



Host plant availability potentially limits butterfly distributions under cold environmental conditions

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Species ranges are shaped by both climatic factors and interactions with other species. The stress gradient hypothesis predicts that under physiologically stressful environmental conditions abiotic factors shape range edges while in less stressful environments negative biotic interactions are more important. Butterflies provide a suitable system to test this hypothesis since larvae of most species depend on biotic interactions with a specific set of host plants, which in turn can shape patterns of occurrence and distribution. Here we modelled the distribution of 92 butterfly and 136 host plant species with three different modelling algorithms, using distribution data from the Swiss biodiversity monitoring scheme at a 1×1 km spatial resolution. By comparing the ensemble prediction for each butterfly species and the corresponding host plant(s), we assessed potential constraints imposed by host plant availability on distribution of butterflies at their distributional limits along the main environmental gradient, which closely parallels an elevational gradient. Our results indicate that host limitation does not play a role at the lower limit. At the upper limit 50% of butterfly species have a higher elevational limit than their primary host plant, and 33% have upper elevational limits that exceed the limits of both primary and secondary hosts. We conclude that host plant limitation was not relevant to butterfly distributional limits in less stressful environments and that distributions are more likely limited by climate, land use or antagonistic biotic interactions. Obligatory dependency of butterflies on their host plants, however, seems to represent an important limiting factor for the distribution of some species towards the cold, upper end of the environmental gradient, suggesting that biotic factors can shape ranges in stressful environments. Thus, predictions by the stress gradient hypothesis were not always applicable.

Understanding causal mechanisms determining species distributions is an important topic in biogeography and macroecology (Brown et al. 1996). Species distributions are limited by the range of abiotic conditions under which individuals of a species can survive and reproduce. Biotic factors further constrain this fundamental niche to the realized niche, which encompasses all the conditions under which a species actually occurs (Hutchinson 1957). Biotic factors are interspecific interactions that affect the performance of species positively or negatively and, therefore, likely strongly influence range limits (Brown et al. 1996). Such influences are probably context dependent and likely show geographical and environmental patterns. For example, the stress gradient hypothesis predicts that abiotic conditions limit ranges when resource availability is low and under unfavourable biophysical conditions (high altitude/latitude, dry environments). Negative

biotic interactions (mainly competition) limit ranges under less physiologically stressful conditions, i.e. lower altitude/latitude, more humid environments (Bertness and Callaway 1994). While observational studies support this hypothesis (Callaway 1992, Merrill et al. 2008), it has not received much attention so far (but see Normand et al. 2009, Meier et al. 2011 for large scale examples in plants).

Species distribution models (SDMs) correlate species occurrence patterns with independent sets of variables to identify parameters relevant to the distribution of species. Frequently, SDMs incorporate climatic factors (Huntley et al. 1995) and variables describing land-cover patterns (Pearson et al. 2004, Pompe et al. 2008). The incorporation of biotic interactions into SDMs presents a challenge to present research (Kissling et al. 2012, Wisz et al. 2013). So far, few studies incorporate biotic interactions into species

distribution models. Most such studies focus on tree species, while for animals only a few single-species studies exist (Araújo and Luoto 2007, Heikkinen et al. 2007, Schweiger et al. 2008, Meier et al. 2010). Heikkinen et al. (2007) show that species distribution models of tree-hole breeding owls in Finland could be improved by incorporating variables expressing presence of woodpeckers. For common tree species in the Swiss Alps, performance of species distribution models is superior to a simple climatic model when the abundances of other tree species are included as predictor variables (Meier et al. 2010). According to Meier et al. (2011), biotic interaction with competing species generally increases towards the southern latitudinal distribution limit of the European beech *Fagus sylvatica*. In another example, the distribution of the butterfly *Parnassius mnemosyne* in Europe is tightly linked to the distribution of its four host plants (Araújo and Luoto 2007). Additionally, Schweiger et al. (2008) show that the distribution of the butterfly *Boloria titania* is limited by both its larval host plant *Polygonum bistorta* and other factors, most likely climate. These studies suggest a frequent role for biotic interactions in limiting the geographic distributions of species.

Most butterflies depend on a limited set of plant species as food resources during larval development. Such dependencies generally determine local occurrence patterns of butterfly species. How this translates into effects on large-scale species distributions is particularly important, especially when considering projections under scenarios of climate change, to which butterflies and their host plants may respond differently (Schweiger et al. 2008). Although Schweiger et al. (2012) conclude from a study of a subset of European butterflies that only few butterfly species are significantly limited by their host plants at large spatial scales, their study does not consider that biotic interactions might only be relevant at particular range limits, as is predicted by the stress gradient hypothesis. However, the findings of Meier et al. (2011) challenge the generality of the stress gradient hypothesis by showing that the potential for competition among tree species in Switzerland is especially high under cold, dry and harsh climate, and not under warm, wet and more favourable conditions as predicted by the hypothesis.

In order to improve our understanding of the effects of different drivers on range limits we have tested the hypothesis that abiotic factors are more important under less favourable environments while the biotic relationships between butterflies and their host plants are more important in benign environments. We used the distribution of a large set of butterflies in Switzerland together with topo-climatic variables and the availability of host plants to represent one important biotic factor. Further, we evaluate whether host plant limitation is biased towards certain environmental conditions.

Methods

Study area

Our study area is Switzerland, a country covering over 41 293 km² between 45°N and 48°N and 5°E to 11°E. The country has an altitudinal gradient ranging from 193 to

4634 m a.s.l and includes climatic conditions analogous to large parts of Europe. Mean annual temperatures range from -11°C to 12°C and mean annual rainfall varies from 438 to 2950 mm (Kirchhofer 1982–2000). In the lowlands the main land use is intensified agriculture while in montane areas forests are dominant. Extensively used pastures dominate above the tree line.

Environmental variables

Topo-climatic data were available on a 1 × 1 km grid across Switzerland (Zimmermann and Kienast 1999, Pearman et al. 2011). We extracted variables that are ecologically relevant and non-redundant (Pearson correlation coefficient < 0.7). These variables included growing degree days above 0°C [°C], mean annual precipitation sum [mm], mean annual solar radiation [MJ m⁻²], slope [°] and topographic exposure [unitless]. Topographic exposure describes the relative elevation of the centre of a grid cell compared to its surrounding elevation. It ranged between -2.39 and 3.92 with low values indicating concavity and high values convexity. We excluded all grid cells that were covered by more than 50% water according to the Swiss 'Arealstatistik 1992/1997' land cover summary (Bundesamt für Statistik, <www.bfs.admin.ch>). Environmental variables were standardized to zero mean and unit variance prior to analysis.

We performed principal components analysis (PCA) on the environmental variables across all grid cells in order to describe the main environmental gradients (Fig. 1). The first principal component explained 47.6% of the variance and described a gradient from grid cells with a predominantly flat topography and warm and dry climates (negative values on the principal component) to grid cells

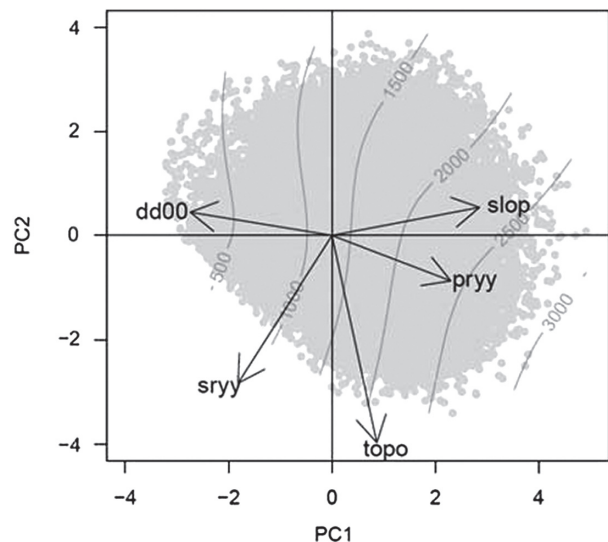


Figure 1. Result of the principal component analysis on the environmental variables used for model calibration. The environmental variables are growing degree days (dd00), solar radiation (sryy), topographic position (topo), annual precipitation (pryy) and slope (slop). The first axis is further used to compare the agreement between the butterfly and host distribution. Contour lines represent the altitudinal gradient and were fitted to the plot a posteriori.

with steep slopes and cold and wet climates (positive values), thus resembling the altitudinal gradient. The second principal component explained 22.2% and described a gradient from grid cells with a convex topography receiving large amounts of solar radiation (negative values) to grid cells with a concave topography and little exposure to sun (positive values). We used the first principal component scores as the main environmental gradient along which we assessed the potential limitation of butterfly species distributions by their host plants.

Survey data

We extracted butterfly and vascular plant survey data from the Swiss biodiversity monitoring programme (<www.biodiversitymonitoring.ch>) from the period 2005–2009. Swiss biodiversity monitoring is realized within the same grid system as used for the environmental data (1 × 1 km) but relies on a subset of 473 sites that are regularly placed all over Switzerland. Each year 20% of the sites that are evenly distributed over the whole country are sampled. Per year and site butterfly occurrence was surveyed four to seven times along a 2.5 km transect within a site covering the whole flight period at different elevations. Presence of vascular plants was recorded once in the high Alps and twice at all lower elevations in the given year along the same transects for 462 sites. We assume that the species distributions were stable during the sampling period, but acknowledge that some species might have experienced small range shifts due to recent warming in Switzerland. However, due to the rotational sampling scheme and the joint surveys of plants and butterflies in the same year, this should not bias the data.

Host plant data

Host plant selectivity was extracted from scientific literature (Ebert and Rennwald 1991a, b, Ebert 1994, Schweizer Bund für Naturschutz 1994, Sonderegger 2005) and complemented by expert knowledge, including information on different levels of fidelity and data quality. We used those plant species that were classified as exclusive host, main host or secondary host, respectively. Host information describing exceptional use, very broad preference (e.g. feeding on most species of an entire family), or uncertain data was excluded from the analysis. For the ease of presentation we grouped the results for exclusive host type (e.g. feeding only on one species) together with those for main host and refer to them as main host. In total, host plant information was available for 169 butterfly species. 184 plant species and 3 genera without any detailed information about the species level were listed as hosts.

Modelling

We separately modelled species distribution for those butterfly and plant species with more than 20 presences and absences, respectively (92 butterflies and 136 plant species). Species distribution models were calibrated using presence/

absence data on each species as response variables and the topo-climatic variables as explanatory variables. We applied three different modelling algorithms, namely generalized linear models (GLMs) using linear and quadratic terms and stepwise selection based on AIC, generalized additive models (GAMs) using a spline smoother with three degrees of freedom, and boosted regression trees (BRTs) allowing for a maximum of 5000 trees, a learning rate of 0.001 and a maximum depth of seven interactions.

Models were validated internally using the True Skill Statistic ($TSS_{GLM} = 0.58 \pm 0.14$ mean \pm SD; $TSS_{GAM} = 0.58 \pm 0.14$; $TSS_{BRT} = 0.77 \pm 0.11$). TSS is a measure of predictive accuracy ranging from -1 (perfect disagreement) to 1 (perfect agreement) and is not influenced by prevalence (Allouche et al. 2006).

We combined the results of the different modelling algorithms and applied an ensemble prediction weighted by individual model performance (TSS) to describe the modelled species distribution for the 39 470 grid cells (each 1 × 1 km) across Switzerland. Grid cells with environmental conditions exceeding those of the calibration data by more than 5% were not included in the prediction. Predicted probabilities of occurrence were transformed into presence/absence maximizing the model accuracy using TSS. Species distribution modelling was conducted with BIOMOD (Thuiller et al. 2009).

Comparing distribution of host and butterfly

We evaluated the agreement between the modelled distribution of a given butterfly species and the modelled distribution of its host plant(s) in order to evaluate potential host plant limitation. If more than one host species was given, we considered the host to be present if at least one of the host species was modelled as present. We assessed the agreement between host and butterfly distribution separately for both the main hosts alone and the main plus secondary hosts. If host information was not species specific (e.g. species feeds on species from a whole genus), we considered all modelled species of that genus.

Agreement was estimated via the relative proportion of modelled presences and absences of hosts and butterfly along the main environmental gradient as described by GAMs. The main environmental gradient was determined using the first axis of the principal component analysis on the climatic data used for model calibration (Fig. 1), and was used as the independent variable in the GAMs. Agreement per grid cell is given by the four possible outcomes: neither host nor butterfly are modelled as present (Fig. 2A, B), both host and butterfly are modelled as present (Fig. 2C, D), only the host is modelled as present (Fig. 2E, F), or only the butterfly is modelled as present (Fig. 2G, H). We separately modelled the agreement levels ‘only host present’, ‘host and butterfly present’ and ‘only butterfly present’ as the binomial response variables and as a function of the main environmental gradient in GAMs. The results were plotted and the type of agreement was estimated visually for the upper and the lower limits of joint occurrence (Fig. 2, Fig. 3.). All statistical analyses were performed using the R environment (R Development Core Team).

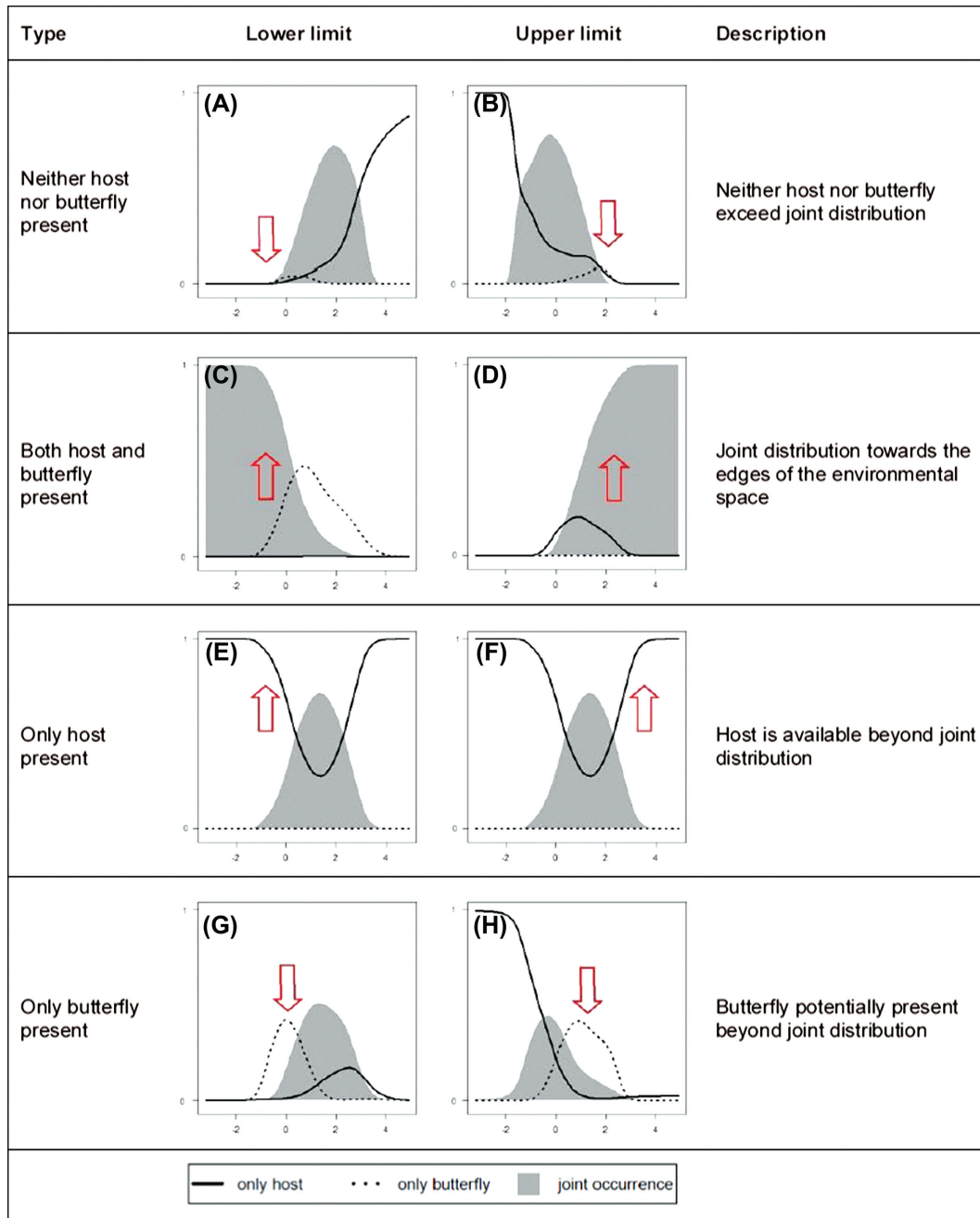


Figure 2. Different types of agreement between the modelled distribution of host plants and butterflies. Graphs are showing the proportion of grid cells containing presences of host, butterfly or both along the main environmental gradient. Arrows indicate where a certain type of agreement occurs. Panel letters are used to enable a direct reference in the text. The x-axis is the first axis of a principal component analysis of a PCA of the environmental data (Fig. 1). See methods section for further description.

Results

Most frequently, the modelled host distribution exceeded the butterfly distribution along the main environmental gradient (Table 1). Most of the butterfly species showed a unimodal response to the main environmental gradient, meaning that the modelled altitudinal limits occurred within the study area (e.g. Fig. 3B). However, patterns of agreement between butterfly and host plant distribution differed quite strongly between lower and upper environmental limits.

At the lower environmental limit hosts were present beyond the modelled range limits of most butterfly species (69% when considering main hosts, 81% when considering main and secondary hosts; e.g. Fig. 3D). Much less frequently, neither the distribution of the butterfly nor the distribution of the host exceeded the joint distribution (19% main host; 5% main and secondary host). The modelled butterfly distribution exceeded modelled host plant distribution only once for main host and three times for main host and secondary host.

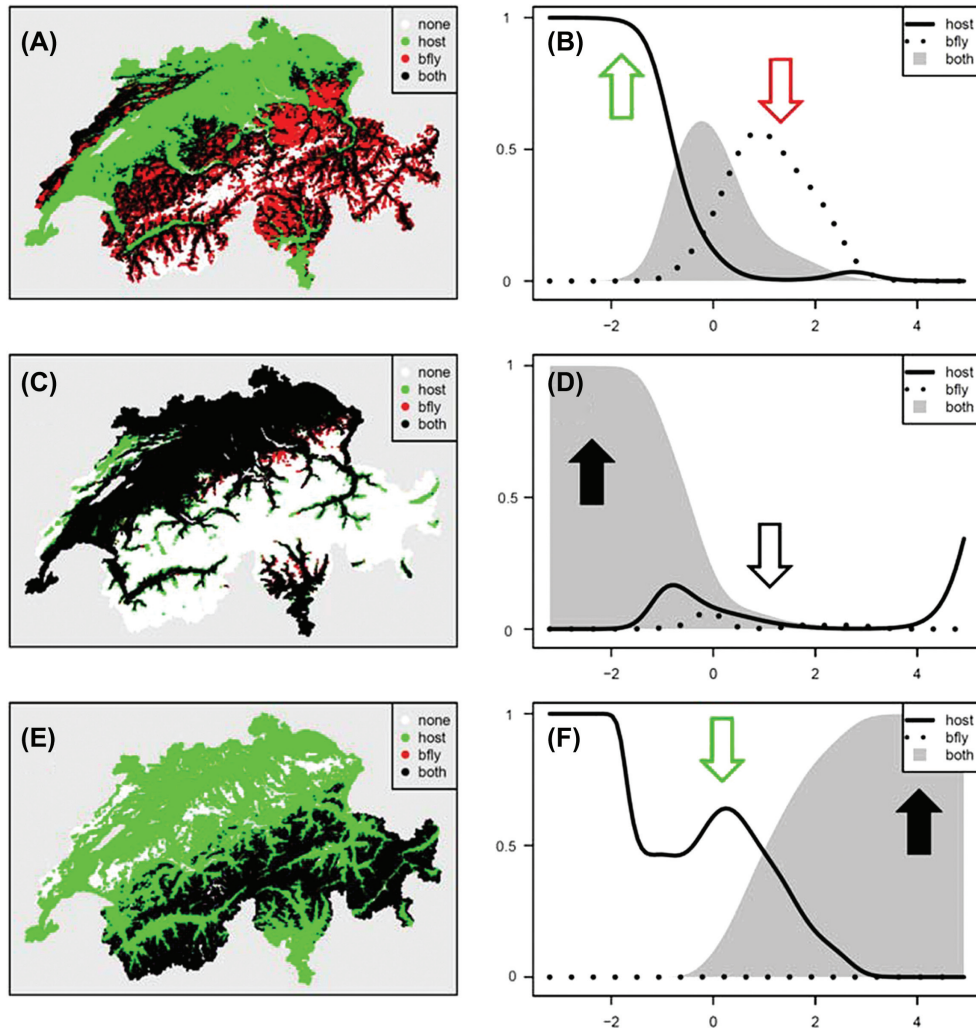


Figure 3. Modelling results for three different butterfly species and their host plants. Panels (A) and (B) show the agreement of the modelled distribution of *Polyommatus semiargus* and its main host plant *Trifolium pratense*. In panel (A) either none of the two species is modelled as present ('none', white), only host is present ('host', green), only butterfly is present ('bfly', red) or host and butterfly are both present ('both', black). Panel (B) shows the modelled proportions of the distributional agreement along the main environmental gradient (i.e. the first principal component). At the lower limit (green arrow) of the joint distribution the host plant is available but the butterfly does not occur. At the upper limit (red arrow), the potential distribution of the butterfly exceeds the distribution of the host. Panels (C) and (D) show the agreement between *Celastrina argiolus* and its host plants *Frangula alnus* and *Cornus sanguinea*. At the lower environmental limit both butterfly and host plants are modelled present (filled black arrow) and none of the two exceed the upper joint distributional limit (empty black arrow). Panels (E) and (F) show the agreement between *Erebia pandrose* and its host plants *Festuca halleri*, *F. ovina*, *F. quadriflora*, *F. violacea* and *Sesleria caerulea*. Here, host plants are present beyond the lower limit of the butterfly (green arrow) and butterfly and host plants are modelled present towards the upper environmental limit (filled black arrow).

Towards the upper limit of the joint distribution the modelled butterfly distribution frequently exceeded the modelled distribution of host species, 54% in relation to main host and 33% in relation to main and secondary host respectively (e.g. Fig. 3B). For less than half of the butterfly species the modelled distribution of host species exceeded the modelled butterfly distribution (18 and 44% respectively). A joint upper limit of modelled host and butterfly occurred for 29 and 21% of the butterfly species (e.g. Fig. 3D).

Discussion

Species ranges are shaped by a multitude of factors, with climatic variables usually being considered among the most

influential, at least at large spatial scales. Nonetheless, in recent years the importance of biotic interactions has been increasingly acknowledged (Araújo and Luoto 2007, Meier et al. 2010, Schweiger et al. 2010) and evidence is increasing that range limits are influenced by different factors, depending on location (Normand et al. 2009, Meier et al. 2011). Our results confirm this latter point, and we find indications that species interactions can have a strong effect in limiting species distributions.

The limitation patterns that we find do not support the stress gradient hypothesis for many butterfly species. We found potential host plant limitation for more than half of the species towards harsher environmental conditions, based on comparison between the modelled distribution of butterflies and their host plants (Table 1). This potential

Table 1. Number and proportion of butterfly species showing a certain pattern of agreement with the host distribution towards the lower or upper limit of the joint distribution. Joint distribution can be either exceeded by the host ('only host') or the butterfly distribution ('only butterfly'), or by neither of the two ('none') or the joint distribution is not limited ('host and butterfly').

	Lower environmental limit		Upper environmental limit	
	Main host	Main + secondary host	Main host	Main + secondary host
Total number of species	26	43	28	43
Neither host nor butterfly	5 (19%)	2 (5%)	8 (29%)	9 (21%)
Host and butterfly	3 (12%)	4 (9%)	0 (0%)	1 (2%)
Only host	18 (69%)	35 (81%)	5 (18%)	19 (44%)
Only butterfly	0 (0%)	2 (5%)	15 (54%)	14 (33%)

limitation is indicated by the fact that many butterflies are present at the upper range limit of their hosts (Fig. 2B, Fig. 3D), or the modelled distribution of the butterfly even exceeds the modelled distribution of the host plants (Fig. 2H, Fig. 3B).

A joint upper limit of host and butterfly distribution may either be caused by the coincidence that both are directly limited by the same abiotic factors or that only the host is limited by abiotic factors and the butterfly is indirectly limited by the absence of its host towards harsher conditions. While the former is unlikely given the quite distinct physiologies of plants and butterflies, the latter is supported by study of Gross and Price (2000) who found that the northern range margin of the bird *Phylloscopus humei* is limited by climate-induced disappearance of its arthropod food. Gutierrez and Thomas (2000) showed that the butterfly *Gonepteryx rhamni* extended its range in Great Britain after planting of host plants outside their natural ranges. Also in Great Britain, Pateman et al. (2012) report that the butterfly *Aricia agestis* extended its northern range limit only due to a shift in host plant utilization that was induced by a slight increase of temperature.

Under simulated climate change Pelini et al. (2009) found that the availability of a host plant and its interaction with climatic variables plays a key role for the survival of two butterfly species at their northern range edge in western North America. Boggs and Inouye (2012) found that one abiotic variable, namely snow melt date, can both directly and indirectly influence population dynamics of the butterfly *Speyeria mormonia* in North America, only that indirect effects were not found via larval host plants but nectar plants. Also, Cormont et al. (2013) found host plant mediated effects of climate change on the persistence of Alcon blue butterfly populations in the Netherlands using a complex modelling approach.

Since we find indications of host plant limitation at the harsher end of the environmental gradient for the majority of the butterfly species we analysed (i.e. the modelled butterfly distribution tightly matches or even exceeds the modelled distribution of the host(s)), our study extends previous findings to a more general level and to a larger spatial scale. By including context-dependency for the factors limiting species distributions, this work supports stronger host plant

limitation than reported by Schweiger et al. (2012). That study addressed the agreement between the distributions of butterflies and host plants on a European scale and on a coarser grid (10 × 10 km) and highlights the importance of host plant limitation against a background of climate change. Past climate change is important in this discussion because post-glacial recolonisation might not be finished for some plant species that have not yet filled their climatic niches (Araújo and Pearson 2005, Svenning et al. 2008).

While butterflies overall have good dispersal abilities it seems possible that host plant availability still acts as a limiting factor at colder range edges. Future climate change will certainly affect chances of butterfly populations persisting especially when plants and butterflies react asynchronously, which could cause a spatial mismatches between butterfly and host distributions (Walther et al. 2002, Schweiger et al. 2012). Moreover, specialist species seem to be most susceptible to such changes (Warren et al. 2001).

Ecological and evolutionary adjustments, such as the shift to other host plants, can help to reduce the pressure of climate change on butterfly populations at least for some species (Pateman et al. 2012). In Switzerland it has been observed that for example *Cupido minimus* feeds on *Astragalus penduliflorus* at the upper elevational limit, while almost everywhere else it feeds on *Anthyllis*. Also, *Maculinea arion* showed a recent shift from *Thymus* to *Origanum* recently and it is not yet clear if it is in relation to climate change.

Host plant limitation is also indicated in our results when modelled butterfly distribution exceeded the distribution of the host plants (Fig. 3B). This would be the case when the model describes the potential non-host related niche of the butterfly that is broader than the aggregated niche of the hosts. However, other reasons might be responsible for this, too. For example, butterflies may locally feed on other species than those that are known to be main or secondary hosts, e.g. *Boloria titania* feeds mainly on *Polygonum bistorta* but may exceptionally use *Viola* species (Stettmer et al. 2007, Schweiger et al. 2008). Further, some butterfly species are rather mobile in their adult stage and can move far away from their larval habitat, extending the observed range beyond the range of the host plants. For very mobile species, this leads to low performance in model validation (e.g. *Vanessa cardui* TSS = 0.2; *Gonepteryx rhamni* TSS = 0.46; *Papilio machaon* TSS = 0.32; TSS from internal validation of GAMs).

Host plant limitation does not seem to play an important role at the lower limit of modelled butterfly distributions since most of the host plants occur far beyond the distribution of the corresponding butterfly (Fig. 2E). In general, such a pattern is supported by Quinn et al. (1998) who conclude from a study on 43 butterfly species in Great Britain that butterflies tend to feed on widespread species and occupy only small proportions of host plant range. Thus, factors other than host plant availability must be responsible for shaping range limits of most butterfly species at the less harsh range margins. Merrill et al. (2008) and Schweiger et al. (2012) suggest climatic variables as likely explanations but human land use might also play an important role here (see also Araújo and Rahbek 2006). McArthur (1972) observed that many species appear to have their range limited by habitat specialization rather than by any other factor (see also

Hardie and Hutchings 2010). Many butterfly species have retreated in the last decades from low altitude portions of their ranges in Switzerland, likely because of intensified agriculture (e.g. *Cupido minimus*, *Lasiommata maera*, *Maculinea arion*). However, land-use patterns in Switzerland are highly correlated with elevation and, therefore, it is difficult to disentangle effects of climate from effects of land use change.

Another important factor that limits species distributions at the warm range margins might be additional biotic interactions as predicted by the stress gradient hypothesis (Bertness and Callaway 1994, Callaway and Walker 1997). Further, we considered presence or absence of host plants but not host plant abundance or host plant species richness, which intuitively seem relevant. Quinn et al. (1998) showed that polyphagous butterflies tend to occur disproportionately in areas of high host plant richness. Evolutionary factors can also be considered influential via shared traits of closely related species. Many species from the genus *Erebia* or the family Satyridae generally feed on widely available grasses. Therefore, host plant limitation at the lower as well as the upper limit is likely not so relevant for these groups.

Our results support the stress gradient hypothesis to some extent in that under low abiotic stress, negative biotic interactions appear to be important in shaping the distribution of a species, while under harsh conditions abiotic factors are more important and only positive interactions influence distributional limits considerably. The influence of biotic factors on range margins seems to be caused by interplay between positive and negative interactions (Daleo and Iribarne 2009, Boggs and Inouye 2012) showing rather complex patterns along stress gradients (Maestre et al. 2006). Tight biotic interactions like the obligatory dependency of butterflies on its host plants might represent an important limiting factor for some, but not all, species distributions towards the cold end of environmental gradients in the Swiss Alps.

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Supplementary material (Appendix ECOG-00195 at <www.oikosoffice.lu.se/appendix>). Appendix 1.