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ORIGINAL PAPER

# Assessing the vulnerability of European butterflies to climate change using multiple criteria

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**Abstract** Vulnerability of 100 European butterfly species to climate change was assessed using 13 different criteria and data on species distributions, climate, land cover and topography from 1,608 grid squares $30' \times 60'$ in size, and species characteristics increasing the susceptibility to climate change. Four bioclimatic model-based criteria were developed for each species by comparing the present-day distribution and climatic suitability of the occupied grid cells with projected distribution and suitability in the future using the HadCM3-A2 climate scenario for 2051–2080. The proportions of disadvantageous land cover types (bare areas, water, snow and ice, artificial surfaces) and cultivated and managed land in the occupied grid squares and their surroundings were measured to indicate the amount of unfavourable land cover and dispersal barriers for butterflies, and

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topographical heterogeneity to indicate the availability of potential climatic refugia. Vulnerability was also assessed based on species dispersal ability, geographical localization and habitat specialization. Northern European species appeared to be amongst the most vulnerable European butterflies. However, there is much species-to-species variation, and species appear to be threatened due to different combinations of critical characteristics. Inclusion of additional criteria, such as life-history species characteristics, topography and land cover to complement the bioclimatic model-based species vulnerability measures can significantly deepen the assessments of species susceptibility to climate change.

**Keywords** Bioclimatic model · Climate change · Land cover · Lepidoptera · Range shift · Species characteristics · Susceptibility · Topographical heterogeneity

## Introduction

Climate change increasingly affects species' distributions and the persistence of populations (Parmesan and Yohe 2003; Thomas et al. 2004; Thuiller et al. 2005b; Parmesan 2006). In order to target conservation actions to mitigate the harmful impacts of climate change on biodiversity, it is imperative to assess which species will be most strongly affected, and where and when (Bomhard et al. 2005; Lawler et al. 2006).

Recent assessments of species vulnerability to climate change-induced threats have mainly been based on the outcomes of bioclimatic envelope models (Pearson and Dawson 2003; Peterson 2003; Settele et al. 2008). These modelling approaches correlate current species distributions with climate variables, and then forecast spatial shifts in climatically suitable areas under selected climate change scenarios (e.g. Peterson et al. 2004; Thuiller et al. 2005b; Heikkinen et al. 2006; Lawler et al. 2006). Using these models, vulnerability of a species has been assessed by comparing the differences in the projections of climatically suitable areas at present versus the future (Bakkenes et al. 2002; Midgley et al. 2003; Gómez-Mendoza and Arriaga 2007; Settele et al. 2008); forecasts of large range reductions, or small overlap between current and future ranges, indicate high vulnerability.

Although bioclimatic model-based range projections provide useful first estimates of species vulnerability, such assessments are limited in a number of ways. First, very little attention has been paid to the spatial location of future suitable areas (i.e. distance between present and future suitable areas; Midgley et al. 2003), or to changes in climatic suitability of presently occupied locations (but see Skov and Svenning 2004; Ohlemüller et al. 2006a). Second, the limitations to species migration due to physical obstacles and human habitat transformation have rarely been considered (Bomhard et al. 2005; Broennimann et al. 2006; Thuiller et al. 2006), although the challenges for species tracking the changing climate are greater than ever before (Huntley 1998; Bourn and Thomas 2002).

Third, the ability of species to move to new areas also depends on their dispersal ability (Peters and Darling 1985; Brereton et al. 1995; Maes and Van Dyck 2001), as well as on the range and commonness of the preferred habitats. Habitat specialists are considered to be more prone to climate change than generalists (Peters and Darling 1985; Dennis and Shreeve 1991; Warren et al. 2001; Jiguet et al. 2007). Thus integrating even rather simple measures of dispersal ability and habitat specificity in bioclimatic model-based risk assessments might improve identification of the most vulnerable species (Dennis and Shreeve 1991; Brereton et al. 1995; Beaumont and Hughes 2002; Midgley et al. 2006).

Moreover, geographically localized species that often have narrow climatic envelopes are likely to be more susceptible to climate change impacts than more widespread species (Brereton et al. 1995; Thuiller et al. 2005a; Broennimann et al. 2006), which should be taken into account. The fourth limitation in most bioclimatic model-based assessments is that the potential impacts of topographical heterogeneity have not been taken into account (Luoto and Heikkinen 2008). This is a drawback because areas in heterogeneous terrain provide a greater diversity of ecological niches and may enhance the persistence of biodiversity (Peters and Darling 1985; Nichols et al. 1998; Konvicka et al. 2006; Ruggiero and Hawkins 2008), also under changing climate conditions (Peterson 2003; Hannah et al. 2005; Guralnick 2007).

Butterflies represent an ideal group to investigate the impacts of climate change because their distributional information is abundant in many regions, their taxonomy is well understood, and they are likely to respond rapidly to climate change (Peterson et al. 2004; Parmesan 2006; Menéndez 2007; Pöyry et al. 2009). Settele et al. (2008) provided the first large-scale analysis for European butterflies of the risks stemming from the projected climatic changes, and the magnitude of potential range losses. In this study, we extend the vulnerability assessments of Settele et al. (2008) in a number of important ways. The risk assessment in Settele et al. (2008) was based on climatic envelopes and their changes, whereas the criteria employed in the present study also include estimates of changes in climatic suitability, landscape hostility and topographical heterogeneity of the occupied areas, and estimates based on species characteristics.

Specifically, we address the following questions: (i) Are the same species most at risk across the whole set of different criteria?, (ii) Do vulnerability estimates based on land cover, topographical heterogeneity and species characteristics corroborate vulnerability measures based on bioclimatic models?, (iii) Do the most vulnerable species concentrate in certain biogeographical areas?

## Methods

### Species data

The study by Settele et al. (2008) included 294 European butterfly species. However, following Luoto and Heikkinen (2008) and Marmion et al. (2009a), we used here a smaller but equally representative set of European butterfly species. This is a subset of 100 butterfly species (22% of the 451 European butterfly species; see Luoto and Heikkinen 2008 for more details) from the Distribution Atlas of European Butterflies (Kudrna 2002). Species with less than 10 records in the data set and species with insufficiently known distribution range were excluded from the analysis. The remaining 332 species were assigned to six broad categories according to their biogeographical distribution, based on information from Kudrna (2002) and Tshikolovets (2003). The six biogeographical categories were (1) bimodal/sporadic (BS), (2) Southern Europe (SE), (3) Mountains of Central and Southern Europe (MCSE), (4) Central Europe (CE; including species ranging from Central to Southern Europe), (5) Northern Europe (NE) and (6) Whole Europe (WE). From each of these categories, a set of species was selected to the overall set of 100 species using a stratified random sampling (see Table 2). The selection was constrained, so that the relative proportions of species representing different biogeographical categories were the same both in the 332-species set and in the final 100-species set.

Species distribution data in Kudrna (2002) is given using 2,620 grid squares of $30' \times 60'$ (i.e. half a degree by one degree) in size. However, we used only 1,608 grid squares and excluded most of the eastern European countries (Russia, Belarus, Ukraine and Moldova) due to undersampling in these areas. A species was recorded as present in each of the 1,608 $30' \times 60'$ grid cells in which it had been observed since 1950 (Kudrna 2002).

## Climate data

Data on the observed climate records for the time period 1901–2000 were obtained from the Climatic Research Unit (CRU) climatological database (New et al. 2002; Mitchell et al. 2004). We aggregated averages for the time period 1961–1995 ('present-day' climate) from the original $30' \times 30'$ spatial resolution to the $30' \times 60'$ grid to match the species data and used them for calibrating the models. The modelling was based on three climate variables that have been successfully used in earlier studies on the biogeographical distribution modelling of European butterflies (e.g. Hill et al. 1999, 2002, 2003; Luoto et al. 2006). The three variables included provide indices of known limitations to butterfly growth and survival: annual daily temperature sum above 5°C (GDD5; surrogate for the development threshold for butterfly larvae), mean temperature of the coldest month (MTCO; related to overwintering survival) and water balance (moisture availability for both larvae and adult butterflies), as shown by Hill et al. (2003). Water balance was calculated as the monthly difference between precipitation and potential evapotranspiration, and by summing the separate monthly differences. The potential evapotranspiration was calculated following Skov and Svenning (2004):

$$\mathrm{PET} = 58.93 \times \mathrm{T}(_{\text{above } 0^{\circ}\mathrm{C}})/12 \qquad (1)$$

This is a simple but widely used index that requires only monthly average values of temperature and precipitation (Skov and Svenning 2004, and the references therein). Despite its simplicity, this measure of PET has been found to provide a valuable variable for the broad-scale distribution modelling of different taxa (see Skov and Svenning 2004; Svenning and Skov 2004; Ohlemüller et al. 2006a, b; and Luoto and Heikkinen 2008 for successful applications).

In addition, we employed the projected mean values of the same three climate variables for the period 2051–2080. For the purpose of this study, we used climate data only from one scenario, the simulation of the HadCM3 General Circulation Model with the A2 emissions scenario (modified from Mitchell et al. 2004). The A2 scenario (medium–high emission scenario) describes a very heterogeneous world with a continuously increasing population and regionally oriented economic development. Global concentrations of $CO_2$ are projected to increase from 380 ppm in 2000 to 700 ppm in 2080, and temperature to increase by 2.8°C (IPCC 2001).

## Bioclimatic model-based measures of risk

The climatic suitability of the $30' \times 60'$ grid cells at present and in the future for each of the 100 butterfly species was modelled with the statistical method Random forest (RF), using the BIOMOD (Thuiller 2003) user interface embedded in the R environment software (R Development Core Team 2004). We first calibrated the models with present species distributions and climate data, and then projected them into the HadCM3A2 climate scenario data to predict the future distribution of the species. Recent applications in species distribution modelling have shown that RF provides high classification accuracy, and it often outperforms other modelling techniques (Lawler et al. 2006; Prasad et al. 2006; Cutler et al. 2007; Marmion et al. 2009b). A study by Marmion et al. (2009a), based on the same data as the present study, showed that RF provides a higher prediction accuracy than the most other state-of-the-art modelling techniques. More specifically, 81% of the 100 study species had AUC (the area under the curve) values higher than 0.80 when modelled using RF, and thus showed a good or excellent model performance (cf. Swets 1988).

Random forest (RF) represents a model-averaging approach which belongs to the machine learning methods (Breiman 2001). It generates hundreds of trees based on randomly selected subsets of the data points and random subsets of the predictor variables. Trees are grown to maximum size without pruning and then used to predict the out-of-bag observations. The predictions from the trees are then averaged. For more information on RF see Breiman (2001), Prasad et al. (2006) and Cutler et al. (2007).

The RF yielded probability of occurrence values in each $30' \times 60'$ grid cell for each species. In cases, where the probability values were converted into presence–absence records of species in a cell, we used a cut-off based on the prevalence (the ratio of presence squares to the total sample) of species in the 1,608 grid squares (Liu et al. 2005). We compared the predicted species distributions and climatic suitability of grid cells in 1961–1995 to those in 2051–2080 to generate four measures of species vulnerability to climate change. The approach proposed by Ohlemüller et al. (2006a) was adopted to carry out the following comparisons.

(1) *Change in climatically suitable area* (*cut-off, full dispersal*): We calculated the climatically suitable area for each species in each period based on predicted presence-absence. The sums of climatically suitable areas (species predicted present) were compared between 2051–2080 and 1961–1995; higher negative values in percentage change indicated higher loss of climatically suitable area. This measure is based on the assumption that species can reach all new areas that become climatically suitable.

(2) *Change in climatically suitable area* (*cut-off, no dispersal*): Otherwise as (1), but assuming that species are unable to move from one grid cell to another and can occur in a cell in 2051–2080 if it was predicted to be present in that cell in 1961–1995, and if the climatic suitability remains.

(3) *Change in distance to the nearest climatically suitable cell* (*cut-off, full dispersal*): The distance of the climatically suitable cell to the nearest climatically suitable cell in 1961–1995 (predicted distribution) was recorded, and the distance between a climatically suitable cell in 2051–2080 and that in 1961–1995 was calculated. The distance in the latter period was subtracted from the distance in 1961–1995. High values represent increasing distance to the nearest climatically suitable cell in the future and potentially high susceptibility to climate change.

(4) *Change in average climatic suitability of already occupied cells* (*no cut-off*): Here, we studied how much average probability of occurrence (i.e. predicted climatic suitability) for each species, based on the prediction in 1961–1995, would change in the period 2051–2080. Only areas where a species had been recorded to occur in Kudrna (2002) were taken into account when calculating these measures. Thus, here, we compared the probabilities of occurrence for each species in 1961–1995 in each occupied cell with the probabilities of occurrence in the same cells in 2051–2080. Large negative values indicate more strongly decreasing suitability. We deliberately focused here only on the climatic changes in occupied grid cells, because pure

> bioclimatic models are known to occasionally overestimate the suitable area for the species as they do not consider effects of land cover, distribution of suitable habitats and environmental factors other than climate (Pearson and Dawson 2003; Svenning and Skov 2004).

The full dispersal and no dispersal assumptions used here are the two most common assumptions in bioclimatic envelope modelling studies, which give projections based on the two most extreme potential future trends. However, as both of these assumptions are likely to be unrealistic for many butterfly species, we will include estimates of the actual dispersal ability of the species in our vulnerability assessments (Section "Species characteristics increasing vulnerability").

## Local land cover hostility

Due to the spatial variation in both natural land cover types and anthropogenic land cover alterations, certain areas are less favourable for persistence of butterfly populations than others (Blair and Launer 1997; Kocher and Williams 2000; Hogsden and Hutchinson 2004; Stefanescu et al. 2004). Moreover, it is likely that the impacts of hostile landscape will be amplified due to climate change (Warren et al. 2001; Bomhard et al. 2005; Franco et al. 2006).

We assessed the vulnerability of the studied 100 butterfly species by comparing the mean proportions of the unfavourable land cover types in the $30' \times 60'$ grid cells occupied by a given species. We extracted the data on land cover for each of the 1,608 grid cells from the Global Land Cover 2000–Europe data base ('GLC–Europe dataset'; see http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=955). This dataset is a pan-European classification system which represents a consistent classification for the whole of Europe at a resolution of 1 km.

We acknowledge here that the GLC–Europe dataset was originally not designed to measure the distribution of optimal habitats for butterflies, such as calcareous unimproved grasslands, or certain types of wetlands (van Swaay 2002; Peterson et al. 2004; van Swaay et al. 2006). However, this database is useful for measuring the approximate proportion of certain unfavourable land cover types in the 1,608 grid cells which may critically affect the persistence and dispersal of butterflies. In the present study, we deliberately focused on using only a limited set of five GLC–Europe land cover classes which are amongst the best overall representatives of unfavourable habitats for the butterfly species included in the study. Based on this, we developed a systematic comparison of the baseline hostility of the inhabited areas across all the 100 studied species.

First, from the 22 land cover types included in the GLC–Europe dataset, we identified four types as hostile habitats for butterflies: (i) bare areas (gravel, sandy and rocky areas), (ii) water bodies, (iii) snow and ice and (iv) artificial surfaces and associated areas (in essence, urban areas). The summed cover of these four land cover types (their proportion of the total cover of all land cover types) in each grid cell was calculated. Next, the mean values of summed proportion across the occupied cells were calculated for each species separately. Higher values indicate less favourable landscapes for local butterfly populations to persist, and increased obstacles for species to move between the suitable habitat patches (Thomas et al. 1998). Second, we calculated the proportion of cultivated and managed land in each grid cell from the GLC–Europe dataset. This measure was taken as a complementary indication of an unfavourable landscape, as cultivated and managed land in the GLC–Europe dataset predominantly includes intensively managed agricultural environments showing decreased habitat quality for butterflies (Bourn and Thomas 2002; Stefanescu et al. 2004).

We did not integrate vulnerability measures based on projected future land cover into our analysis because no dataset for the future distributions of land cover types is included in the GLC–Europe dataset. Therefore, it was assumed that future land cover is the best conservatively described by the current GLC–Europe dataset. In addition, we focused in our study on land cover types which are hostile to butterflies; their cover (particularly that of gravel, sandy and rocky areas, water bodies, and urban areas) is unlikely to decrease. Thus, the current GLC–Europe dataset also gives a useful conservative prognosis of the minimum amount of unfavourable land cover for butterflies under future conditions.

### Long-distance dispersal barriers

In order to assess the long-distance dispersal barriers for the studied butterfly species, we calculated the summed cover of the four hostile land cover types (bare areas, water bodies, snow and ice, and artificial surfaces and associated areas) in a buffer zone of 200 km surrounding the focal $30' \times 60'$ grid cell. For each species, we measured the mean summed proportion of the four land cover types in the buffer zone across all the grid cells occupied by the species. Similarly, the proportion of cultivated and managed land was calculated for the buffer zone. High values indicate increased difficulties for the species to move over long distances from the currently occupied areas, and high vulnerability to climate change (cf. Broennimann et al. 2006).

### Topographic heterogeneity

We calculated the topographic heterogeneity of the grid cells occupied by a given butterfly species using the global digital elevation model (GTOPO30) with a horizontal grid spacing of 30 arc seconds (approximately 1 km; for more details see http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html). Each 30 arc seconds GTOPO30 pixel in each of the 1,608 $30' \times 60'$ grid cells was assigned to one of the subjectively defined 16 topographic classes using ArcGIS Spatial Analyst extension 9.2 (ESRI, Redlands, USA). This categorization was based on altitude, slope direction and slope inclination of the pixels (Table 1). Based on the cover of these 16 topography classes, and following Nichols

**Table 1** The 16 topographic classes used in describing the topographical heterogeneity of the 1,608 $30' \times 60'$ grid cells in Europe

| | Altitudinal classes | | | |
|---|---|---|---|---|
| | 0–500 m | ≥500 m and <1000 m | ≥1000 m and <2000 m | ≥2000 m |
| Sites on slopes with inclination >3% | | | | |
| S–SW (180° ≤ slope direction < 225°) | 1 | 2 | 3 | 4 |
| N–NE (slope direction <45°) | 5 | 6 | 7 | 8 |
| NE–S (45° ≤ slope direction < 180°) | | | | |
| or SW–N (225° ≤ slope direction < 360°) | 9 | 10 | 11 | 12 |
| Sites with level terrain (inclination ≤3%) | 13 | 14 | 15 | 16 |

The categorization was based on information on altitude, slope direction and slope inclination of the 30 arc seconds GTOPO30 pixel. Each pixel in each of the $30' \times 60'$ grid cells was assigned to one of the 16 classes et al. (1998), an index of topographic heterogeneity (H′) was calculated for each 30′ × 60′ grid cell with the Shannon index (Magurran 1988) as:

$$H = -\Sigma(P_{\mathrm{i}}\log[P_{\mathrm{i}}])$$

where $P_{\mathrm{i}}$ is the cover of 30 arc seconds GTOPO30 pixels belonging to the topographic class i/the total cover of all 30 arc seconds GTOPO30 pixels in the 30′ × 60′ grid cell. In the final step, mean topographic heterogeneity value was computed separately for each species across the grid cells which they inhabit.

### Species characteristics increasing vulnerability

A number of species characteristics have been identified that are likely to increase susceptibility to climate change (Peters and Darling 1985; Brereton et al. 1995; Beaumont and Hughes 2002), and specifically for butterflies by Dennis and Shreeve (1991), Dennis (1993) and Pöyry et al. (2009). The studied European butterfly species were ranked using three such criteria: (i) dispersal ability, (ii) geographical localization and (iii) habitat specialization.

Species were subjectively ranked according to their dispersal ability using five categories: (1) very sedentary; (2) sedentary; (3) limited mobility; (4) mobile; (5) highly mobile/migratory. The ranking was made first separately by JP (with advice from Zdravko Kolev) and JS, and then a consensus of their initial rankings was developed. Assessments of dispersal ability were based on information obtained from the literature (Bink 1992; Shreeve 1995; Komonen et al. 2004), own field experience, and comparisons with ecologically similar species. Sedentary species are considered to be more susceptible than mobile species to a changing climate (Dennis and Shreeve 1991; Brereton et al. 1995; Pöyry et al. 2009).

Geographically localized species, i.e. species with narrow geographic distributions, are presumed to be more sensitive to climate change than widespread species (Peters and Darling 1985; Beaumont and Hughes 2002; Thuiller et al. 2005a; Broennimann et al. 2006). We ranked the study species using the prevalence of species in the 1,608 30′ × 60′ grid squares (cf. Dennis and Shreeve 1991). Low prevalence values suggest increased vulnerability to climate change. We acknowledge here that low prevalence does not necessarily always directly imply a narrow geographic distribution. However, in our data, a very clear majority of the low-prevalence species have narrow ranges in Europe, as exemplified by species such as *Archon apollinus*, *Colias aurorina*, *Erebia epistygne*, *E. eriphyle* and *E. polaris* (Kudrna 2002).

Habitat specialists are species with narrow habitat requirements, which may be particularly vulnerable to changes in climatic conditions (Peters and Darling 1985; Dennis and Shreeve 1991; Jiguet et al. 2007). We assessed habitat specialization in two ways. First, we adopted the biotope profile definition of van Swaay et al. (2006), and recorded the number of biotopes which the species inhabits in Europe (for details see van Swaay et al. 2006). Small values indicate a limited range of habitats, which is likely to increase the susceptibility to climate change. Second, we used the habitat specialist categorization of van Swaay et al. (2006) that includes four classes: grassland specialists, forest specialists, wetland specialists and generalist butterfly species. Based on the differences between the population declines in these species groups (van Swaay et al. 2006), we considered that grassland specialists are most vulnerable to climate change impacts, generalist species least vulnerable, and wetland and forest specialists intermediately vulnerable (see also van Swaay 2002).

### Summed vulnerability values

The studied 100 species were ranked according to the 13 vulnerability criteria, and from each criterion the 10 most highly ranked species (in the case of ties amongst criteria values or categorical criteria, a set of species closest to 10%) were identified as the most vulnerable ones. However, topographical heterogeneity was not used as a criterion for mountain species, on the basis of the assumption that these species may benefit more from wide areas of high altitude habitats than from high topographical heterogeneity per se (see Wilson et al. 2005). Finally, the most sensitive species were identified by summing the incidences in which a given species was included into the set of most vulnerable species across all the 13 criteria.

## Results

### Relationships between vulnerability criteria

Pair-wise correlations amongst the 13 vulnerability criteria measured for the study species varied considerably (Appendix), about half of them being statistically significant. Thus, the same species were classified as susceptible to climate change impacts in approximately half of the pair-wise vulnerability criteria comparisons, but there was also much disparity between the criteria. The highest correlations were between the proportion of cultivated and managed land in the focal cell and in the 200-km buffer ($r_S = 0.893$, $P < 0.001$), and between the four bioclimatic envelope model-based criteria. The highest negative correlation was between species prevalence and mean topographical heterogeneity of the occupied grid cells ($r_S = -0.727$, $P < 0.001$), showing that geographically limited European butterfly species often occur in topographically heterogeneous mountainous areas.

### Criteria based on bioclimatic models

Three northern species (*Boloria chariclea*, *Erebia polaris* and *Oeneis bore*) and one species occurring throughout Europe (*Boloria selene*) ranked amongst the most vulnerable species according to all four criteria based on bioclimatic models (Table 2). According to the same criteria, southern European species appeared to be the least vulnerable. The scatter plot of criteria ‘Change in range size—full dispersal’ versus ‘Change in range size—no dispersal’ (Fig. 1a) showed a positive correlation ($r_S = 0.641$, $P < 0.001$), highlighting the fact that the most vulnerable species are projected to loose considerable amounts of climatically suitable area regardless of whether they can track the changing climate or not. However, species in the middle of the plot show more variation, indicating that the potential range expansion/contraction will vary greatly between different species on the basis of their capability to move to new areas.

**Table 2** Assessment of the vulnerability of 100 European butterfly species to climate change impacts, using four bioclimatic model-based criteria, four land cover-based criteria, topographical heterogeneity of the occupied grid cells, and four species characteristics potentially increasing species susceptibility to climate change

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Apatura ilia* | CE | 18.41 | −57.50 | 77.36 | −0.53 | 4.19 | **45.63** | *10.38* | **44.21** | 0.39 | *4* | 4 | 2 | 24.00 | 2 |
| *Apatura iris* | CE | −15.88 | **−69.69** | 103.81 | **−0.59** | 7.05 | 43.13 | 14.48 | **41.72** | 0.34 | *4* | 4 | 2 | 27.67 | 3 |
| *Aporia crataegi* | WE | 14.37 | −46.60 | 82.57 | −0.40 | 12.25 | 36.94 | 22.43 | 33.49 | 0.39 | *5* | *8* | *3* | 39.12 | 0 |
| *Archon apollinus* | SE | 236.49 | −49.32 | 87.83 | −0.40 | **45.65** | 20.12 | **42.75** | 23.07 | 0.57 | **1** | **2** | 3 | **0.68** | 5 |
| *Argynnis niobe* | WE | 22.77 | −49.15 | 80.79 | −0.42 | 11.22 | 36.31 | 20.71 | 34.99 | 0.41 | 3 | *8* | *3* | 29.23 | 0 |
| *Argynnis paphia* | WE | −13.55 | −52.56 | 79.88 | −0.44 | 12.83 | 36.87 | 24.08 | 33.54 | 0.36 | *4* | 5 | 2 | *48.45* | 0 |
| *Aricia anteros* | SE | 218.10 | −30.95 | 74.57 | −0.32 | 9.81 | 39.29 | 31.80 | 34.28 | *0.77* | 2 | 4 | **1** | 1.99 | 1 |
| *Aricia morronensis* | SE | 162.73 | −66.36 | 98.57 | *−0.26* | *1.84* | 43.74 | 24.74 | 38.54 | *0.78* | 2 | 4 | 3 | **0.87** | 1 |
| *Aricia nicias* | BS | 28.51 | **−76.75** | **134.39** | −0.53 | 17.51 | *6.33* | 24.29 | *8.97* | **0.26** | 2 | 7 | **1** | 4.54 | 4 |
| *Boloria aquilonaris* | NE | **−33.11** | −64.40 | **176.09** | −0.51 | 16.24 | 14.03 | 26.72 | *13.26* | **0.31** | 2 | 6 | 2 | 23.76 | 3 |
| *Boloria chariclea* | NE | **−95.00** | **−97.50** | **350.09** | **−0.63** | 15.59 | *0.45* | 30.05 | *0.43* | 0.55 | 3 | 5 | 3 | **1.24** | 5 |
| *Boloria dia* | CE | 65.11 | −34.67 | *65.92* | −0.37 | 4.46 | **45.68** | *11.44* | **43.36** | 0.43 | 3 | 7 | *3* | 25.19 | 2 |
| *Boloria euphrosyne* | WE | −20.89 | −57.82 | 95.05 | −0.45 | 12.29 | 27.10 | 23.48 | 25.63 | 0.39 | 3 | 7 | *3* | *46.77* | 0 |
| *Boloria graeca* | MCSE | 186.92 | −47.66 | 79.40 | −0.35 | *2.95* | 33.06 | 22.65 | 30.87 | NM | 3 | 3 | **1** | 1.87 | 1 |
| *Boloria pales* | MCSE | 34.00 | −50.50 | 86.13 | −0.44 | *3.82* | 20.32 | 12.89 | 31.56 | NM | 3 | 3 | **1** | 4.42 | 1 |
| *Boloria selene* | WE | **−44.31** | **−72.77** | **128.86** | **−0.56** | 13.17 | 29.63 | 22.85 | 27.82 | 0.32 | 3 | 6 | *3* | *50.31* | 4 |
| *Boloria thore* | BS | −6.49 | −54.55 | 90.88 | −0.51 | 10.76 | *3.35* | 17.29 | *13.24* | 0.59 | 3 | 5 | *3* | 3.05 | 0 |
| *Brenthis ino* | WE | **−23.50** | −66.17 | 122.71 | **−0.56** | 11.21 | 30.20 | 19.22 | 29.36 | **0.29** | 3 | 5 | **1** | 35.26 | 4 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Carcharodus flocciferus* | CE | 127.33 | −30.81 | 72.74 | −0.36 | 7.90 | 37.93 | 17.85 | 36.46 | 0.55 | 2 | 6 | *3* | 13.74 | 0 |
| *Carcharodus orientalis* | SE | *254.05* | −31.89 | 76.66 | −0.35 | **27.12** | 30.59 | **42.29** | 26.09 | 0.70 | 2 | 6 | **1** | 2.43 | 3 |
| *Carterocephalus silvicolus* | NE | −16.86 | **−71.65** | **301.14** | **−0.60** | 16.31 | 21.93 | 25.17 | 18.68 | **0.07** | 2 | 4 | 2 | 12.50 | 4 |
| *Charaxes jasius* | SE | 145.96 | *−21.21* | *66.26* | −0.36 | **29.46** | 29.91 | **45.61** | 24.02 | 0.65 | 3 | 6 | *3* | 6.16 | 2 |
| *Coenonympha arcania* | CE | 25.63 | −33.05 | *67.05* | −0.33 | 7.56 | 42.01 | 16.31 | 40.03 | 0.40 | 2 | 7 | *3* | 34.70 | 0 |
| *Coenonympha dorus* | SE | 165.33 | *−25.13* | 68.30 | −0.35 | 7.17 | 39.25 | 27.57 | 33.18 | 0.68 | 2 | 4 | **1** | 4.91 | 1 |
| *Coenonympha glycerion* | WE | 7.44 | −61.86 | 91.10 | −0.53 | 7.21 | 41.09 | 13.04 | 39.55 | **0.30** | 2 | 7 | **1** | 24.07 | 2 |
| *Colias aurorina* | SE | 181.87 | −51.65 | 75.82 | −0.44 | 10.95 | 30.19 | **46.12** | 20.74 | 0.83 | **1** | 5 | **1** | **0.68** | 4 |
| *Colias myrmidone* | CE | 33.78 | **−81.76** | **124.18** | **−0.57** | *1.98* | **51.89** | *2.51* | **52.50** | 0.37 | 2 | 5 | **1** | 3.30 | 6 |
| *Colias phicomone* | MCSE | 42.31 | −47.69 | 95.91 | −0.46 | *3.86* | 14.78 | *11.39* | 26.32 | NM | 3 | **2** | **1** | 3.42 | 2 |
| *Cupido argiades* | CE | 98.14 | −28.90 | 70.36 | *−0.31* | 5.66 | **45.32** | 13.47 | 41.33 | 0.41 | *4* | *8* | *3* | 21.02 | 1 |
| *Cupido osiris* | SE | *220.30* | −44.67 | 72.50 | −0.45 | 7.69 | 35.16 | 23.52 | 31.94 | 0.68 | 2 | 7 | **1** | 7.15 | 1 |
| *Erebia embla* | NE | **−29.73** | −65.41 | **143.27** | **−0.57** | 13.71 | *3.56* | 22.87 | *2.68* | **0.18** | 2 | 5 | 2 | 8.15 | 4 |
| *Erebia epistygne* | MCSE | 92.04 | −57.21 | 87.88 | −0.48 | *2.05* | 35.50 | 24.30 | 31.96 | NM | 2 | **2** | *3* | **1.12** | 2 |
| *Erebia eriphyle* | MCSE | **−39.29** | **−71.43** | 103.69 | **−0.54** | 4.68 | *0.94* | *5.66* | 23.25 | NM | 2 | **1** | **1** | **1.24** | 6 |
| *Erebia ligea* | WE | −19.30 | −58.87 | 97.45 | −0.48 | 13.14 | 18.49 | 22.38 | 20.74 | 0.43 | 3 | 4 | 2 | 28.61 | 0 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Erebia melas* | SE | 202.12 | −47.62 | 79.62 | *−0.30* | 8.55 | 40.76 | 24.89 | 38.01 | *0.77* | 3 | 5 | *3* | 1.62 | 0 |
| *Erebia ottomana* | SE | 174.34 | −33.19 | 72.40 | −0.49 | *3.09* | 42.50 | 20.81 | 38.91 | *0.80* | 3 | 6 | *3* | 2.30 | 0 |
| *Erebia pandrose* | BS | **−25.64** | −48.29 | 96.66 | −0.44 | 13.88 | 7.70 | 23.89 | *13.85* | 0.65 | 2 | **2** | **1** | 10.14 | 3 |
| *Erebia polaris* | NE | **−92.39** | **−95.65** | **170.38** | **−0.55** | 14.93 | *0.32* | 32.80 | *0.32* | 0.48 | 2 | **2** | *3* | **1.12** | 6 |
| *Erebia pronoe* | MCSE | 55.28 | −45.96 | 79.70 | −0.45 | *2.80* | 22.39 | *7.69* | 33.65 | NM | 3 | 4 | **1** | 3.67 | 1 |
| *Erynnis marloyi* | SE | *364.52* | −43.01 | 81.30 | −0.39 | **27.14** | 26.49 | 41.70 | 22.99 | 0.72 | **1** | 5 | **1** | **1.37** | 4 |
| *Euchloe belemia* | SE | 180.42 | *−4.20* | *63.74* | *−0.30* | 8.38 | **52.63** | 26.74 | **42.37** | 0.57 | 3 | 4 | *3* | 2.80 | 2 |
| *Euphydryas aurinia* | WE | 13.51 | −54.26 | 90.05 | −0.43 | 10.38 | 34.37 | 23.68 | 31.58 | 0.41 | 2 | 7 | **1** | 25.87 | 1 |
| *Euphydryas maturna* | WE | 60.47 | **−70.93** | 98.68 | **−0.54** | 9.21 | 40.36 | 15.64 | 35.20 | **0.21** | 2 | 5 | 2 | 9.51 | 3 |
| *Favonius quercus* | CE | **−33.13** | −58.63 | 92.70 | −0.49 | 14.24 | 39.10 | 25.92 | 34.13 | 0.34 | 2 | 5 | 2 | 39.05 | 1 |
| *Glaucopsyche alexis* | WE | 88.97 | −29.66 | 71.66 | *−0.31* | 13.20 | 35.21 | 22.38 | 32.38 | 0.45 | 2 | 6 | **1** | 28.73 | 1 |
| *Glaucopsyche melanops* | SE | 142.78 | *−18.56* | *63.56* | −0.34 | 7.66 | 43.84 | 24.66 | 36.38 | 0.62 | 2 | 3 | *3* | 5.22 | 0 |
| *Hamearis lucina* | CE | 64.76 | −36.38 | 72.14 | −0.36 | 6.98 | 41.91 | 15.02 | 40.53 | 0.47 | 2 | 6 | *3* | 22.89 | 0 |
| *Heteropterus morpheus* | CE | 84.15 | −52.13 | 72.32 | −0.44 | 8.72 | **47.15** | 16.98 | **41.82** | **0.24** | 2 | 7 | *3* | 13.93 | 3 |
| *Hipparchia briseis* | SE | 91.28 | −44.19 | 72.10 | −0.38 | 7.39 | 44.33 | 18.37 | 39.71 | 0.57 | 3 | 4 | *3* | 16.11 | 0 |
| *Hipparchia fatua* | SE | 199.17 | −28.33 | 74.50 | −0.40 | **32.40** | 23.58 | **45.45** | 22.26 | *0.75* | 2 | 5 | *3* | 2.24 | 2 |
| *Hipparchia fidia* | SE | 114.44 | −32.22 | 70.02 | −0.35 | 9.44 | 39.12 | 27.38 | 33.92 | 0.65 | 2 | 4 | *3* | 4.66 | 0 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Hipparchia semele* | CE | −23.23 | −53.85 | 94.56 | −0.47 | 15.52 | 36.98 | 26.87 | 33.60 | 0.34 | 3 | *9* | *3* | 37.75 | 0 |
| *Hipparchia senthes* | SE | *333.12* | *−3.90* | *60.15* | *−0.29* | **38.12** | 24.89 | **47.39** | 21.07 | 0.70 | 3 | 5 | *3* | 2.55 | 2 |
| *Hipparchia volgensis* | SE | *221.60* | −33.80 | 73.80 | −0.34 | 14.66 | 43.58 | 30.92 | 36.06 | *0.75* | 3 | 7 | *3* | 1.80 | 0 |
| *Leptotes pirithous* | SE | 160.00 | −27.14 | 69.58 | −0.33 | 20.70 | 34.90 | 35.76 | 29.51 | 0.63 | *4* | 6 | *3* | 12.13 | 0 |
| *Lycaena ottomana* | SE | *242.86* | −28.06 | 74.13 | −0.35 | 19.32 | 34.14 | 33.90 | 33.94 | *0.73* | 2 | 5 | **1** | 1.74 | 1 |
| *Maniola bathseba* | SE | 109.41 | *−22.94* | 67.70 | −0.34 | 7.50 | 43.11 | 24.31 | 37.88 | 0.65 | 3 | 4 | *3* | 5.22 | 0 |
| *Melanargia arge* | SE | 188.64 | −55.68 | 94.02 | −0.51 | **28.03** | 33.09 | **60.78** | 18.85 | 0.66 | 3 | NM | NM | 1.49 | 2 |
| *Melanargia occitanica* | SE | 127.23 | *−25.13* | *67.58* | −0.34 | 8.09 | 43.77 | 26.46 | 35.26 | 0.68 | 3 | 3 | *3* | 4.48 | 0 |
| *Melitaea didyma* | CE | 80.04 | −26.01 | 67.85 | *−0.26* | 8.39 | 44.00 | 18.44 | 40.11 | 0.52 | *4* | 4 | **1** | 27.74 | 1 |
| *Melitaea parthenoides* | SE | 31.05 | −57.53 | 89.67 | −0.50 | 5.07 | 37.93 | 16.10 | 36.46 | 0.51 | 2 | 6 | **1** | 9.14 | 1 |
| *Melitaea varia* | MCSE | 40.30 | −44.03 | 78.91 | −0.43 | 5.94 | 12.95 | 17.93 | 21.14 | NM | 3 | 5 | *3* | 1.80 | 0 |
| *Nymphalis c-album* | WE | −11.27 | −48.16 | 81.49 | −0.41 | 12.82 | 36.47 | 22.95 | 33.02 | 0.34 | *4* | 6 | *3* | *52.92* | 0 |
| *Nymphalis egea* | SE | 216.39 | *−19.67* | 68.06 | *−0.26* | **29.99** | 29.15 | **44.77** | 23.32 | 0.70 | *4* | 4 | *3* | 7.71 | 2 |
| *Nymphalis io* | WE | −16.51 | −47.69 | 81.01 | −0.42 | 13.51 | 36.61 | 24.65 | 32.98 | 0.32 | *5* | *8* | *3* | *54.48* | 0 |
| *Nymphalis polychloros* | CE | 16.77 | −38.11 | 74.86 | −0.38 | 11.71 | 42.27 | 21.55 | 38.51 | 0.38 | *5* | 5 | *3* | 39.18 | 0 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Nymphalis urticae* | WE | −22.31 | −48.35 | 84.21 | −0.41 | 14.09 | 31.53 | 25.40 | 28.65 | 0.34 | *5* | *8* | *3* | *62.44* | 0 |
| *Ochlodes sylvanus* | WE | −16.46 | −51.22 | 79.19 | −0.44 | 13.07 | 36.54 | 23.48 | 32.65 | 0.34 | 3 | 6 | *3* | *51.18* | 0 |
| *Oeneis bore* | NE | **−85.54** | **−89.16** | **200.79** | **−0.55** | 13.59 | *0.30* | 26.68 | *0.36* | 0.47 | 2 | 5 | *3* | **1.12** | 5 |
| *Oeneis glacialis* | MCSE | 17.56 | −37.40 | 88.23 | −0.42 | 4.94 | *5.83* | *9.51* | 21.34 | NM | **1** | 4 | **1** | 1.93 | 2 |
| *Oeneis jutta* | NE | 0.00 | −60.26 | **169.51** | −0.51 | 13.49 | 8.38 | 24.36 | *5.99* | **0.17** | 2 | 4 | 2 | 10.51 | 2 |
| *Papilio alexanor* | SE | 170.67 | −39.42 | 83.79 | −0.39 | **24.54** | 20.62 | **44.89** | 18.10 | *0.78* | 2 | 5 | *3* | 2.05 | 2 |
| *Papilio machaon* | WE | −3.85 | −40.82 | 71.18 | −0.35 | 14.34 | 36.11 | 24.41 | 32.09 | 0.37 | *5* | *9* | *3* | *55.78* | 0 |
| *Pararge achine* | CE | 31.05 | −66.67 | 89.22 | −0.50 | 6.48 | 38.18 | 13.05 | 35.18 | 0.34 | 2 | 4 | 2 | 12.94 | 0 |
| *Pararge aegeria* | WE | −19.79 | −49.65 | 87.40 | −0.42 | 14.73 | 36.99 | 26.34 | 32.85 | 0.36 | 2 | 6 | 2 | *54.42* | 0 |
| *Pararge maera* | WE | 28.63 | −38.55 | 75.41 | −0.34 | 12.93 | 33.08 | 23.13 | 31.00 | 0.41 | 3 | 6 | *3* | 43.28 | 0 |
| *Pararge megera* | CE | 2.92 | −37.48 | 69.63 | −0.34 | 14.91 | 41.35 | 25.20 | 36.82 | 0.40 | 3 | 4 | *3* | *48.76* | 0 |
| *Pararge roxelana* | SE | *249.77* | −25.81 | 73.60 | −0.32 | **23.52** | 33.91 | 36.19 | 31.12 | 0.71 | 2 | 3 | 2 | 3.48 | 1 |
| *Parnassius mnemosyne* | CE | 129.07 | −29.94 | 69.86 | −0.35 | 8.11 | 36.70 | 18.85 | 37.67 | 0.57 | 2 | 6 | **1** | 16.36 | 1 |
| *Parnassius phoebus* | MCSE | 1.48 | −35.56 | 81.50 | −0.43 | 4.39 | *4.90* | *9.14* | 22.76 | NM | 2 | 6 | **1** | 1.93 | 1 |
| *Plebejus argyrognomon* | CE | 117.88 | −30.91 | 70.02 | −0.39 | 5.33 | 7.38 | *11.58* | **43.14** | 0.45 | 2 | 7 | **1** | 14.93 | 2 |
| *Plebejus glandon* | MCSE | 42.40 | −48.80 | 97.61 | −0.44 | 4.28 | 14.77 | 13.83 | 25.67 | NM | 2 | 5 | **1** | 2.11 | 1 |
| *Plebejus orbitulus* | BS | −8.33 | −45.83 | 72.53 | −0.46 | 6.18 | *4.49* | 13.52 | *17.03* | 0.64 | 2 | 3 | **1** | 2.55 | 1 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Polyommatus albicans* | SE | 155.48 | −49.68 | 77.61 | −0.35 | *3.54* | **52.01** | 18.21 | **44.27** | 0.69 | **1** | **2** | *3* | 1.99 | 4 |
| *Polyommatus dolus* | SE | 144.00 | −42.40 | 82.26 | −0.45 | 15.54 | 29.82 | **41.87** | 23.24 | *0.75* | 2 | 3 | *3* | 1.55 | 1 |
| *Polyommatus escheri* | SE | 144.54 | −44.96 | 83.39 | −0.41 | 10.95 | 34.82 | 26.20 | 30.92 | 0.67 | 2 | *9* | **1** | 8.64 | 1 |
| *Polyommatus nivescens* | SE | *231.30* | −41.74 | 74.38 | −0.40 | 10.17 | **45.00** | 25.09 | 39.87 | 0.72 | **1** | 3 | *3* | 1.49 | 2 |
| *Pyrgus armoricanus* | CE | 127.03 | *−24.62* | 70.07 | *−0.31* | 10.23 | 40.41 | 21.70 | 36.18 | 0.53 | 3 | 6 | **1** | 14.86 | 1 |
| *Pyrgus carthami* | CE | 65.03 | −50.92 | 82.49 | −0.42 | *3.80* | 42.27 | *11.54* | **41.78** | 0.53 | 2 | 7 | **1** | 12.25 | 2 |
| *Pyrgus onopordi* | SE | 156.46 | −36.84 | 69.33 | −0.44 | 9.04 | 35.68 | 25.35 | 29.35 | 0.61 | 2 | 7 | **1** | 5.35 | 1 |
| *Pyrgus serratulae* | CE | 72.40 | −46.59 | 76.90 | −0.40 | 3.88 | 31.84 | 13.18 | 38.92 | 0.53 | 3 | 4 | **1** | 13.81 | 1 |
| *Satyrium ilicis* | CE | 42.65 | −36.73 | 73.85 | −0.35 | 10.33 | 43.14 | 20.08 | 39.36 | 0.43 | 2 | 3 | 2 | 27.24 | 0 |
| *Satyrium pruni* | CE | 6.70 | −67.25 | 91.98 | −0.53 | 7.35 | 42.81 | 13.90 | 40.05 | **0.31** | 2 | 6 | 2 | 20.40 | 1 |
| *Satyrium spini* | CE | 95.68 | −25.91 | *65.78* | *−0.31* | 7.54 | 43.48 | 16.50 | 41.03 | 0.54 | 2 | 6 | *3* | 22.51 | 0 |
| *Satyrium w-album* | CE | −10.90 | −55.64 | 77.71 | −0.47 | 12.65 | 40.59 | 23.58 | 35.03 | 0.32 | 2 | 4 | 2 | 29.23 | 0 |
| *Scolitantides baton* | CE | 77.82 | −34.68 | 70.45 | −0.40 | 10.36 | 34.23 | 22.09 | 30.83 | 0.52 | 2 | 7 | **1** | 11.07 | 1 |
| *Scolitantides bavius* | SE | 130.81 | −68.18 | 76.84 | −0.43 | 6.35 | **47.39** | 21.36 | 39.35 | 0.72 | **1** | 5 | **1** | **1.18** | 4 |
| *Scolitantides vicrama* | CE | 179.74 | *−15.36* | *67.15* | *−0.27* | 16.31 | 42.58 | 21.23 | 40.58 | 0.52 | 2 | 6 | **1** | 9.70 | 1 |

**Table 2** continued

| Species | Bio-geography | Bioclimatic model-based criteria | | | | Land cover-based criteria | | | | Topography | Species characteristics and vulnerability | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range shift, full dispersal | Range shift, no dispersal | Nearest cell | Climatic suitability | Focal grid cell | | 200 km buffer | | Topogr. hetero-geneity | Dispersal ability | Biotope range | Habitat spec. | Prevalence | Summed vulnera-bility |
| | | | | | | Hostile land | Cultivated land | Hostile land | Cultivated land | | | | | | |
| *Thecla betulae* | CE | 8.13 | −47.64 | 68.27 | −0.42 | 10.03 | 42.40 | 18.20 | 38.06 | **0.31** | 3 | 6 | *3* | 30.04 | 1 |
| *Zerynthia cerisyi* | SE | *333.33* | *−19.05* | *66.53* | −0.32 | 13.83 | **48.00** | 23.37 | **43.09** | 0.61 | 3 | 6 | **1** | 2.92 | 3 |

The 10 (10%), or the nearest number, most vulnerable species in each criteria category are indicated with **bold figures**, and the 10 (or the nearest number) least susceptible species with *italicizing*. Summed vulnerability indicates the number of times a given species was ranked among the most vulnerable species across all 13 criteria

Nearest cell = average distance to nearest climatically suitable grid cell in the future; Climatic suitability = average change in climatic suitability of occupied cells between present and future climates; Hostile land = Average proportion of bare areas, water bodies, snow and ice, and artificial surfaces and associated areas; Cultivated land = Average proportion of cultivated and managed land; Topogr. heterogeneity = Average topographical heterogeneity of occupied cells; Biotope range = number of preferred biotopes in Europe; Habitat spec. = Habitat specialization, 1—grassland specialist, 2—wetland or forest specialist, 3—generalist; NM = Vulnerability not measured

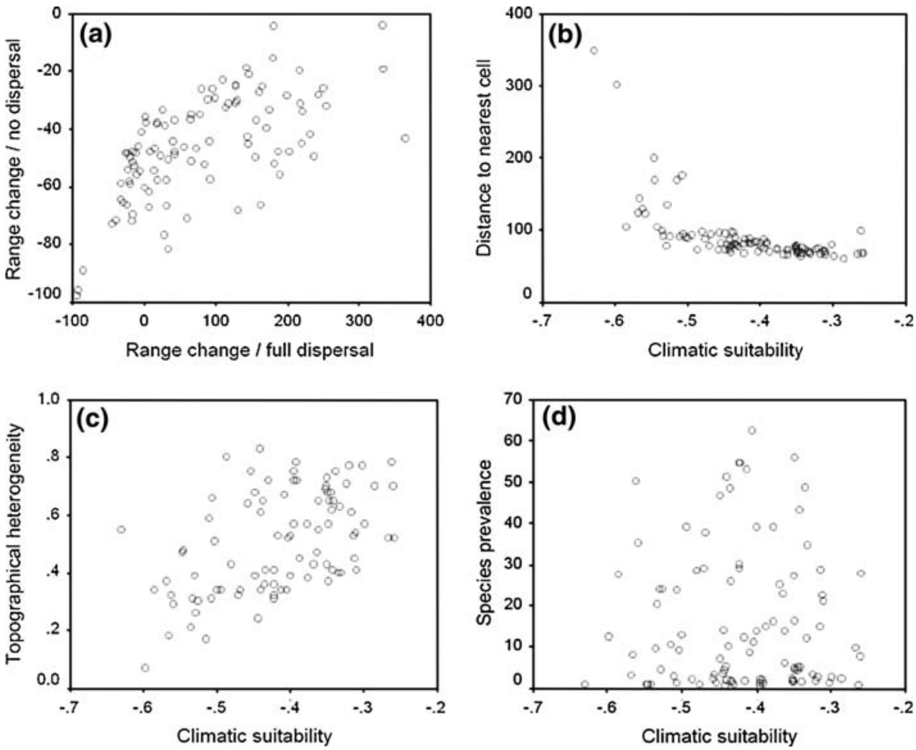


**Fig. 1** Pair-wise relationships of vulnerability of 100 European butterfly species to climate change based on **a** projected range size change based on full dispersal assumption versus projected range size change based on no dispersal assumption; and projected change in climatic suitability of occupied areas versus **b** mean distance to nearest suitable grid cell in the future, **c** topographical heterogeneity of the occupied areas, and **d** species prevalence

The relationship between the change in climatic suitability of occupied grid cells and distance to the nearest suitable cell in the future (Fig. 1b; $r_s = -0.779$, $P < 0.001$) showed that species such as *Boloria chariclea*, whose current areas will become most unsuitable, will have their nearest suitable areas furthest away. In addition, species for which the currently occupied areas will decrease most in climatic suitability often inhabit landscapes that are topographically flatter than average (Fig. 1c). These two factors, taken together, may cause boosted adverse impacts for species such as *Carterocephalus silvicolus*, *Erebia embla* and *Euphydryas maturna* (Table 2). There is no clear trend between species prevalence and change in climatic suitability of occupied areas ($r_S = 0.002$, $P = 0.981$; Fig. 1d). Thus some of the geographically limited species, e.g. *Erebia polaris* and *Oeneis bore*, will face a notable decrease in climatic suitability in their current range areas whereas some other low-prevalence species (e.g. *Aricia morronensis*) may be less affected (Table 2).

## Criteria based on land cover

Species inhabiting areas with the greatest amount of hostile land cover were mainly southern European butterfly species, such as *Archon apollinus*, *Hipparchia senthes* and

*Hipparchia fatua*. According to the amount of hostile land cover types in the 200-km buffer surrounding the occupied grid cells, the same species along with *Melanargia arge* are again highly ranked. By contrast, the group of butterfly species whose occupied areas and the surrounding 200-km buffer areas encompass large amounts of cultivated and managed land include a different set of species, e.g. *Euchloe belemia*, *Polyommatus albicans* and *Colias myrmidone* (Table 2). Some of these species are poor dispersers (e.g. *Polyommatus albicans*), which may thus experience amplified difficulties in tracking climatically suitable areas across highly managed landscapes.

## Species characteristics

Seven species were classified as very sedentary (Table 2). Although these species may, in principle, find new suitable areas in close vicinity (Fig. 2a), detrimental impacts may arise from joined impacts with other vulnerability factors, such as hostility of inhabited areas, habitat specialization and geographical localization, as in the case of *Erynnis marloyi* and *Colias aurorina* (Table 2). About half (49) of the studied species were classified as sedentary. Some of them (e.g. *Carterocephalus silvicolus* and *Oeneis jutta*) may face notable

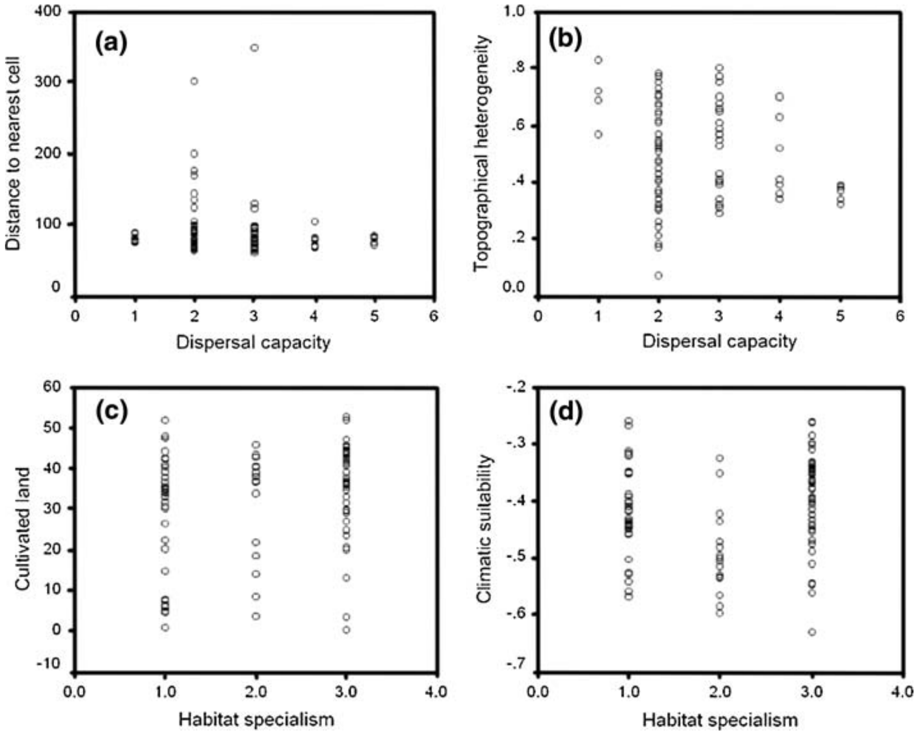


**Fig. 2** Pair-wise relationships of vulnerability of 100 European butterfly species to climate change based on dispersal capacity versus **a** mean distance to the nearest suitable grid cell in the future, and **b** topographical heterogeneity; habitat specialization versus **c** proportion of cultivated and managed land in the occupied areas, and **d** projected change in climatic suitability of occupied areas

challenges due to long distances to the nearest suitable areas in the future (Fig. 2a), and as their currently occupied areas are topographically rather homogenous (Fig. 2b).

Seven species thrive in only very few biotopes (Table 2). In addition, 36 species belong to grassland specialists. Many of these species, e.g. *Colias myrmidone* and *Scolitantides bavius*, inhabit areas where cultivated and managed land are abundant (>30%; Fig. 2c). In addition, the climatic suitability of occupied areas is expected to decrease notably for many of the grassland specialist species (Fig. 2d), the most affected species being *Colias myrmidone*.

### Vulnerability and biogeographical groups

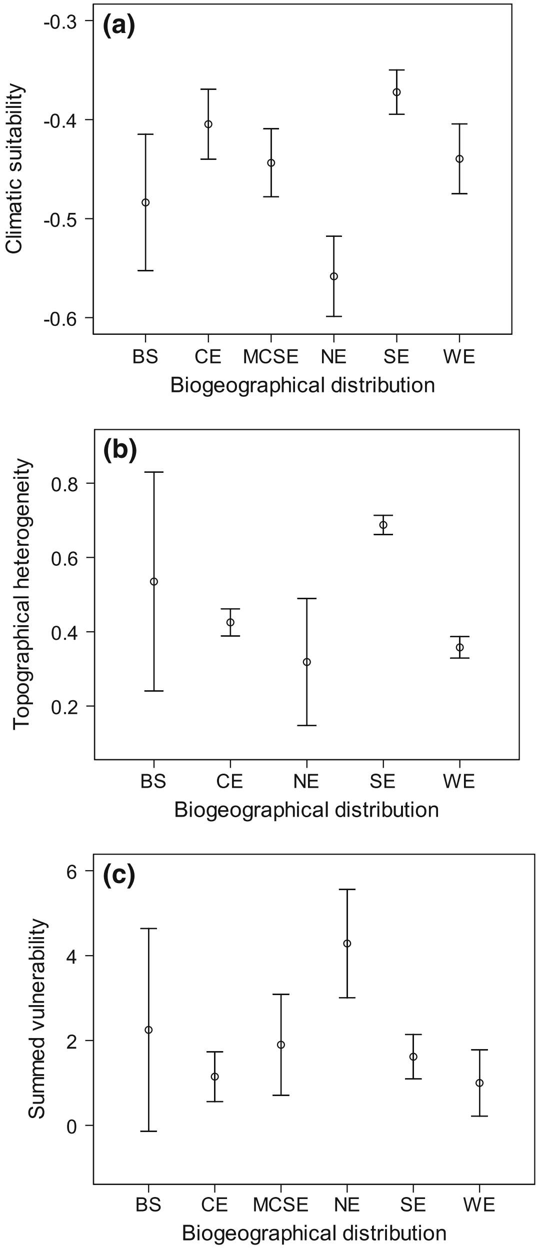
With respect to the changes in climatic suitability of occupied areas, southern European butterfly species were predicted to be on average least affected, followed by central European species, whereas the northern European species are likely to be most affected (Fig. 3a). In many cases, the 95% confidence intervals for the mean values of climatic suitability changes overlap between the biogeographical distribution groups, southern European and northern European species being most distinctly separated from the others. A similar trend also emerged for all the other three criteria based on bioclimatic models.

As regards topographical heterogeneity, southern European species appeared on average as the least affected species (mountain species excluded), as they occupy topographically heterogeneous areas (Fig. 3b). Northern European species and species occurring throughout Europe may generally have more difficulties in finding climatic refugia in currently occupied areas than other species. As regards species prevalence, southern European species and species of central and southern European mountains have on average more geographically localized distributions and, in this respect, they are more sensitive to climate change than other species groups. Investigation of the summed vulnerability of species suggests that northern European butterfly species are, in general, more susceptible to climate change impacts than species from other biogeographical groups, and that species occurring throughout Europe are least susceptible (Fig. 3c, Table 2). However, in some of the biogeographical groups (especially species with a bimodal/sporadic distribution), there is much within-group variation in the summed vulnerability values for species.

## Discussion

Bioclimatic envelope models are increasingly applied to predict the potential impacts of climate change on biodiversity (Heikkinen et al. 2006; Beale et al. 2008; Beaumont et al. 2007). These models allow consideration of how climate change may affect tens or even hundreds of species simultaneously, and provide useful first approximations of the magnitude of potential range shifts of species, and identification of locations and species that may be at greater risk (Pearson and Dawson 2003; Thuiller et al. 2005b; Virkkala et al. 2008). However, the projections from bioclimatic envelope models may vary based on the modelling technique adopted (Lawler et al. 2006; Pearson et al. 2006), the choice of future climate scenarios (Beaumont et al. 2007), and the life-history traits and geographical characteristics of the modelled species (Luoto et al. 2005; McPherson and Jetz 2007; Pöyry et al. 2008). Further uncertainty is caused by the extrapolation of species range shift projections into non-analogue climate (Fitzpatrick and Hargrove 2009). The studied

**Fig. 3** Mean **a** projected change in climatic suitability of occupied areas, **b** topographical heterogeneity of occupied areas, and **c** summed vulnerability in the six biogeographic distribution categories, and the 95% confidence intervals for the mean. Mountain species of central and southern Europe were excluded from **b**. BS = species with a bimodal/sporadic distribution, SE = southern European species, MCSE = Mountain species of central and southern Europe, CE = central European species, NE = northern European species, WE = species occurring throughout Europe



species may also match weakly with their presumed climatic determinants (Beale et al. 2008) and the predictions of climate-induced future species' distributions may be complicated by the complexity of the ecological impacts and biotic interactions involved (Mustin et al. 2007; Schweiger et al. 2008).

The numerous uncertainties associated with the bioclimatic envelope models suggest that it is imperative also to include other relevant vulnerability criteria in the assessments of species susceptibility to climate change. The results presented here, indeed, show that simultaneous investigation of several complementary vulnerability criteria can significantly extend the assessments based solely on projections of the bioclimatic envelope models.

## Criteria based on bioclimatic models

Bioclimatic envelope model-based assessments of species vulnerability to climate change have hitherto focused on projected range size changes, based on two assumptions of species ability to migrate into new areas, i.e. full dispersal or no dispersal (e.g. Bakkenes et al. 2002; Peterson et al. 2004; Lawler et al. 2006; Gómez-Mendoza and Arriaga 2007). Settele et al. (2008) reported that depending on the scenario used in the modelling, 3–24% of the European butterflies may lose more than 95% of their present climatic niche under the no dispersal assumption. The projections of the potential changes in the species distribution range developed in Settele et al. (2008) and, in this study, are partly concordant and partly contradictory. For certain central European species, such as *Apatura ilia*, *Favonius quercus* and *Hipparchia semele*, northern European species, such as *Boloria chariclea*, *Carterocephalus silvicolus* and *Erebia embla*, and species occurring throughout Europe (e.g. *Erebia ligea*, *Nymphalis io* and *Nymphalis urticae*), the projected losses of climatic niche are comparable. The two studies agree especially in suggesting that northern European butterfly species are at risk to lose large amounts of their current climatically suitable areas. However, predictions for southern European species are in many cases contradictory, this study suggesting potential range expansions, whereas Settele et al. (2008) suggested range contractions. Three factors may contribute to these discrepancies: the differences between (i) selected climate variables, (ii) modelling techniques and (iii) the ways of converting species occurrence probability values into species presence/absence predictions. In any case, the observed differences echo the concerns put forward that outputs from bioclimatic modelling studies may be sensitive to the choice of climatic predictor variables (Beaumont et al. 2005) and choice of modelling techniques (Pearson et al. 2006). Thus, it is useful to compare the outputs from different modelling settings and to identify species and areas, where projections from different models agree and disagree, and to generate interpretations on them with caution.

Some recent studies go beyond the basic way of using the outputs from bioclimatic envelope models to assess species vulnerability. Skov and Svenning (2004) and Ohlemüller et al. (2006a) included ‘extended’ bioclimatic model-based criteria such as measures of the change of climatic suitability within species current ranges, and/or distance to future suitable areas in their vulnerability assessments. However, both in Ohlemüller et al. (2006a) and in the present study, all the vulnerability rankings for the studied species from the bioclimatic model-based criteria were significantly inter-correlated. Thus identifying species at risk solely on the basis of extended sets of bioclimatic model-based criteria is likely to give an incomplete picture of the overall threats.

## Species characteristics and vulnerability

The concept of life-history characteristics increasing species vulnerability to climate change was already introduced by Peters and Darling (1985). Brereton et al. (1995) also suggested that sensitivity of some groups of species to climate change appears to be intimately linked with certain characteristics, such as geographical localization (see also Thuiller et al. 2005a; Walker and Preston 2006). Beaumont and Hughes (2002) identified seven endemic Australian butterfly species as potentially very vulnerable to climate change, using two bioclimatic model-based criteria and six species life-history characteristics. The species identified as most threatened were projected to face drastic changes in their climatically suitable area, to have narrow climatic ranges, and were also poor dispersers and/or geographically localized species. Habitat specialization has been found to be intimately linked with increased extinction risk of regional plant populations (Walker and Preston 2006), and with stronger bird population declines and changes in climate (Jiguet et al. 2007). Warren et al. (2001) showed that habitat specialists and sedentary butterfly species in the UK have fared significantly worse than the wider-countryside generalist species and that such species may have difficulties in adapting to warming climate.

Hitherto the most multi-faceted systematic assessment of multiple butterfly species vulnerability to climate change is the article by Dennis and Shreeve (1991). These authors argued that vulnerability criteria based on species range and distribution may alone be poor predictors of the effects of future events. This is because some species with currently extremely restricted ranges may respond positively to warming climate whereas other, more widespread species, may decline under the same conditions. In our results, species prevalence did not show any correlation with projected climatic suitability of the occupied areas, and the low-prevalence species varied in their estimated mobility, range of habitats and habitat specialization. Thus, the ability of the species with restricted distributions to respond to climate change may indeed depend critically on many other factors than merely geographical distribution.

Some examples of individual species demonstrate clearly the importance of using species characteristics in vulnerability assessments to complement criteria based on bioclimatic models. For example, *Archon apollinus*, *Colias aurorina*, *Erynnis marloyi*, *Lycaena ottomana* and *Scolitantides bavius* are five southern European species with restricted distributions, all of which are projected to gain considerable amounts of new climatically suitable areas. However, all these species have one or more characteristics (low mobility, limited range of habitats, or grassland habitat specialization) which may prevent them from taking advantage of the warming climate. By contrast, some other low-prevalence species, such as *Eribia melas*, *Erebia ottomana* and *Nymphalis egea,* are less limited by their special characteristics, and will have better possibilities to track the changing climate.

## Land cover and topography

The ability of species to respond to climatic changes does not depend only on the magnitude of projected changes and on species characteristics but also on the structure of the landscape which they inhabit and over which dispersal is occurring (Pearson and Dawson 2003, Skov and Svenning 2004; Broennimann et al. 2006). We assessed the potential impacts of land cover on persistence and dispersal of the studied European butterfly species on the basis of the landscape features of the currently occupied areas and areas adjacent to them. Water bodies, urban areas, bare areas and snow and ice were taken as the most unfavourable land cover types, and areas that harbour large amounts of such habitat types are likely to provide decreased possibilities for species to adapt or migrate under climate change (see e.g. Blair and Launer 1997; Hogsden and Hutchinson 2004). Modern-day intensified agricultural practices can also pose negative impacts on the persistence of species populations (Kerr and Cihlar 2004), and limit the capability of many groups of species to respond to climate change (Erasmus et al. 2002), including butterflies (Kocher and Williams 2000; Stefanescu et al. 2004; Franco et al. 2006). Furthermore, it is likely that the impacts of changes in certain land cover types on butterfly species will be intimately linked with the changing climate, for example, via the increasing transformation of semi-natural grasslands to forest following marginalisation and abandonment, or further intensification of the use of agricultural land.

Against this background, it is probable that species, such as *Archon apollinus*, *Hipparchia senthes* and *Hipparchia fatua*, will face increased difficulties under climate change, as large proportions of the landscape which they inhabit may become unfavourable. Species, such as *Euchloe belemia* and *Colias myrmidone* may experience difficulties due to the high proportions of managed and cultivated land in their current range area. This factor is intimately linked with habitat specialization of the species. Severe population declines in butterfly species dependent on unimproved grasslands has been recorded (Bourn and Thomas 2002; Stefanescu et al. 2004; van Swaay et al. 2006). Therefore, sedentary grassland specialist butterfly species (e.g. *Colias myrmidone* and *Scolitantides bavius)* whose current occurrences are located in agriculturally dominated landscapes may be amongst the most vulnerable species, and have few possibilities to move to the new climatically suitable areas (cf. Erasmus et al. 2002; Peterson et al. 2004).

Recent studies have shown that topographic heterogeneity is intimately intermingled with climatic diversity and habitat diversity (Ruggiero and Hawkins 2008). In areas with wide topographical variation stronger local gradients in climate exist than in the lowlands, causing more abrupt changes in vegetation structure which in turn affects the distribution of animal species (Ruggiero and Hawkins 2008). Consequently, under changing climate conditions, species inhabiting topographically heterogeneous landscapes have a wider range of habitats and microclimates in the adjacent areas, and required distances for range shifts are shorter than in flat lowlands (Peterson 2003; Hannah et al. 2005; Guralnick 2007). Amongst the species studied here, several southern European species (e.g. *Colias aurorina*, *Erebia ottomana* and *Papilio alexanor*) occur in topographically very diverse areas, and may have better possibilities to track their climate optima than species whose populations are in the flattest landscapes in Europe (e.g. *Euphydryas maturna*, *Erebia embla* and *Oeneis jutta*). In flat lowlands, the interplay between several factors such as dispersal ability, degree of habitat specialization and the permeability of the landscape may ultimately determine the ability of species to respond to climate change (Hannah et al. 2005).

Finally, it should be noted that topographical heterogeneity probably plays a less essential role for the persistence of species inhabiting high montane habitats. As the climate warms, these species are forced to move uphill and ultimately their habitable climate regime will disappear (Peterson 2003; Wilson et al. 2005; Menéndez 2007).

## Limitations

One limitation in the present study is that although our ranking of the dispersal ability of the butterfly species is based on several sources, in essence, it is an evaluation based on expert opinion. Acquisition of accurate measures of dispersal ability is complicated, because empirical data on the mobility of most European butterfly species are rare (Dennis and Shreeve 1991). The ability of butterfly species to track the changing climate will also depend on the distribution of suitable host plants (Peterson et al. 2004; Araújo and Luoto 2007; Schweiger et al. 2008). However, we did not include host plants in the present assessment, because detailed information on the range of host plants of all the study species throughout Europe was not available (cf. Dennis and Shreeve 1991; Braschler and Hill 2007). The persistence of species and their possibilities to shift their ranges may also depend on specific types of grasslands, e.g. calcareous unimproved grasslands, or certain types of wetlands (van Swaay 2002; Peterson et al. 2004; van Swaay et al. 2006), and thus data on distribution of such habitats would be useful. Unfortunately, data on the geographic distribution of such specific habitats data for the whole of Europe, or even for many European Union countries, does not exist.

## Conclusions

Our results show that important extensions to pure bioclimatic model-based assessments of species vulnerability to climate change can be made by the inclusion of additional criteria. Overall, our results suggest that northern European species are likely to be the most vulnerable species among European butterflies, and species occurring throughout Europe the least vulnerable (cf. Thuiller et al. 2005a, b). However, behind these general patterns, there is considerable species-to-species and criterion-to-criterion variation which should be taken into account. Most importantly, species which might be expected to benefit from warming climate based on bioclimatic model projections may be threatened due to certain critical characteristics, such as low mobility and habitat specialization, hostile landscapes, and lack of climatic refugia. In conclusion, the development of vulnerability assessments for species and targeting conservation actions to mitigate climate change impacts would benefit from moving forward from separate judgments based solely on either bioclimatic models or species characteristics to fruitful combinations of the two approaches, complemented further by aspects of land cover and topography.

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## Appendix

See Table 3.

**Table 3** Spearman rank correlations for the 13 vulnerability criteria (four bioclimatic model-based criteria, four land cover-based criteria, topographical heterogeneity of the occupied grid cells, and four species characteristics potentially increasing species susceptibility) used in assessing the vulnerability of 100 European butterfly species to climate change impacts

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Range change/full dispersal | | <0.001 | <0.001 | <0.001 | 0.883 | 0.003 | 0.001 | 0.016 | 0.042 | 0.396 | 0.540 | <0.001 | <0.001 |
| 2. Range change/no dispersal | 0.641 | | <0.001 | <0.001 | 0.408 | 0.010 | 0.059 | 0.011 | 0.209 | 0.505 | 0.430 | 0.788 | <0.001 |
| 3. Average distance to nearest climatically suitable grid cell in the future | −0.585 | −0.876 | | <0.001 | 0.619 | <0.001 | 0.477 | <0.001 | 0.136 | 0.240 | 0.129 | 0.400 | <0.001 |
| 4. Average change in climatic suitability of occupied cells between present and future climate | 0.630 | 0.841 | −0.779 | | 0.489 | <0.001 | 0.024 | <0.001 | 0.213 | 0.655 | 0.094 | 0.981 | 0.816 |
| 5. Average proportion of unfavourable land cover (bare areas, water bodies, snow and ice, and urban areas) in the current range area | 0.015 | 0.084 | 0.050 | 0.070 | | 0.001 | <0.001 | <0.001 | 0.528 | 0.124 | 0.022 | 0.353 | 0.816 |
| 6. Average proportion of cultivated and managed land in the current range area | 0.298 | 0.255 | −0.487 | 0.393 | −0.326 | | 0.078 | <0.001 | 0.289 | 0.280 | 0.062 | 0.017 | 0.813 |
| 7. Average proportion of unfavourable land cover in the 200-km buffer zone surrounding occupied grid cells | 0.322 | 0.190 | −0.072 | 0.226 | 0.764 | −0.177 | | −<0.001 | 0.669 | 0.542 | 0.003 | 0.014 | <0.001 |
| 8, Average proportion of cultivated and managed land in the 200-km buffer zone surrounding occupied grid cells | 0.240 | 0.253 | −0.467 | 0.363 | −0.501 | 0.893 | −0.443 | | 0.325 | 0.166 | 0.605 | 0.005 | 0.684 |
| 9. Dispersal capacity of species | −0.204 | 0.127 | −0.150 | 0.126 | 0.064 | 0.107 | −0.043 | 0.099 | | 0.048 | <0.001 | <0.001 | 0.034 |
| 10. Number of preferred biotopes in Europe | −0.086 | 0.068 | −0.119 | 0.045 | 0.155 | 0.110 | −0.062 | 0.140 | 0.199 | | 0.630 | <0.001 | 0.005 |
| 11. Habitat specialization | −0.062 | 0.080 | −0.154 | 0.169 | 0.230 | 0.188 | 0.297 | 0.053 | 0.358 | 0.049 | | 0.188 | 0.921 |
| 12. Species prevalence | −0.513 | −0.027 | −0.085 | 0.002 | 0.094 | 0.239 | −0.245 | 0.280 | 0.454 | 0.472 | 0.133 | | <0.001 |
| 13. Average topographical heterogeneity of occupied cells | 0.775 | 0.519 | −0.393 | 0.499 | 0.025 | 0.025 | 0.455 | −0.044 | −0.224 | −0.296 | 0.011 | −0.727 | |

The *lower left part* of the matrix indicates the Spearman's correlation coefficients amongst the 13 vulnerability criteria and the *upper right-hand part* of the matrix the *P* values for the corresponding correlationships

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