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SPECIAL ISSUE

Increasing range mismatching of interacting species under global change is related to their ecological characteristics

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ABSTRACT

Aim We investigate the importance of interacting species for current and potential future species distributions, the influence of their ecological characteristics on projected range shifts when considering or ignoring interacting species, and the consistency of observed relationships across different global change scenarios.

Location Europe.

Methods We developed ecological niche models (generalized linear models) for 36 European butterfly species and their larval host plants based on climate and land-use data. We projected future distributional changes using three integrated global change scenarios for 2080. Observed and projected mismatches in potential butterfly niche space and the niche space of their hosts were first used to assess changing range limitations due to interacting species and then to investigate the importance of different ecological characteristics.

Results Most butterfly species were primarily limited by climate. Species dwelling in warm areas of Europe and tolerant to large variations in moisture conditions were projected to suffer less from global change. However, a gradient from climate to host plant control was apparent, reflecting the range size of the hosts. Future projections indicated increased mismatching of already host-plant-limited butterflies and their hosts. Butterflies that utilize plants with restricted ranges were projected to suffer most from global change. The directions of these relationships were consistent across the scenarios but the level of spatial mismatching of butterflies and their host plants increased with the severity of the scenario.

Main conclusions Future changes in the co-occurrence of interacting species will depend on political and socio-economic development, suggesting that the composition of novel communities due to global change will depend on the way we create our future. A better knowledge of ecological species characteristics can be utilized to project the future fate and potential risk of extinction of interacting species leading to a better understanding of the consequences of changing biotic interactions. This will further enhance our abilities to assess and mitigate potential negative effects on ecosystem functions and services.

Keywords

Climate change, climate envelope, Europe, host-plant-constrained range, species distribution model, species interaction.

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INTRODUCTION

Bioclimatic envelope models (Pearson & Dawson, 2003; Heikkinen *et al.*, 2006) are widely used to provide first estimates about the projected impacts of global change on future distributions of many species (e.g. Pompe *et al.*, 2008; Settele *et al.*, 2008; Heikkinen *et al.*, 2010). However, it is increasingly being realized that their ability to provide realistic projections is limited (Davis *et al.*, 1998; Pearson & Dawson, 2003), and a number of uncertainties remain to be considered (Luoto *et al.*, 2005; Heikkinen *et al.*, 2006; Pöyry *et al.*, 2008). Here, we address four such limitations.

Firstly, although climate is a major determinant of species distributions at broad macroecological scales (Pearson & Dawson, 2003; Luoto *et al.*, 2007) it also interacts with many other factors (Dormann *et al.*, 2008; Schweiger *et al.*, 2010). In particular, land use may significantly affect future species range changes (Hill *et al.*, 2001), and should be taken into account alongside climatic changes (Pompe *et al.*, 2008).

Secondly, climate change can alter soil water availability, which in turn may affect the distribution of suitable habitat for different species (Berry *et al.*, 2002). However, there are notable differences in the measures of water availability, stemming from dissimilarities in the algorithms used for calculation (Hickler *et al.*, 2009). These discrepancies affect the outcomes of ecological niche models, especially when projected into the future (Rickebusch *et al.*, 2008). Usually basic climatic variables are used to describe water availability while a mechanistic understanding of the water balance of terrestrial ecosystems, incorporating vegetation structure and ecosystem functioning, might provide more realistic projections (Hickler *et al.*, 2009).

Thirdly, the importance of biotic interactions in assessing future species performance and distribution has become apparent (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007; Preston *et al.*, 2008; Schweiger *et al.*, 2010). Using land-cover data to predict species distributions indirectly incorporates some species interactions (Heikkinen *et al.*, 2007). However, direct interactions need to be modelled on a species-to-species basis to avoid spatial over-predictions of suitable environment due to a lack of information on relevant interacting species (Heikkinen *et al.*, 2007; Schweiger *et al.*, 2008). So far very few studies have investigated future changes in the spatial matching of interacting species, using only a limited set of species (Araújo & Luoto, 2007; Preston *et al.*, 2008; Schweiger *et al.*, 2008).

Fourthly, different aspects of global change should be incorporated into the modelling simultaneously and based on the very same basic assumptions. However, most studies so far have only addressed land-use or climate change separately, or obtained scenarios for climate and land-use change from separate assumptions (but see Pompe *et al.*, 2008). Here, we synchronize the scenarios for both climate and land use in a consistent manner by using the same set of storylines. These storylines cover an adequately broad range of potential developments in environmental policy, demography, socio-economics and technology (Spangenberg *et al.*, 2012; Stocker *et al.*, 2012).

Using species distribution models and climate, soil water content and land-use data, we investigate here the ecological niches of a selected set of European butterflies and their co-occurrence with their larval host plants. To develop future species range projections, we apply integrated scenarios that are consistent with three socio-economic storylines developed for the EU-funded project ALARM (Settele *et al.*, 2005): a sustainable policy scenario (SEDG), a business-as-might-be-usual scenario (BAMBU) and a liberal, growth-focused policy scenario (growth applied strategy, GRAS; Spangenberg *et al.*, 2012). Based on these projections, we investigate the changes in distributional matches of the butterflies and their hosts, and the consistency of the observed trends across the three scenarios.

By analysing distributional mismatches, we study potentially different responses of two aspects of ecological niche models. Usually, the geographic niche space (i.e. the modelled range) of trophically dependent species is represented independently of the host plant, i.e. neglecting species trophic dependences. In contrast, host-plant-constrained niche models consider the co-occurrence of the interacting species as a prerequisite of the biotic dependency. Since biotic interactions can change under global change (Schweiger *et al.*, 2010), the host-plant-independent range can be expected to vary substantially more than that of the host-plant-constrained range. In this study, we investigate future changes in the host-plant-independent range and the host-plant-constrained range and how much they differ from each other.

While Schweiger *et al.* (2008) showed that indirect effects of global change can be detrimental for a particular butterfly species due to asymmetric changes in the distribution of its host plant and the butterfly itself, we investigate here whether such an effect can be generalized to a larger set of European butterflies. Moreover, we also study whether particular ecological characteristics of the butterfly species can alter the level of response. The expectation here is that changes in the host-plant-independent range depend on species range size and climatic niche position and breadth (Thomas *et al.*, 2004; Thuiller *et al.*, 2004; Parmesan, 2006; Pöyry *et al.*, 2009), and that changes in the host-plant-constrained range additionally depend on factors influencing species interactions (trophic interactions in particular), such as the level of dietary specialization and the distributional range and climatic niche properties of the host plants (Thuiller *et al.*, 2004; Kotiaho *et al.*, 2005). Information on these mechanisms will be used to draw conclusions on the question of what determines observed species range boundaries (Brown *et al.*, 1996; Pearson & Dawson, 2003) and which factors (abiotic or biotic) and which ecological characteristics are most critical for future changes and potential threats to butterfly species.

METHODS

Study area, plant, butterfly and environmental data

The study covered the area of the European Union, excluding Bulgaria and Romania due to lack of available data, plus Norway and Switzerland. Host plant distribution was obtained from 1720 Universal Transverse Mercator (UTM) grid cells (*c.* 50 × 50 km^2) from the Atlas Florae Europaeae database (AFE database; Lahti & Lampinen, 1999) maintained by the Botanical Museum of the University of Helsinki. Butterfly distributions were available from about 7000 georeferenced localities. These data also constitute the basis for *The distribution atlas of European butterflies* (Kudrna, 2002), but here we resampled the localities to the same UTM grid as for plants.

Selection of the butterfly species was constrained by the availability of information on host plants and the incompleteness of the AFE database, which currently covers only 20% (4123 taxa) of the plant species in Europe. We used 44 butterfly species for which host plant information was obtained from 12 field guides across Europe (see Appendix S1 in Supporting Information) and for which distributional data for all their host plants were available in the AFE database.

Monthly interpolated climate data were obtained at a 10′ grid resolution (New *et al.*, 2000; Mitchell *et al.*, 2004). Mean values of the following 18 climate variables for the period 1971–2000 were derived: mean annual temperature (°C); range in annual temperature (°C); mean quarterly temperature (e.g. March–May = spring; °C); range in quarterly temperature (°C); diurnal temperature range per year (°C); diurnal temperature range per quarter (°C); annual summed precipitation (mm); range in annual precipitation (mm); quarterly summed precipitation (mm); range in quarterly precipitation (mm); annual water deficiency (annual equilibrium evapotranspiration minus annual precipitation; mm); range in annual water deficiency (mm); mean annual cloudiness (%); mean quarterly cloudiness (%); accumulated growing degree days with a base temperature of 5 °C until February, April, June and August.

In addition to these 18 climate variables, we calculated soil water content for the upper horizon (0.5 m) with the dynamic vegetation model LPJ-GUESS (Hickler *et al.*, 2004, 2009; Smith *et al.*, 2007). This model provides a process-based representation of the water balance in terrestrial ecosystems as it considers feedback mechanisms by changing vegetation structure such as leaf area index and ecosystem functioning, e.g. effects of changes in photosynthetic demand and elevated CO_2 on stomatal conductance (Hickler *et al.*, 2009).

Percentage cover of the following five land-cover classes (Mücher *et al.*, 2000) were provided by Rounsevell *et al.* (2006) for the same 10′ grid cells: forest, grassland, arable land, urban and others comprising natural and semi-natural areas, water bodies, inland rocks and ice.

Global change scenarios

Global change scenarios were generated based on storylines developed within ALARM (Settele *et al.*, 2005; Spangenberg *et al.*, 2012), including down-scaled climate scenarios from global atmosphere–ocean general circulation models (AOGCM) (Fronzek *et al.*, 2012) and spatially explicit land-use change scenarios (Rounsevell *et al.*, 2006). These storylines cover a broad range of potential developments in demography, socio-economics and technology during the 21st century. The resulting greenhouse gas emission scenarios are very close to IPCC SRES scenarios (Nakicenovic & Swart, 2000; for more details see Spangenberg *et al.*, 2012).

The scenario of moderate change (SEDG) assumes that policy will integrate social, environmental and economic aspects to enhance the sustainability of societal development. Climatic projections are based on the IPCC B1 scenario. Under this scenario, the mean expected temperature increase in Europe by 2080 is 2.4 °C. Grasslands are projected to decrease by about 1%, while forests and areas used for bioenergy are projected to increase by about 4% (Rounsevell *et al.*, 2006).

The scenario of intermediate change (BAMBU) assumes free trade, growth and globalization and implementation of policy decisions already made in the EU. Climatic projections are based on the IPCC A2 scenario, with a mean expected increase in temperature of 3.1 °C. Under BAMBU, grasslands decrease by about 10%, and forests and areas for bioenergy increase by about 1% and 9%.

The scenario of maximum change (GRAS) assumes that free trade, growth and globalization will be the main policy objectives. Climatic projections are based on the IPCC A1FI scenario and the mean expected increase in temperature is 4.1 °C. Grasslands decrease by about 9%, and forests and areas for bioenergy increase by about 1% and 9%.

Based on the storylines, integrated projections of future changes in climate, including soil water content, and land use were developed on the 10′ grid of Europe. Monthly projected climate and soil water content data were averaged for the period 2051–80. Annual projected changes in land use were modelled in a spatially explicit way on the same 10′ grid until 2080 (Rounsevell *et al.*, 2006).

Ecological niche modelling

Classical methods of variable reduction usually yield unstable results in the presence of highly collinear predictors (e.g. Harrell, 2001; Dormann, 2007; Dormann *et al.*, 2008). To avoid such problems among the climate variables, we performed a hierarchical cluster analysis based on the complete linkage method and Pearson correlation coefficients (r) lower than 0.3. From each of the resulting four clusters (representing four groups among which the variables show very little correlation) the ecologically most meaningful variable was selected for modelling: (1) accumulated growing degree days with a base temperature of 5 °C until August (GDD5); (2) soil water content for upper horizon (SWC); (3) range in annual temperature; and (4) range in annual precipitation.

Prior to the modelling, all land use and the selected climate variables were averaged across the UTM grid to match the spatial resolution of the species data. Ecological niche models relating the environmental variables to presence and absence data were developed for each plant and butterfly species separately using generalized linear models (GLM) with a binomial error distribution and a logit link function. We allowed for curvilinear effects by incorporating both first- and second-order terms. All terms were scaled to a mean of zero and standard deviation of one prior to the modelling. Models were checked for spatial autocorrelation with Moran's *I* correlograms of model residuals, but none was detected. The models were simplified by stepwise regression, while minimizing Akaike's information criterion (AIC).

Host plant models were developed across the whole study area. In contrast, we wanted the butterfly models to be independent of the distribution of the host plants. However, this aim may be hard to achieve if a species distribution model is developed across the whole study area, due to the possibility that species co-occurrence will be indirectly incorporated into the modelling (Davis *et al.*, 1998; Heikkinen *et al.*, 2007). In such cases, absences that are in fact a consequence of interacting species may be falsely attributed to the explanatory variables. Such falsely modelled relationships may introduce bias to future projections of the focal species, especially when responses of the focal species and interacting species differ (Schweiger *et al.*, 2008). To avoid this, we included in the calibration of the butterfly models only those grid cells where at least one host plant species of the modelled butterfly is currently present. This approach is quite conservative, since it also disregards grid cells were the modelled butterfly is reported to be present but none of its host plants are. In cases like these it is hard to decide which data set might be wrong, i.e. whether the butterfly is falsely reported as present (for instance, quite dispersive species might be observed outside their breeding ranges), the host plant was not detected or the butterfly utilizes host plants which were not reported in the sources we used. To avoid calibrating our butterfly models with potentially wrong presence data, we decided to apply this conservative approach. However, the number of disregarded presence grid cells was generally small (median = 8.5) and model quality did not suffer (see Appendix S2). With this approach, we avoided a potentially false attribution of absences to climate and land-use conditions in areas outside the range of the host plants. Consequently, we were able to model the geographical representation of potential niche space inside and outside the current range of the host plants. These areas are identified only through suitable climate and land use and will be referred to as the 'host-plant-independent range'.

Models were calibrated on an 80% random sample of the initial data set, and model accuracy was evaluated on the remaining 20%. Agreements between observed presences and absences and projected distributions were evaluated by the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell, 1997) and by the frequencies of falsely modelled absences (modelled as absent while actually being present; J. Hanspach *et al.*, unpublished data). Thresholds for calculating presence–absence projections were obtained by a maximizing kappa approach (Manel *et al.*, 2001). The AUC values were generally high for all models (range = 0.78–0.99, median = 0.92 for plants, and range = 0.61–0.99, median = 0.84 for butterflies), but occasionally high frequencies of falsely modelled absences indicated weak model performance for some butterfly species (for model coefficients, AUC values and false absence rate see Appendices S3 & S4). Therefore, we excluded eight species with a false absence rate higher than 50% from the subsequent analysis. This resulted in 36 species with corresponding information on 115 host plants (Table 1).

The models developed at the UTM grid were then downscaled to the 10′ grid for current and projected future environmental conditions according to the three ALARM scenarios. The overlaps of the host-plant-independent range of the butterflies with the aggregated niche spaces of their host plants indicate areas where climate conditions are suitable for both the butterfly and its host plants. We will refer to these areas as the 'host-plant-constrained range'. We also acknowledge that there are many additional potential obstacles to colonization, such as dispersal limitations or hostile habitats, due to which the species may not reach all the otherwise suitable areas.

Ecological characteristics of the butterflies

The following ecological characteristics were obtained from modelled current (host-plant-independent) niche space: (1) present-day range size (number of occupied 10′ grid cells); four variables describing basic climatic niche characteristics of the butterfly species, including (ii) mean (niche position) and (iii) standard deviation (niche breadth) of GDD5, and (iv) mean and (v) standard deviation of SWC across the modelled niche space; and five variables describing basic trophic niche characteristics of the butterfly species, i.e. (vi) host range size (number of 10′ grid cells occupied by the host plants), and (vii)–(x) the same four climatic niche characteristics of the host plants as used for the butterflies, i.e. mean and standard deviation of GDD5 and SWC (Table 1). For each butterfly species, trophic niche characteristics were calculated on the aggregated total area of all their host plants. In addition (xi) the number of host plants (trophic niche breadth) was extracted from the literature (Appendix S1).

Percentage changes in host-plant-independent range, calculated as (future projected niche space/present niche space −1) × 100, and modulating effects of host plants, calculated as the difference between changes in host plant-constrained range and host plant-independent range, were related to the ecological characteristics with linear mixed effects models where the three ALARM scenarios were considered as a random factor. High levels of collinearity (higher than 0.5) between mean GDD5 and mean SWC (butterflies, Pearson $r = -0.86$; host plants, Pearson $r = -0.85$) were detected. Hierarchical variation partitioning (Mac Nally, 2002) revealed that mean SWC of both butterflies and host plants explained less variance in changes of the host-plant-independent range than mean GDD5 and was thus not included in the initial models. All remaining variables were scaled to a mean of zero and standard deviation of one prior to the modelling. Models were simplified according to AIC and model comparisons based on a likelihood ratio test.

Percentage changes in host-plant-constrained range of the butterflies were then related to the remaining variables of both

Table 1 Ecological characteristics of 36 analysed butterfly species and their host plants based on modelled current potential distribution, except for the number of host plants, which was based on the literature (Appendix S1).

	Butterfly						Host plants				
		Position		Breadth				Position		Breadth	
Species	*R*	GDD5	SWC	GDD5	SWC	*H*	*R*	GDD5	SWC	GDD5	SWC
Anthocharis cardamines	14,035	1341	0.46	396	0.11	28	22,046	1393	0.47	635	0.14
Anthocharis euphenoides	3767	2048	0.38	620	0.09	2	3843	1829	0.44	666	0.16
Anthocharis gruneri	1951	1535	0.41	590	0.09	1	3210	1936	0.43	591	0.14
Apatura ilia	4749	1633	0.41	256	0.1	7	20,900	1350	0.47	604	0.14
Apatura iris	5669	1502	0.42	217	0.1	8	20,931	1343	0.48	595	0.14
Euchloe crameri	2888	2164	0.37	583	0.09	7	16,047	1581	0.45	579	0.15
Euchloe simplonia	371	580	0.68	354	0.16	2	4198	1634	0.47	513	0.15
Euchloe tagis	915	2318	0.38	645	0.09	7	7870	1798	0.44	563	0.12
Favonius quercus	4687	1513	0.41	269	0.08	10	15,269	1693	0.44	543	0.13
Libythea celtis	8652	1527	0.43	480	0.15	1	2733	2320	0.43	488	0.12
Limenitis populi	6167	1371	0.44	266	0.09	2	20,104	1312	0.48	576	0.14
Lycaena alciphron	3447	1721	0.41	361	0.12	4	20,844	1332	0.48	590	0.14
Lycaena candens	216	1847	0.31	257	0.06	1	19,958	1273	0.48	527	0.14
Lycaena dispar	4023	1688	0.4	269	0.1	6	21,282	1441	0.46	629	0.13
Lycaena hippothoe	9990	1156	0.47	376	0.12	4	21,806	1376	0.47	620	0.14
Lycaena ottomana	497	2103	0.39	504	0.15	1	19,958	1273	0.48	527	0.14
Lycaena phlaeas	12,595	1595	0.43	456	0.11	11	22,222	1403	0.47	646	0.14
Lycaena tityrus	7691	1629	0.42	342	0.11	3	20,454	1306	0.48	563	0.14
Lycaena virgaureae	9505	1291	0.43	341	0.1	4	21,753	1377	0.47	623	0.14
Phengaris nausithous	1976	1416	0.41	225	0.08	1	9285	1527	0.44	314	0.12
Phengaris teleius	2478	1612	0.4	247	0.12	1	9285	1527	0.44	314	0.12
Nymphalis io	13,350	1511	0.44	333	0.12	1	19,423	1291	0.49	543	0.13
Parnassius apollo	2781	1359	0.5	506	0.17	9	16,026	1358	0.49	605	0.14
Parnassius mnemosyne	2697	1560	0.46	616	0.15	4	11,847	1349	0.46	478	0.14
Parnassius phoebus	464	832	0.63	306	0.14	2	4434	743	0.65	373	0.12
Pieris bryoniae	8557	898	0.57	387	0.13	4	3230	1442	0.52	485	0.13
Pieris callidice	547	875	0.61	368	0.15	5	5734	956	0.6	548	0.13
Pieris krueperi	463	2419	0.33	365	0.03	1	3057	1923	0.37	501	0.09
Pyrgus cacaliae	349	736	0.74	402	0.1	3	19,208	1229	0.49	483	0.13
Pyrgus carlinae	179	820	0.57	320	0.09	3	14,746	1646	0.43	474	0.12
Pyrgus sidae	862	2323	0.41	653	0.16	2	8490	1639	0.41	363	0.1
Satyrium ilicis	7710	1785	0.41	339	0.1	7	15,001	1690	0.44	545	0.13
Vanessa atalanta	14,618	1467	0.44	458	0.12	4	19,739	1297	0.48	545	0.14
Zegris eupheme	1174	2202	0.29	472	0.05	2	8198	1947	0.4	528	0.1
Zerynthia polyxena	2095	2171	0.42	502	0.14	4	6750	1952	0.41	459	0.09
Zerynthia rumina	2116	2292	0.36	613	0.08	5	7234	2017	0.41	496	0.1

R, range size (number of occupied 10′ grid cells); Position, climatic niche position according to accumulated growing degree days until August (GDD5) and soil water content (SWC) averaged over modelled occupied grid cells; Breadth, climatic niche breadth measured as standard deviation of GDD5 and SWC; *H*, number of host plants. Characteristics of host plants were calculated for an aggregated modelled host plant distribution, except for the number of host plants, which was based on the literature (Appendix S1).

minimally adequate models, i.e. to both relevant climatic and trophic niche characteristics. Independent effect sizes of the remaining variables were investigated by hierarchical variation partitioning separately for the three ALARM scenarios.

All calculations were performed in the statistical environment R v.2.5.1 (R Development Core Team, 2007) using the libraries Hmisc (Harrell, 2009), nlme (Pinheiro *et al.*, 2009) and hier.part (Walsh & Mac Nally, 2005).

RESULTS

Determinants of current distribution: climate and land use versus host plants

Comparative analyses of host plant distribution, host-plant-independent range and constrained range, respectively, indicated that most butterflies are currently predominantly limited

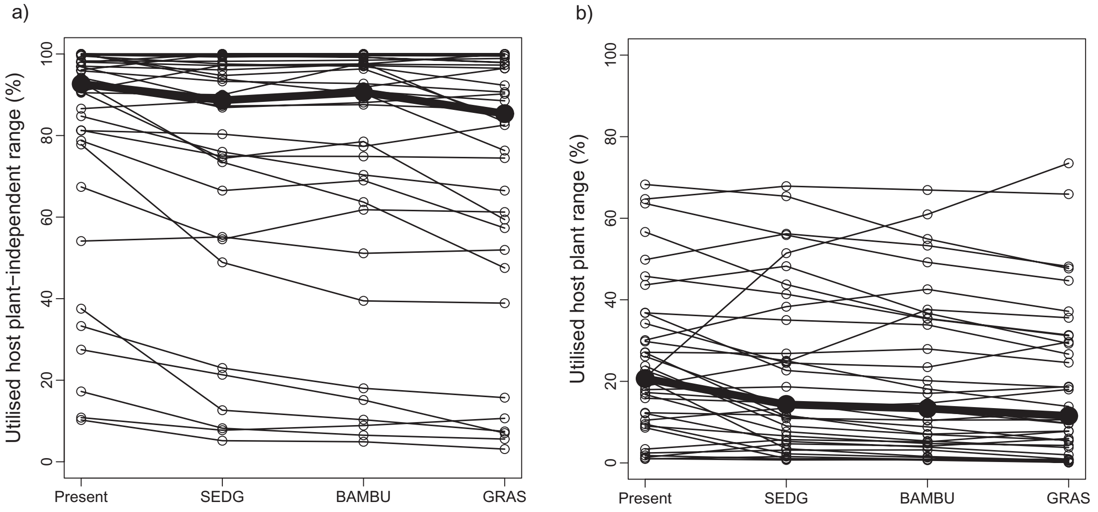

Figure 1 Utilization of the potential range of 36 butterfly species for current conditions and three global change scenarios (SEDG, BAMBU, GRAS) in Europe. (a) Utilization of modelled host-plant-independent range (percentage overlap of modelled host-plant-independent and constrained ranges). (b) Utilization of host plant range (percentage overlap of aggregated modelled host plant distribution and host-plant-constrained ranges). Open circles and thin lines, single species; filled circles and bold lines, median. Note that lines are not meant as transient changes but are drawn for a better visualization of differences among present conditions and future scenarios for each single species.

by climate and land use and less by the distribution of their host plants. Most modelled ranges of butterfly species largely occupy the whole of their host-plant-independent range (median = 92.7%), i.e. only few species showed large areas of host-plant-independent range outside the distribution of their host plants (Fig. 1a). Furthermore, the majority of butterfly species made incomplete use of the aggregated distributional range of their host plants (median = 20.7%), i.e. there were large areas outside the host-plant-independent range where at least host plant presence would allow occurrence of the butterflies (Fig. 1b). Nevertheless, not all species used 100% of their host-plant-independent range, and the impact of host-plant limitations varied considerably across species (Fig. 1). The impact of limitation by the hosts increased when their range sizes decreased ($P < 0.001$, $R^2 = 0.57$; Appendix S5), while the relationship with the number of host plants (trophic breadth) was weaker, though statistically significant ($P = 0.014$, $R^2 = 0.16$). Moreover, this relationship showed a more triangular pattern with generalist species being less constrained by their host plants and specialist species being occasionally very limited by their hosts (Appendix S6).

Range limitations due to climate and host plants are projected to increase consistently across the three global change scenarios. The study species were projected to use less of their host-plant-independent range (median for SEDG = 88.6%, median for BAMBU = 90.6%, median for GRAS = 85.4%; Wilcoxon signed rank test all $P < 0.001$; Fig. 1a), and an increasing number of them were also projected to make incomplete use of the space provided by their host plants (median for SEDG = 14.3%, median for BAMBU = 13.3%, median for GRAS = 11.5%; Wilcoxon signed rank test all $P < 0.024$; Fig. 1b).

Future changes in host-plant-independent range and host-plant-constrained range

Between 64% and 72% of the butterfly species, depending on the global change scenario, were projected to show a loss of host-plant-independent range (median ranges from −17.8% to –45.0%; Table 2). Projected maximum losses of host-plant-independent range varied between 93% and 99%, while maximum gains varied between 249% and 384% (Table 2; Fig. 2). Both largest losses and largest gains were projected for the maximum change scenario GRAS.

Changes in host-plant-constrained range largely reflected the changes in host-plant-independent range (Fig. 2). However, there were several examples where increased mismatching of host-plant-independent range and projected distribution of the host plants resulted in restricted host-plant-constrained range. Yet, changes in the latter (median ranges from −25.4% to –54.5%) were generally more forceful than the changes in host-plant-independent range (Table 2; Fig. 2). As an example, the host-plant-independent ranges of *Pieris bryoniae* (6–13% increase) and *Anthocharis euphenoides* (1–23% increase) were projected to change only marginally, but their host-plant-constrained ranges were projected to diminish up to 67% and 81%, respectively (Table 2; see maps in Appendix S7). Also, species which seemed to profit notably from global change by increased host-plant-independent range, such as *Anthocharis gruneri* (221–334% increase) or *Pyrgus sidae* (122–231% increase), were projected to increase their host-plant-constrained range much less (37–53% and 19–57%, respectively; Table 2; Appendix S7). Most worrying were cases in which the effects of shrinking climatically suitable areas are projected

Table 2 Percentage changes in host-plant-independent range (i.e. independent of the distribution of host plants; Ind) and host-plant-constrained range (i.e. constrained by the occurrence of host plants; Con) of 36 butterfly species for three future global change scenarios SEDG, BAMBU and GRAS for 2080 relative to the modelled number of currently occupied 10′ grid cells.

	SEDG		BAMBU		GRAS	
Species	Ind	Con	Ind	Con	Ind	Con
Anthocharis cardamines	−19.4	−19.6	−29.7	−30.0	−37.2	−37.5
Anthocharis euphenoides	22.8	−58.6	17.2	−67.8	0.8	−80.0
Anthocharis gruneri	221.2	53.3	263.4	37.2	334.4	40.2
Apatura ilia	−57.6	−57.8	−61.1	−61.1	−62.7	−62.8
Apatura iris	−63.2	−63.2	−72.3	−72.3	−84.0	−84.0
Euchloe crameri	−57.4	−66.4	−65.6	−76.5	−69.8	−84.6
Euchloe simplonia	−11.6	−31.4	6.7	−41.2	−50.1	−87.3
Euchloe tagis	−20.4	−50.0	−35.7	−67.4	−48.3	−74.2
Favonius quercus	−25.2	−25.9	−46.5	−46.2	−60.0	−59.9
Libythea celtis	53.0	9.3	41.0	15.6	51.6	49.1
Limenitis populi	3.7	3.6	10.0	10.2	−12.6	−12.0
Lycaena alciphron	−17.7	−20.0	−43.2	−45.1	−34.2	−37.8
Lycaena candens	68.1	37.8	−18.1	−29.1	6.0	−30.6
Lycaena dispar	33.6	26.6	95.5	88.4	92.3	62.4
Lycaena hippothoe	−17.9	−17.9	−33.1	−33.1	−45.2	−45.1
Lycaena ottomana	196.0	201.5	170.0	155.0	260.6	246.1
Lycaena phlaeas	−24.4	−24.8	−40.0	−40.4	−48.5	−49.5
Lycaena tityrus	−45.6	−46.1	−52.8	−53.2	−58.9	−59.5
Lycaena virgaureae	1.3	1.1	−26.0	−26.0	−44.7	−44.8
Phengaris nausithous	−93.1	−92.8	−97.3	−97.2	−99.1	−99.1
Phengaris teleius	−77.9	−77.4	−80.5	−80.2	−88.6	−88.6
Nymphalis io	−1.6	−9.2	−8.7	−14.6	−18.4	−21.8
Parnassius apollo	−38.4	−39.6	−51.5	−52.7	−68.7	−70.9
Parnassius mnemosyne	−6.7	−21.2	−19.3	−29.3	−9.9	−34.4
Parnassius phoebus	−84.3	−83.2	−91.2	−90.5	−99.4	−99.3
Pieris bryoniae	7.9	−45.5	5.5	−49.5	12.8	−65.8
Pieris callidice	−87.2	−87.3	−91.6	−90.9	−97.8	−98.0
Pieris krueperi	63.7	62.0	−5.6	−10.1	14.0	16.0
Pyrgus cacaliae	−57.9	−60.5	−64.5	−67.9	−89.1	−91.7
Pyrgus carlinae	−46.4	−45.2	−45.3	−41.9	−68.2	−64.5
Pyrgus sidae	127.5	57.1	121.5	19.9	230.5	56.1
Satyrium ilicis	1.3	−7.2	−6.5	−12.2	−20.5	−27.4
Vanessa atalanta	−12.7	−17.4	−30.6	−34.0	−43.4	−47.0
Zegris eupheme	−55.3	−59.9	−65.2	−71.2	−84.0	−87.4
Zerynthia polyxena	249.2	182.7	299.1	266.0	383.6	339.4
Zerynthia rumina	−52.8	−56.5	−59.9	−63.1	−66.3	−69.1
Median	−17.8	−25.4	−31.9	−41.6	−45.0	−54.5

to be further amplified by increasing mismatches with the host plants (e.g. *Euchloe tagis*; see Table 2; Appendix S7).

Ecological characteristics

Percentage changes in the host-plant-independent range of the butterflies were predominantly affected by climatic niche characteristics and were less severe in species with high levels of mean accumulated growing degree days (GDD5), standard deviation of soil water content (SWC) and GDD5 of the host plants (Table 3). Modulating effects of host plants, i.e. deviations from changes in host-plant-independent range (Fig. 2), were largely affected by trophic niche characteristics of the butterflies; and negative effects of mismatching decreased with increasing range of the host plants but also increased with standard deviation of SWC of the host plants (Table 3). Both patterns were reflected by factors influencing changes in the host-plant-constrained range (Table 3). In summary, butterfly species that can cope with high values of GDD5 (i.e. inhabit warm areas in Europe), can utilize a broad range of SWC, and whose host plants cover a large range are projected to suffer less from, or even profit from, global change.

While the direction of the effects of species characteristics on changes in the host-plant-constrained range was consistent across all three global change scenarios, their importance differed (Fig. 3). Butterfly climatic niche position, according to GDD5, and niche breadth, according to SWC, dominated the response of species to global change under all three scenarios. However, the impact of trophic niche characteristics (plant niche position and breadth) increased slightly with the severity of the scenario. Furthermore, the dominating role of climatic niche position of the butterflies under the moderate change scenario SEDG shifted to climatic niche breadth under the increasingly severe scenarios BAMBU and GRAS (Fig. 3).

DISCUSSION

Current range margins

The question of which factors determine species range margins is a key topic in ecology and conservation (Brown *et al.*, 1996), but the underlying mechanisms remain subjects of debate (Davis *et al.*, 1998; Pearson & Dawson, 2003). The prevailing view is that climate limits distributions at cool, higher-latitude range margins, while warm, lower-latitude margins are determined by biotic interactions (Brown *et al.*, 1996). However, such patterns of more or less equal effects of climate and biotic interactions, when considering effects of host plants, are not supported by our results. In fact, climate and land use seem to be the most important factors for the majority of the studied European butterfly species, while many of them are largely unconstrained by the distribution of their host plants and make incomplete use of the space provided by their hosts. It is possible that other biotic interactions such as predation, competition, parasitism or isolation effects due to scarcity of the host plants or suitable microclimates at range margins may contribute to these patterns. However, earlier studies support the viewpoint that climate and land use are probably the major driving factors for butterfly distributions (Quinn *et al.*, 1998; Merrill *et al.*, 2008).

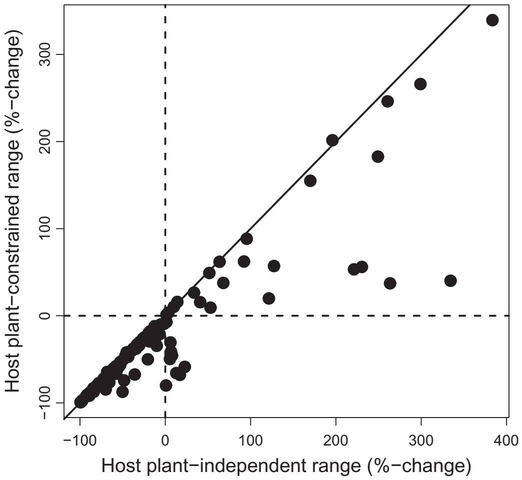

Figure 2 Changes in host-plant-independent and constrained range, respectively, of 36 modelled butterfly species projected for the three global change scenarios SEDG, BAMBU, GRAS.

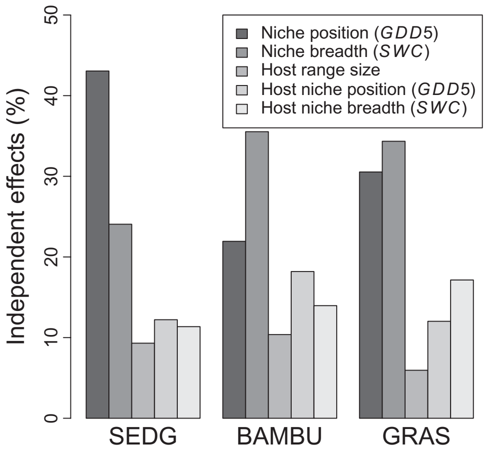

Figure 3 Importance of climatic and trophic niche characteristics for the response of the host-plant-constrained range of 36 modelled butterfly species to three global change scenarios in Europe. Independent effects were obtained by hierarchical variation partitioning and indicate the independent fraction of total explained variation.

Table 3 Model coefficients of three final linear mixed effects models relating percentage changes in host-plant-independent range, modulating effects of host plants, and percentage changes in host-plant-constrained range of 36 modelled butterfly species to their range size, climatic and trophic niche characteristics. The P-value of all coefficients is < 0.024. Cells in grey indicate variables that were excluded from the actual model selection process.

		Butterfly					Host plants					
			Position		Breadth				Position		Breadth	
Response	Int	*R*	GDD5	SWC	GDD5	SWC	*H*	*R*	GDD5	SWC	GDD5	SWC
Host-plant-independent range	−2.4		32.2			37.7			28.9			
Host plant effect	−20.3					−14.7		19.6				−11.7
Host-plant-constrained range	−22.8		23.7			34.1		22.7	19.6			−18.9

Int, intercept; *R*, range size (number of occupied 10′ grid cells); Position, climatic niche position according to accumulated growing degree days until August (GDD5) and soil water content (SWC) averaged over modelled occupied grid cells; Breadth, climatic niche breadth measured as standard deviation of GDD5 and SWC; *H*, number of host plants. Characteristics for host plants were calculated for aggregated modelled host plant distribution, except for the number of host plants, which was based on the literature (Appendix S1).

On the other hand, our findings suggest that there is a gradient in Europe in the relative effects of climate and host plant distribution, ranging from being largely climate controlled to being predominantly controlled by the host plants. These findings are in accordance with nationwide studies of butterflies in Britain, which report that a minority of butterfly species can be strongly constrained by their hosts (Dennis & Shreeve, 1991; Quinn *et al.*, 1998; Hardy *et al.*, 2007). The gradient of relative importance of climate and host plant limitation is best explained by the aggregated range size of the hosts, while host plant specialization is not necessarily a drawback. It is commonly argued that dietary specialists are generally vulnerable to global change (Kotiaho *et al.*, 2005), but our results suggest that, at broad macroecological scales, this applies only for specialization on species with restricted ranges.

Future changes

In the many cases where butterfly species are not greatly constrained by the distribution of their host plants, projected changes of host-plant-independent and constrained ranges, respectively, were similar. Hence, increasing mismatches with their hosts as a consequence of future global change is not a major problem for these species. If their dispersal abilities are sufficient, then at least the presence of the host plants will allow the colonization of suitable new areas, while there is little danger that range shifts of the hosts will affect the remaining originally inhabited areas. In cases like these, having smaller distributional ranges than the hosts may act as a buffer against potential additional threats of global change via disrupted co-occurrence of butterflies and their hosts.

When butterflies are increasingly limited by their hosts, their future range is projected to suffer from increasing mismatch with their hosts. While both better and poorer matching is possible, our results showed no better matching for a single species. Thus, unless these species were capable of rapid evolutionary shifts to alternative hosts (Thomas *et al.*, 2001; Parmesan, 2006; Schweiger *et al.*, 2010), increasing mismatches with their hosts will mean severe additional threats to their future survival.

Ecological characteristics

An important challenge in ecology is to identify ecological species characteristics that are related to declines and extinctions and can thus contribute to the mechanistic understanding of the impacts of global change. Our study reveals some general patterns in these relationships. Projected changes in the host-plant-constrained range of the European butterflies are affected by a combination of both climatic niche characteristics that determine the response of the host-plant-independent range and trophic niche characteristics that determine the impact of the host plants. The projected changes in the host-plant-independent range are mainly related to climatic niche position and breadth, i.e. southern European species and species that are tolerant to a wide range of moisture conditions will suffer less or even profit under global change. These results were anticipated (Brown, 1995) and match findings of earlier studies on plants (Thuiller *et al.*, 2004) and birds (Jiguet *et al.*, 2006). On the other hand, the impact of the host plants was mainly evident via the variation in their range sizes, i.e. butterflies that utilize plants with restricted ranges are projected to suffer most.

Interestingly, both range size and trophic breadth of the butterflies appeared as non-significant factors. Species with restricted ranges are usually thought to face higher risks of extinction (Thomas *et al.*, 2004; Parmesan, 2006), but our results suggest climatic niche position and breadth as the most relevant factors. However, because of constraints in the available data and the chosen modelling approach, our modelled species did not comprise very rare species with highly restricted ranges which might actually be quite vulnerable to global change (Parmesan, 2006). In addition, our results only refer to projected changes in overall range size assuming full dispersal ability. In fact, most of the range-restricted species will lose large amounts of their current distribution (see also Settele *et al.*, 2008, and Heikkinen *et al.*, 2010), while constraints by assumed poor dispersal abilities, weak competition and small local populations (Gaston, 1994; Kotiaho *et al.*, 2005) may reduce their ability to colonize new, otherwise suitable areas.

Dietary specialists are also considered to be particularly threatened by global change (Kotiaho *et al.*, 2005; Schweiger *et al.*, 2010; but see Pöyry *et al.*, 2009). However, our analysis identified range size of the host plants as a major factor instead. Nevertheless, projected presence of the host plants is not the only factor that would affect the performance and occurrence of particular butterfly species. Even when a butterfly and its hosts are projected to co-occur at larger scales, several mechanisms might impede co-occurrence at the local scale. For instance, temporal mismatches due to asymmetric shifts in phenology (for a review see Parmesan, 2006), or changes in the spatial distribution, quantity and quality of the food plants may affect local population performance of the butterfly species (Schweiger *et al.*, 2010). Such effects are likely to accumulate in dietary specialists while generalists may suffer less due to their broader niche and the ability to shift between alternative resources. Taking this into consideration, dietary specialists in general and those that utilize plants with restricted ranges in particular can be considered as particularly threatened by global change.

Differences among global change scenarios

Coreau *et al.* (2009) argue that in addition to improving decision-making in policy and conservation, a combination of scenarios with predictive modelling can be a useful heuristic tool for ecology itself as it has the potential to provide new concepts, methods and knowledge. Our integrated scenario approach enabled us to investigate effects of changes in climate and land use which are based on coherent socio-economic storylines. This approach resulted in simple inferences about future changes based on basic ecological species characteristics.

Further, it showed that the importance of these characteristics differs among the global change scenarios; we observed a shift in the importance of climatic niche position to climatic niche breadth and an increasing impact of interacting species with increasing severity of the scenario. This suggests that the composition of novel communities due to global change (Schweiger *et al.*, 2010) will depend greatly on the way in which we create our future.

CONCLUSIONS

The studied trophic interactions are rather simple, where one species entirely depends on one or several others, but in principle the mechanism of mismatching between interacting species under climate change can be expanded to other inter- and intra-trophic interactions such as mutualism, competition, predation or parasitism. The projected changes in co-occurrence of interacting species will depend on future political and socio-economic development and will be determined by basic ecological characteristics of the species. Basic ecological knowledge of species assemblages can then be utilized to project the future fate and potential risk of extinction of species. Unfortunately, even the basic ecology of species is not readily available for most taxa, butterflies being a fortunate exception in many respects. We conclude that information about simple ecological species characteristics should be improved, and can then be utilized as powerful indicators of species reactions to global change. Further, a better understanding of the consequences of changing biotic interactions will enhance our abilities to assess and counteract potential negative effects on the functioning of ecosystems and their ability to provide ecosystem services (Potts *et al.*, 2010; Schweiger *et al.*, 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Reference list of the field guides used.
Appendix S2 Statistics for Universal Transverse Mercator (UTM) grid cells disregarded for butterfly modelling.
Appendix S3 Standardized plant model coefficients and measures of performance.
Appendix S4 Standardized butterfly model coefficients and measures of performance.
Appendix S5 Relationship between utilized fractions of host-plant-independent range and host range size.
Appendix S6 Relationship between utilized fractions of host-plant-independent range and number of host plants.
Appendix S7 Maps showing examples of increased mismatch between host-plant-independent range and niche space of larval host plants.

BIOSKETCHES

The research of **Oliver Schweiger** focuses on effects of environmental change on population, community and macroecological scales. He is particularly interested in disentangling the scales and interactions of environmental drivers of change, identifying relevant biotic interactions and analysing consequences of global change across organizational levels on the basis of single species, community characteristics, species traits and aspects of ecosystem functioning.

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