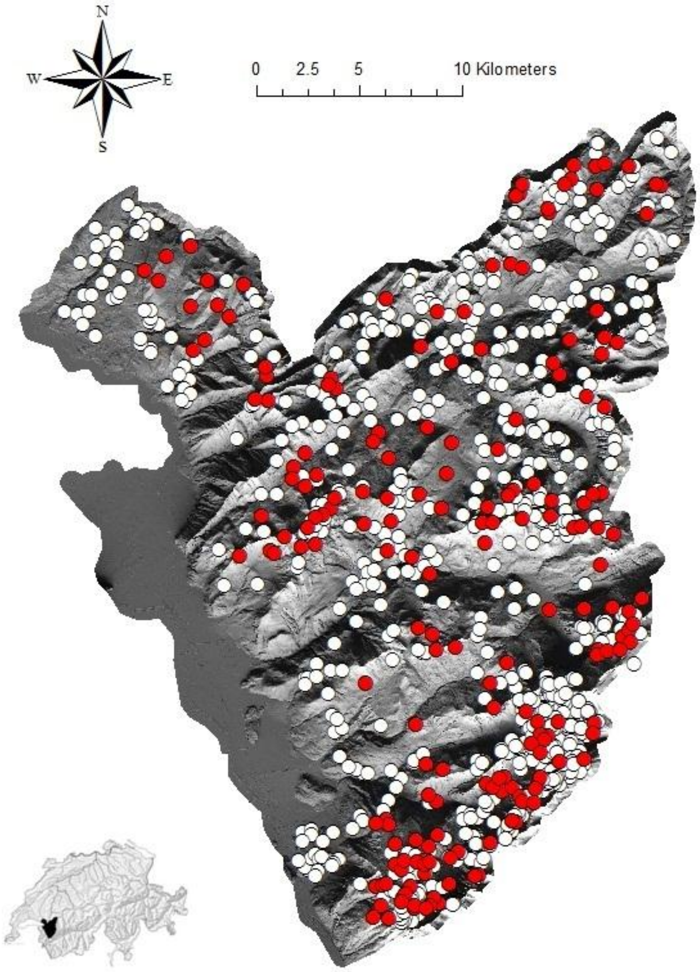

Figure 1: Location of the Study area in the western Alps of Switzerland. All the dots represent vegetation sampling sites. The red dots correspond to the vegetation sites where butterflies have been sampled**.**

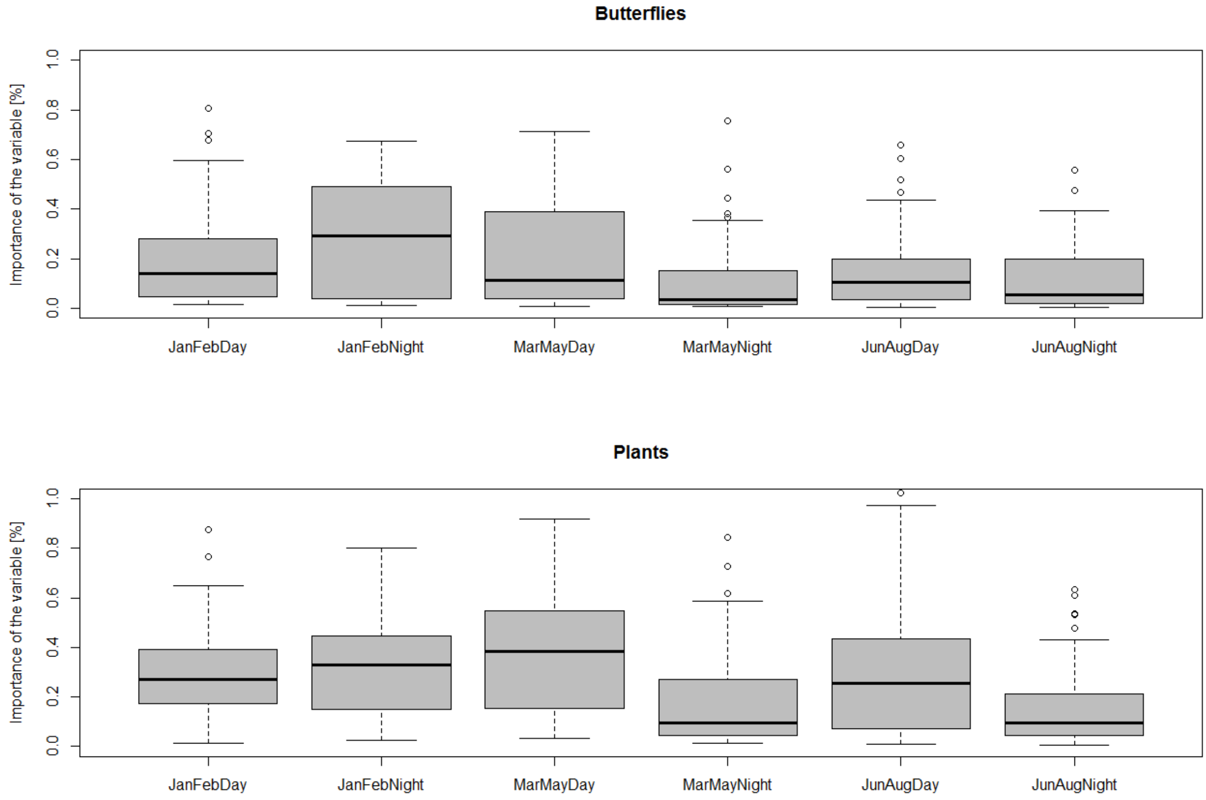

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Figure 2: Importance [%] of the environmental variables in the models for butterflies and for plants.

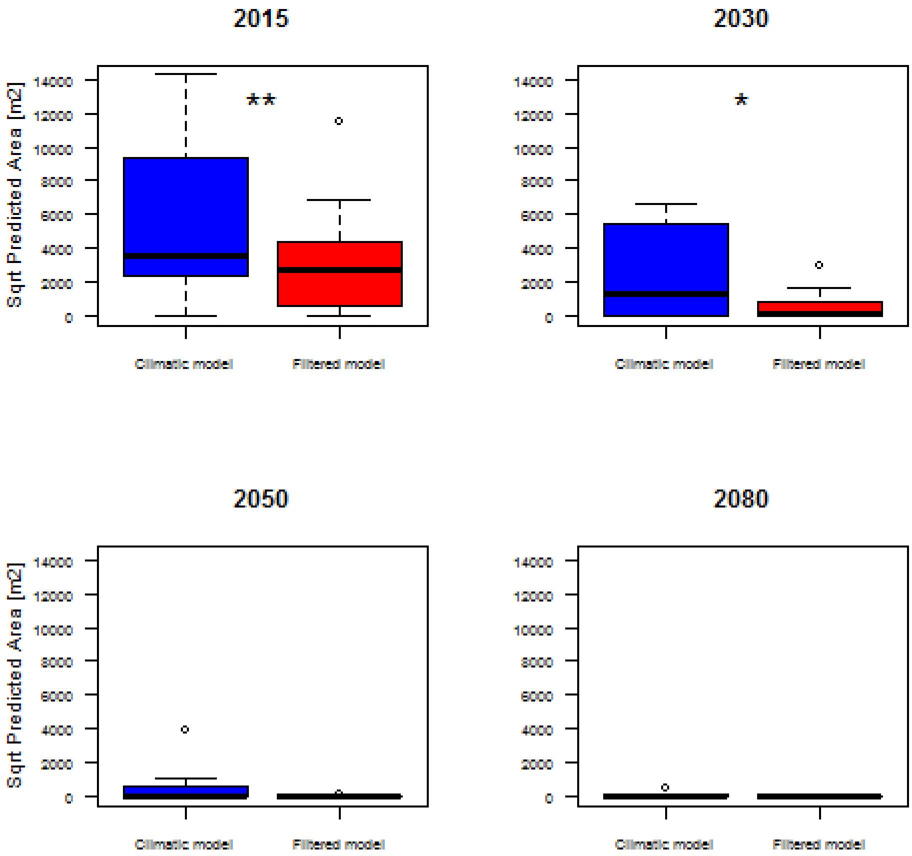

Figure 3: Square root of the predicted distribution area of the butterflies for 2015, 2030, 2050 and 2080 under two different SDM. The butterfly model with no biotic interaction (Climatic model) takes into account only the climatic variables. The butterfly model with biotic interaction (Filtered model) was obtained by filtering the butterfly climatic distribution with the host plant climatic distribution. The filtered model is significantly more restrictive than the butterfly climatic model and predicts a faster decrease of the butterfly distribution area.

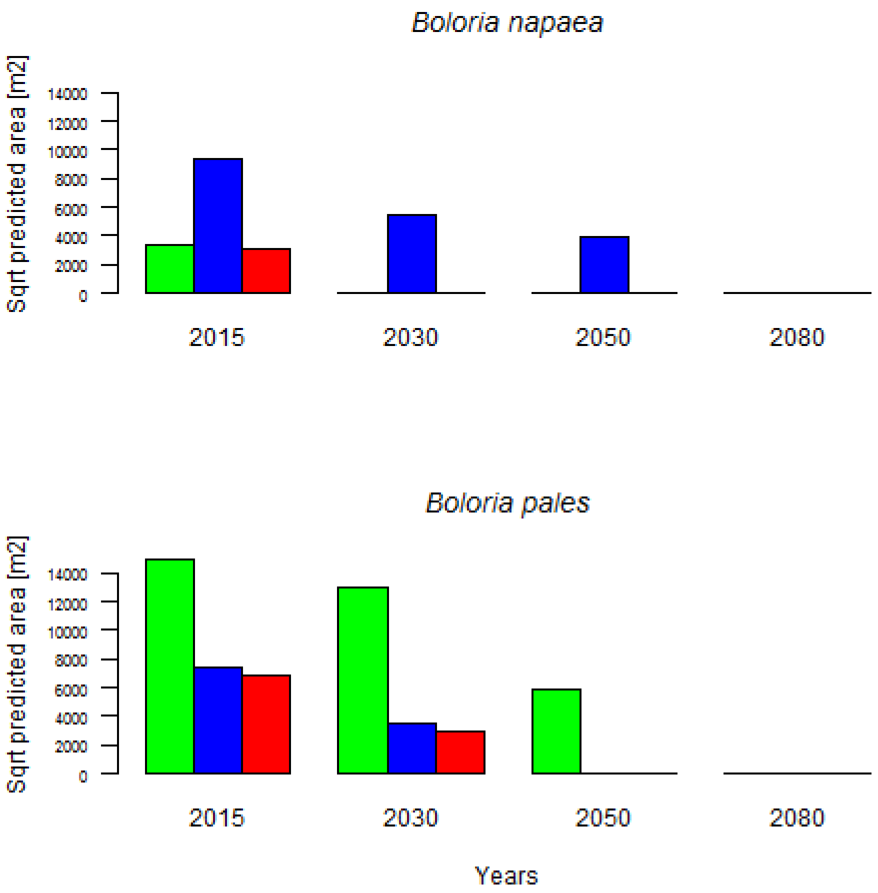

Figure 4: Square root of the area predicted for 2 species (*Boloria napaea* and *Boloria pales)* by the climatic host plant model (in green), the butterfly climatic model (in blue) and the butterfly filtered model (in red) for the years 2015, 2030, 2050 and 2080.