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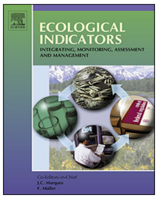

Original Articles

Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient – Implications for conservation in times of climate change

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ABSTRACT

Among the factors that determine habitat quality for butterflies, an adequate microclimate is of crucial importance, especially for the less mobile immature stages. Due to their narrow microclimatic preferences, stenotopic butterflies are potential indicators of specific microclimatic niches. Although the outstanding importance of the microclimate is widely acknowledged, the thermal and hygric requirements of butterflies are usually inferred from habitat structure or regional climate instead of being exactly measured. Here, we present the results of year-round measurements of temperature and relative air humidity at typical oviposition microhabitats of three threatened grassland butterflies (*Erebia medusa*, *Melitaea aurelia* and *Satyrium spini*) inhabiting different zones along a climatic gradient in the Diemel Valley (Central Germany). Furthermore, we analysed how the climate in the study area has changed since the middle of the 20th century.

The interspecific differences in mean temperature and humidity at the oviposition sites roughly reflected the differences in overall distribution of the three species, but separate analyses of day- and nighttime values revealed that local habitat characteristics and radiative heating of the near-ground air layer have a strong modifying effect on the microclimate.

Since the 1950s, the climate in the Diemel valley has become significantly warmer. The magnitude of the observed increase in mean temperature was similar or even greater than the interspecific differences recorded by the microclimatic measurements. This implies that thermophilous species may expand their ranges within the Diemel Valley if climate warming continues. Species living in the relatively cool Upper Diemel Valley such as *E. medusa*, however, may incur population declines because there are few grasslands available at higher elevations or at microclimatically cooler sites such as north-facing slopes.

1. Introduction

Since the beginning of the industrial era, humankind has altered the physical environment of the Earth at an unprecedented rate (Rockstroem et al., 2009). Besides other factors such as land-use change and alterations of the nitrogen cycle, climate warming is one of the main drivers of this global change (Sala et al., 2000). Taxonomic groups with many highly specialised species exhibit particularly fast and strong responses to climatic change and, therefore, are highly suitable as model organisms for assessing the impact of global warming (Parmesan, 2003; Thomas, 2005). Butterflies are one of these indicator groups because many of them exhibit strong climatic associations (Dennis, 2010; Settele et al., 2008; Thomas, 1993). They are frequently used to study the effects of rising temperatures on their phenology (Roy and Sparks, 2000; Van Dyck et al., 2015), habitat preferences, biotic interactions (Boggs and Inouye, 2012) and their latitudinal (Devictor et al., 2012; Thomas et al., 2001a) and altitudinal (Wilson et al., 2005) distribution. There are strong differences between species regarding their response to recent climate change. Thermophilous species usually benefit from global warming and, consequently, extend their ranges polewards and to higher elevations. Taxa adapted to cooler climates, however, often suffer from deteriorating living conditions at the low-latitudinal and low-elevational boundaries of their ranges (Dieker et al., 2011; Konvicka et al., 2003; Wilson et al., 2005). Consequently, they have to move to higher latitudes or elevations. If such movements are not possible, e.g., due to habitat fragmentation or lack of suitable habitats at higher elevations, range retractions are the consequence (Hill et al., 2002; Warren et al., 2001).

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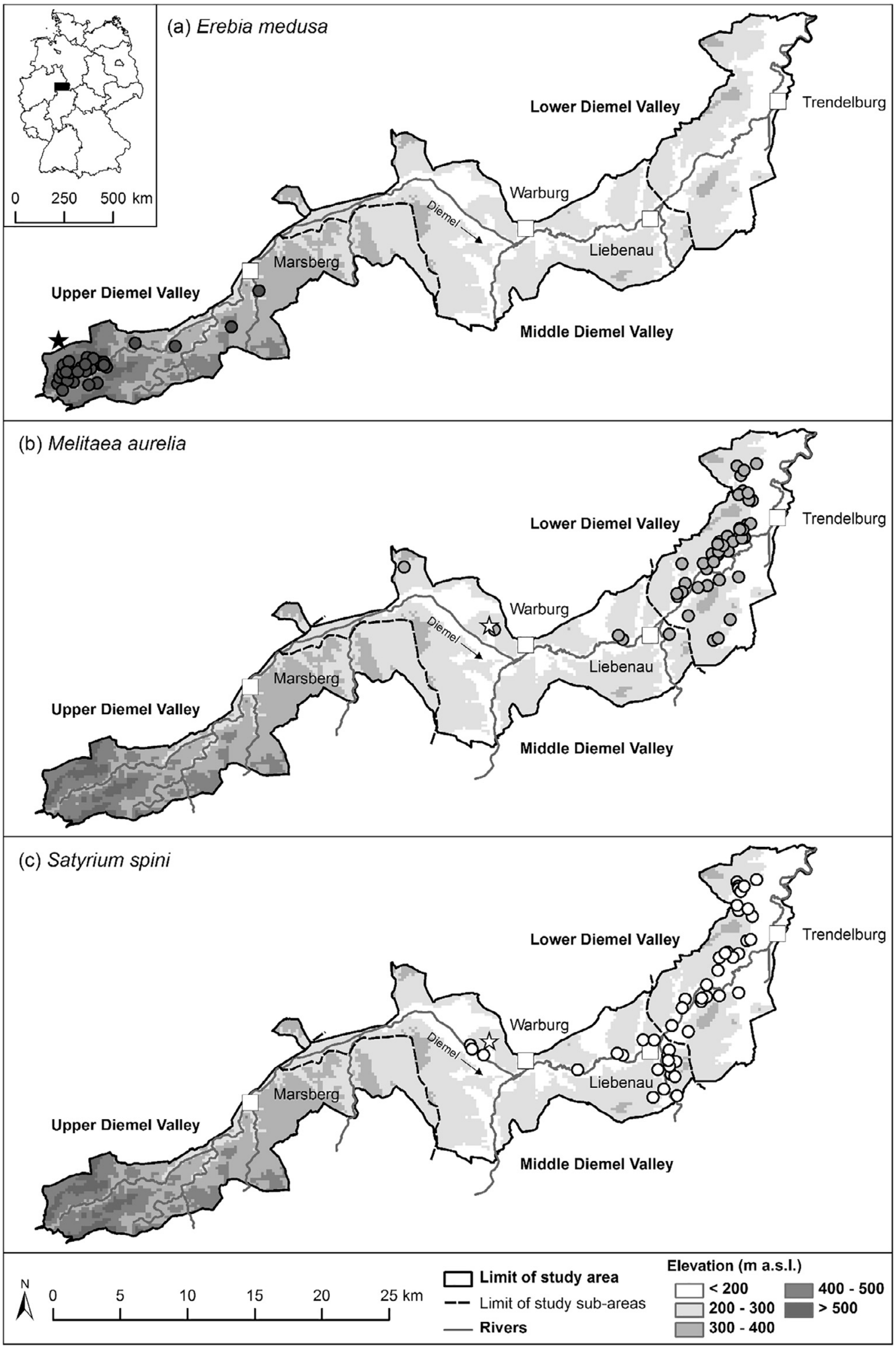

Fig. 1. Distribution of *Erebia medusa*, *Melitaea aurelia* and *Satyrium spini* in the Diemel Valley in Central Germany. Each circle corresponds to an occupied habitat patch. The surveys were carried out in 2009 for *S. spini* and in 2010 for E. *medusa* and *M. aurelia*. The black and white asterisks represent the weather stations in Brilon and Warburg, respectively, from which reference data for temperature and relative humidity were obtained.

The spatial distribution of butterfly populations is crucially determined by habitat quality within patches, whose importance typically equals or exceeds that of patch size and isolation from neighbouring populations (Anthes et al., 2003; Eichel and Fartmann, 2008; Stuhldreher and Fartmann, 2014; Thomas et al., 2001b, 2011). Habitat quality is best defined on the basis of the ecological requirements of the immature stages (eggs, larvae and pupae) because they often have more specific habitat requirements than adults (Fartmann and Hermann, 2006; Garcia-Barros and Fartmann, 2009; Maes et al., 2014). A particularly important feature of habitat quality is the microclimate, because temperature and humidity strongly influence the duration of the embryonic and larval development and the survival rate of the immature stages (WallisDeVries, 2006; WallisDeVries and van Swaay, 2006; Williams, 1981). Therefore, stenotopic butterflies are potential indicators of specific microclimatic niches.

Despite the significance of the microclimate, the thermal and hygric requirements of butterfly species are often not assessed directly by measuring climatological parameters *in situ*, but are either inferred from the preferred habitat characteristics with respect to vegetation structure, soil properties, topography and shading (e.g., Fartmann, 2006a; Kraemer et al., 2012; Loeffler et al., 2013; Thomas et al., 1998; Thomas et al., 1986) or estimated by modelling climate envelopes on the basis of grid data of the distribution of species and climatic parameters (e.g., Hill et al., 2002, 1999; Settele et al., 2008). The former approach allows for rough comparisons of the microclimatic preferences of different species if the underlying observations are made at locations of similar mesoclimate and elevation. However, it does not yield absolute values and therefore is not suited for comparing the preferences of species that live under different regional climates. The latter approach reveals thresholds that define the climatic niche of a species, but as the microclimate within the habitats of butterflies is determined by the interplay of the regional climate and the habitat structure—which can greatly modify temperature and humidity of the near-ground air layer (Kennedy, 1997; Stoutjesdijk and Barkmann, 1992)—these thresholds are just a very rough estimate of what is actually experienced by a butterfly or its immature stages. Despite the limitations of the indirect approaches of investigating the climatic requirements of butterflies, there are relatively few studies in which the microclimate of the larval habitat was measured (but see e.g., Ashton et al., 2009; Turlure et al., 2010; Turlure et al., 2011), and the measurements performed in these studies covered only short periods of time (two months at the longest, Merrill et al., 2008; Roy and Thomas, 2003).

To our knowledge, this is the first paper to present year-round microclimatic measurements in the larval habitats of European butterflies. Three threatened grassland butterflies inhabiting different zones along an elevational and mesoclimatic gradient, the Woodland Ringlet (*Erebia medusa*), Nickerl's Fritillary (*Melitaea aurelia*) and the Blue-spot Hairstreak (*Satyrium spini*), were chosen as model organisms. *E. medusa* is considered to be negatively affected by climate warming (Settele et al., 2008; Stuhldreher et al., 2014), whereas Central European populations of *M. aurelia* and *S. spini* will probably benefit from rising temperatures (Settele et al., 2008). In line with this, several populations of *E. medusa* in the lowlands of the area where this study was conducted went extinct in the second half of the 20th century, whereas *M. aurelia* greatly extended its range (Fartmann, 2004). The study was carried out in the Diemel Valley (Central Germany), the northernmost German "Prime Butterfly Area" (van Swaay and Warren, 2003). We demonstrate how the microclimatic conditions at the oviposition microhabitats differ among the three species, compare them to measurements taken by official weather stations in the same area and discuss the ecological implications of our findings in the context of past and projected future climatic changes in the study area. Finally, we provide recommendations for the conservation of the species in times of global warming.

2. Material and methods

2.1. Study area

The study area, the Diemel Valley, covers an area of about 460 km^2 in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (Fig. 1). It is the largest area of calcareous grassland in the northern half of Germany (Fartmann, 2004). The climate is suboceanic (Mueller-Wille, 1981) and varies greatly with elevation. The Upper Diemel Valley (200–600 m a.s.l.) is the coolest (annual mean temperature [1961–90]: 7.6 °C) and wettest (annual precipitation [1961–90]: 814 mm) part of the study area (all meteorological values were derived from 1-km^2 grid datasets from Germany's National Meteorological Service, pers. comm.). In the Middle Diemel Valley (140–380 m a.s.l.) the precipitation is lower (703 mm) and the temperature is higher (8.2 °C). The Lower Diemel Valley (100–375 m a.s.l.) is similarly warm (8.3 °C), but the precipitation (756 mm) is slightly higher, due to orographic rainfall caused by the eastwardly adjacent hill landscapes of the Reinhardswald and Solling.

2.2. Study species

The three studied butterfly species—*Erebia medusa* Fabricius 1787 [Satyrinae], *Melitaea aurelia* Nickerl 1850 [Nymphalinae] and *Satyrium spini* Denis & Schiffermüller 1775 [Lycaeninae])—are univoltine habitat specialists that are restricted to nutrient-poor semi-natural grasslands, however, they differ in their ecological requirements regarding climate and host plants. *Melitaea aurelia* and *S. spini* are xerothermophilous sub-Mediterranean species that in Central Europe mainly occur in semi-dry and dry calcareous grasslands (Ebert and Rennwald, 1991a,b; Fartmann, 2004; Hermann, 2007; Kolbeck, 2013). In the study area, both are restricted to the warm Middle and Lower Diemel Valley (Fig. 1b, c, Eichel and Fartmann, 2008; Loeffler et al., 2013). *Erebia medusa* has a continental-montane distribution and is slightly less heat-demanding (Ebert and Rennwald, 1991b; Kudrna et al., 2011). In the Diemel Valley, it currently occurs only in the mountainous Upper Diemel (Fig. 1a, Stuhldreher and Fartmann, 2014). Its habitats are semi-dry and nutrient-poor mesic grasslands that are abandoned or characterised by very low land-use intensity (Ebert and Rennwald, 1991b; Fartmann, 2004; Schraml and Fartmann, 2013; Stuhldreher and Fartmann, 2014).

With respect to host plant use in the Diemel Valley, all three species are mono- or oligophagous. *Erebia medusa* attaches the eggs singly to leaves of the grasses *Festuca rubra* agg. and *F. ovina* agg. (Stuhldreher and Fartmann, 2015). The only larval host plant of *M. aurelia* in the Diemel Valley is the herb *Plantago media* (Eichel and Fartmann, 2008). The eggs are laid in clutches on the underside of leaves of *P. media*. Both *E. medusa* and *M. aurelia* overwinter as half-grown larvae. *S. spini* deposits eggs exclusively on the shrub *Rhamnus cathartica*, usually in small batches on the upper side of twig forks of small host plant individuals (Helbing et al., 2015; Loeffler et al., 2013). *Satyrium spini* overwinters in the egg stage. Detailed information on the timing and duration of the life-cycle stages of all three species can be obtained from Figs. A1 and A2 in the Appendix.

At the regional level (North Rhine-Westphalia and Hesse), all three species are considered vulnerable, endangered or critically endangered (HMUELV, 2009; LANUV NRW, 2011). At the national level, *E. medusa* and *M. aurelia* are considered as near threatened, *S. spini* as vulnerable (Reinhardt and Bolz, 2011).

2.3. Microclimatic measurements

During previous studies, the distribution of *E. medusa* and *S. spini* in the Diemel Valley has been documented by exhaustive surveys in 2009 and 2010 that covered all potentially suitable habitat patches in the study area (Loeffler et al., 2013; Stuhldreher and Fartmann, 2014). The distribution of *M. aurelia* was recorded in the same way in 2010. Based on these data, we randomly selected 11 occupied habitat patches per species and placed one data logger in each of them. The three sets of patches covered the entire current range of the respective species in the

Diemel Valley and the full spectrum of environmental conditions of the occupied patches (e.g., elevation, slope, aspect, shading, vegetation structure).

Within each habitat patch, we identified one typical egg-laying site based on the findings of previous studies on the oviposition preferences of *E. medusa* (Fartmann, 2004; Stuhldreher and Fartmann, 2015), *M. aurelia* (Eichel and Fartmann, 2008) and *S. spini* (Helbing et al., 2015; Loeffler et al., 2013) in the Diemel Valley and installed the data loggers next to an egg or clutch at the same height above ground as the eggs. All measurements were taken using Maxim iButton® Hygrochron DS1923 data loggers which recorded air temperature and relative air humidity hourly with an accuracy of 0.5 °C and 0.6%, respectively, for 12 months from 01 September 2011 until 31 August 2012. The data loggers were protected from rain and direct sunlight by a white cap. This prevented the measurements from being affected by heating of the metal cases of the iButtons during periods in which the logger was exposed to direct sunlight, which would have led to unreasonably high temperature recordings.

As the 11 data loggers belonging to the same study species were placed in distinct habitat patches, we considered them to be statistically independent units. The values recorded by the same data logger, however, were not independent of each other. Therefore, we averaged the readings of each data logger over the period under consideration (year, season, month or daytime/nighttime within a season) and based our analyses on these averages. Consequently, the sample size was always 11 temperature or humidity values per species, and the differences between the mean values of different data loggers reflect the microclimatic differences between patches.

The data were analysed in two different ways. First, we calculated yearly, seasonal and monthly averages of temperature and relative humidity for each data logger without distinguishing between day and night. The year was divided into seasons using the meteorological definition, according to which spring begins on 01 March, summer on 01 June, autumn on 01 September and winter on 01 December. Second, we calculated the seasonal averages of temperature and humidity separately for daytime and nighttime to analyse the diurnal variation of both parameters in autumn, winter, spring and summer. As the thermal effects of solar radiation are weak shortly after sunrise and shortly before sunset, “day” was defined as the period from two hours after sunrise to two hours before sunset. Consequently, all measurements that fell within this period were assigned to “day” and all others to “night”. Then, the mean daytime and nighttime values were calculated for each data logger and each season. In both approaches, differences among species with respect to the seasonal averages were analysed by Kruskal-Wallis *H* test and subsequent pair-wise comparisons using the Wilcoxon rank-sum test with correction of the level of significance following the method described by Siegel and Castellan (1988). These analyses were done using the package *pgirmess* (version 1.5.7, Giraudoux, 2013) within the *R* environment (R Development Core Team, 2013).

2.4. Reference data from weather stations

In order to compare the microclimate at the oviposition sites with reference data recorded by official weather stations in the same region, we obtained data from weather stations in Brilon (Upper Diemel Valley, 447 m a.s.l., range of *E. medusa*) and Warburg (Middle Diemel Valley, 236 m a.s.l., range of *M. aurelia* and *S. spini*) from Germany’s National Meteorological Service (Fig. 2) (WebWerdis database, DWD, 2015). The reference data had the same temporal resolution (1 h) as our own measurements and covered the same period. For each of the weather stations, we calculated hourly averages of temperature and humidity separately for each season. These averages were used in Figs. 3 and 4 to contrast the diurnal variation of temperature and humidity at the weather stations to that at the oviposition sites.

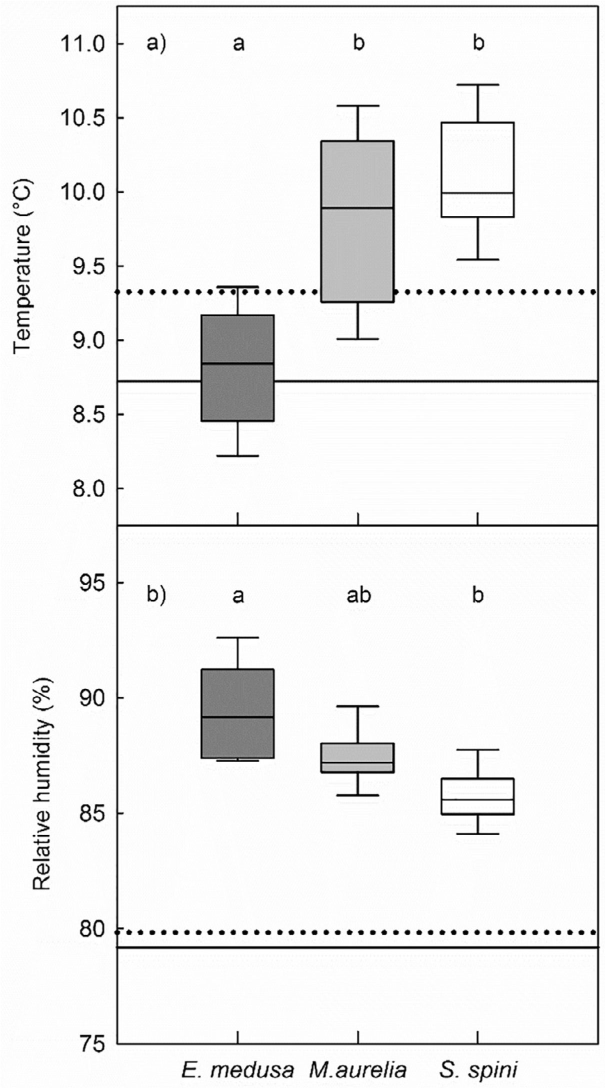

Fig. 2. Microclimatic conditions at oviposition sites of *Erebia medusa*, *Melitaea aurelia* and *Satyrium spini* in terms of (a) annual mean air temperature and (b) annual mean relative air humidity. In each of the three species, the sample size was 11 data loggers. The boxplots show the median of the 11 sites per species, the 1st and 3rd quartile (boxes), and the 10th and the 90th percentile (whiskers). The measurements were taken between 01 September 2011 and 31 August 2012. The solid and dotted lines indicate the annual averages at the weather stations in Brilon (Upper Diemel Valley) and Borgentreich-Bühne (Middle Diemel Valley), respectively, during the same period. Differences among species were analysed by Kruskal-Wallis *H* test and subsequent pair-wise comparisons using the Wilcoxon rank-sum test (for details see Section 2.3).

2.5. Assessment of long-term climate trends

To assess the magnitude of climatic changes that have occurred in the study area since the middle of the 20th century, we analysed time series data for several climatic parameters from two weather stations run by Germany’s National Meteorological Service (WebWerdis database, DWD, 2015). One of the stations was the above-mentioned station in Brilon (Upper Diemel Valley) and the other was Borgentreich-Bühne

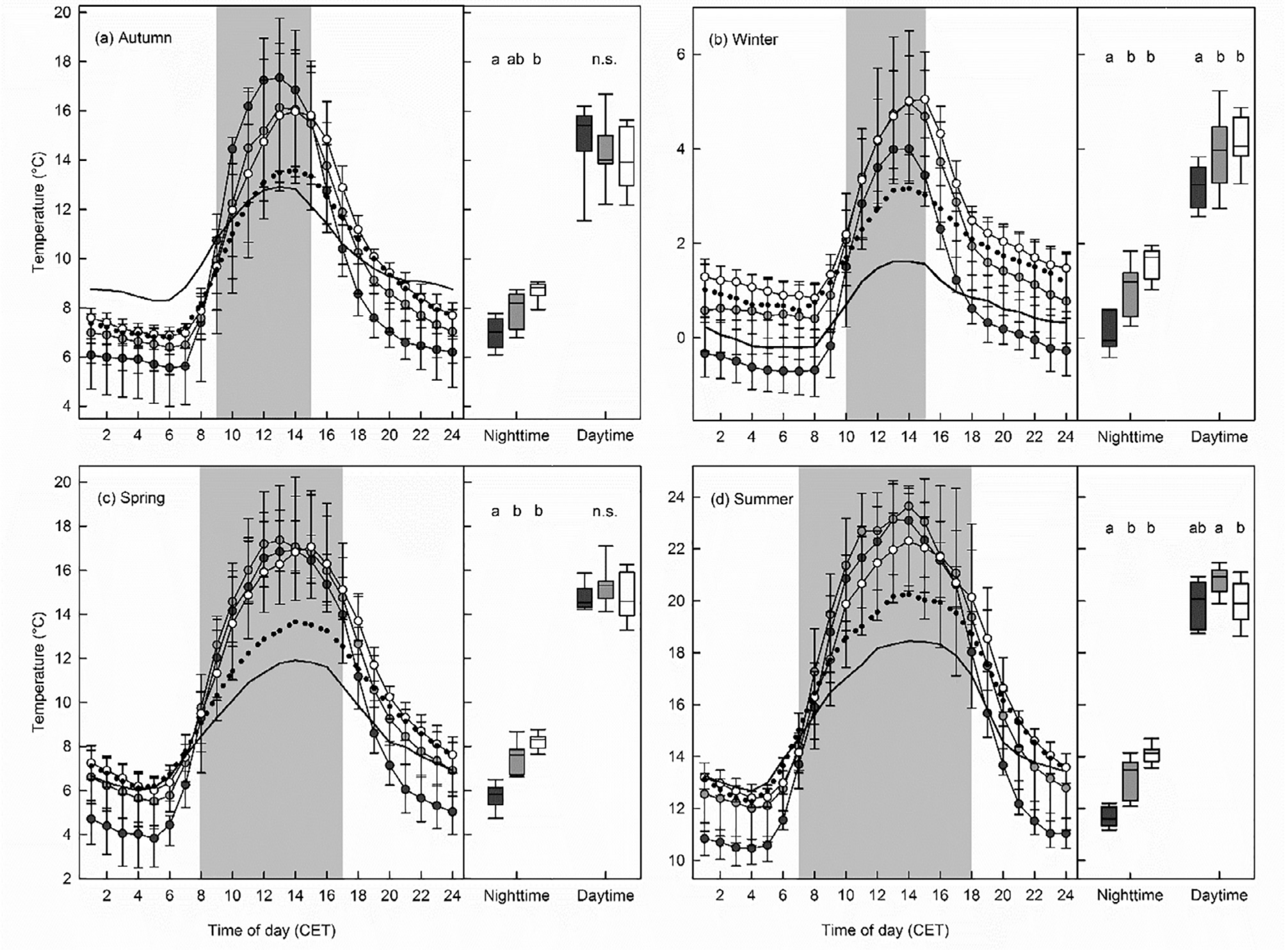

Fig. 3. Diurnal variation of air temperature at oviposition sites of *Erebia medusa* (dark grey), *Melitaea aurelia* (light grey) and *Satyrium spini* (white) in (a) autumn, (b) winter, (c) spring and (d) summer. In each of the three species, the sample size was 11 data loggers. The curves on the left of the diagrams show the hourly averages per season (points = median of the 11 sampled loggers, bars = range of values). The hourly averages of weather stations in Brilon (Upper Diemel Valley) and Warburg (Middle Diemel Valley) are indicated by solid and dotted lines, respectively. The boxplots on the right indicate the mean daytime and nighttime temperatures per season and their variation between sites by displaying the median of the 11 loggers, the 1st and 3rd quartile (boxes) and the 10th and the 90th percentile (whiskers). The calculation of the mean daytime and nighttime temperatures is based on the measurements that were taken within the period delimited by the grey area in the plot and outside of it, respectively. Differences among species were analysed by Kruskal-Wallis *H* test and subsequent pair-wise comparisons using the Wilcoxon rank-sum test (for details see Section 2.3). Different letters indicate significant differences among species. n.s. = not significant.

(Middle Diemel Valley, 240 m a.s.l.) (Fig. 2). It was not possible to use data from the station in Warburg as it was established only in 1998, whereas Borgentreich-Bühne was closed in 2008 and therefore could not be used to obtain hourly reference data (see above).

The time series comprised monthly averages of air temperature and relative air humidity, monthly sums of precipitation and the number of days with a snow depth > 5 cm. The data from the weather station in Brilon covered the period from 1951 to 2011, those from the station in Borgentreich-Bühne the period from 1951 to 2007. The temporal trends were calculated using linear regression analyses (climatic parameter vs. year) and the statistics program *SigmaPlot* 12.5 (Systat Software, 2011).

Estimating the potential impact of expected climate warming on the future distribution of species in a specific region requires knowledge of the vertical lapse rate of the air temperature in that region. The vertical lapse rate determines how far species have to shift their ranges to higher altitudes to track rising temperatures. The temperature lapse rate of the study area was calculated using elevation and annual mean temperature data from the weather stations in Borgentreich-Bühne, Brilon and another at the “Kahler Asten” (839 m a.s.l). The “Kahler Asten” is the highest elevation of the “Rothaargebirge”, a low mountain range southwest of the study area that transitions into the western part of the Upper Diemel Valley. For each of the years between 1951 and 2007 for which data were available from all three weather stations (46 years in total), the annual average temperatures were regressed against elevation. Then the mean slope of the resulting regression lines was calculated to obtain the long-term averages of the regional temperature lapse rate.

2.6. *Potential effects of climate change on species distributions*

To assess the possible effect of continued climate change on the distributions of the study species in the Diemel Valley, the climatic niches of the species were modelled based on current climatic conditions and current distributions of the species. The results were used to evaluate the climatic suitability of the Diemel Valley in the year 2061 under a scenario of moderate climate change that was derived from the assessment of regional long-term climate trends (cf. Section 2.5).

Information on the current climate were obtained from Germany’s

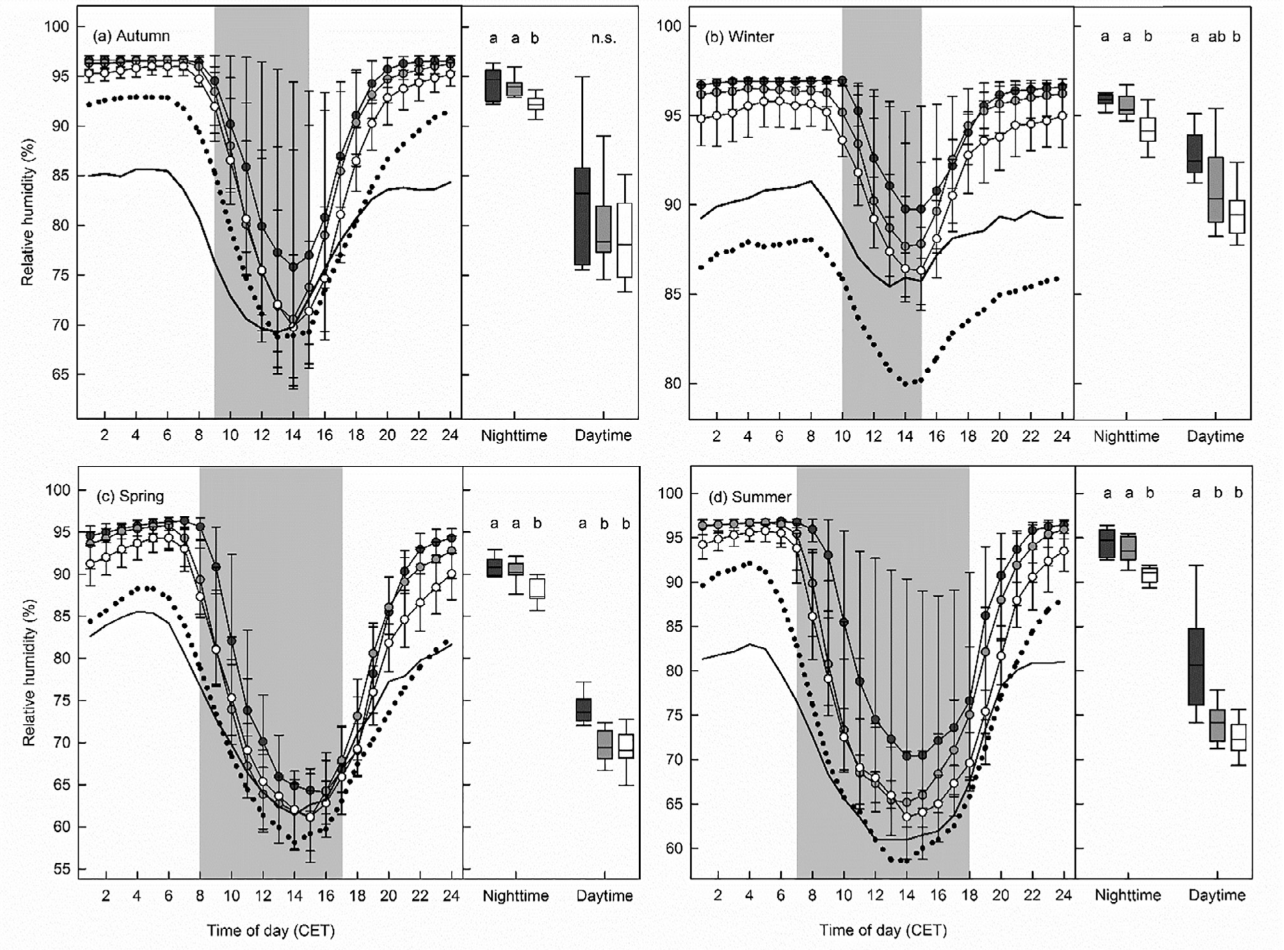

Fig. 4. Diurnal variation of the relative air humidity at oviposition sites of *Erebia medusa* (dark grey), *Melitaea aurelia* (light grey) and *Satyrium spini* (white) in (a) autumn, (b) winter, (c) spring and (d) summer. In each of the three species, the sample size was 11 data loggers. The curves on the left of the diagrams show the hourly averages per season (points = median of the 11 sampled loggers, bars = range of values). The hourly averages of weather stations in Brilon (Upper Diemel Valley) and Warburg (Middle Diemel Valley) are indicated by solid and dotted lines, respectively. The boxplots on the right indicate the mean daytime and nighttime relative humidity per season and its variation between sites by displaying the median of the 11 loggers, the 1st and 3rd quartile (boxes) and the 10th and the 90th percentile (whiskers). The calculation of the mean daytime and nighttime humidity is based on the measurements that were taken within the period delimited by the grey area in the plot and outside of it, respectively. Differences among species were analysed by Kruskal-Wallis *H* test and subsequent pair-wise comparisons using the Wilcoxon rank-sum test (for details see Section 2.3). Different letters indicate significant differences among species. n.s. = not significant.

National Meteorological Service as grid data with a spatial resolution of 1 km2 containing long-term averages of annual mean temperature and annual precipitation for the period 1981–2010 (DWD, 2018). Being averages, the grid data indicate the climatic conditions at the middle of this period (i.e., around 1995) rather than at the end of it when the distributions of the study species were surveyed. Therefore, all values of the annual mean temperature were increased by 0.33 °C (which corresponds to the average increase of 0.22 °C per decade at the weather station in Brilon, cf. Table 2) before being used in the modelling procedure. Precipitation data were not modified because no significant trend of annual precipitation was detected either in Brilon or Borgentreich (cf. Table 2). For each cell of the climate grid data, its status (occupied vs. unoccupied by a certain species) was determined by overlaying it in ESRI ArcMap 10.2.2 with a layer that contained the geometries of all the sites in which the species was present. All cells that intersected with occupied sites were classified as occupied, all others as unoccupied. This resulted in 19, 46 and 56 cells (out of the total of 535 cells that covered the study area) being classified as occupied by *E. medusa*, *M. aurelia* and *S. spini*, respectively.

The climate niches of the study species were calculated by means of Generalised Linear Models (GLM) with binomial error structure and a logit link using the *R* environment. The status of the grid cells was the dependent variable, and annual mean temperature, annual precipitation and the interaction between them served as predictor variables. As indicated above, the ratios between occupied unoccupied grid cells were highly imbalanced. When fitted to such datasets, binomial GLM may yield biased results, especially if the absolute number of presence or absence samples is small (as it is the case here for occupied cells) (King and Zeng, 2001). Therefore, we adopted the following approach. Step 1: For each of the three species, we randomly sampled (without replacement) as many unoccupied grid cells from the total of unoccupied cells as there were occupied cells using the function “sample ()” of the *R* environment and combined them with the occupied cells to obtain balanced datasets of 38, 92 and 112 cells for *E. medusa*, *M.*

Table 1

Seasonal averages of air temperature and relative humidity at oviposition sites of *Erebia medusa*, *Melitaea aurelia* and *Satyrium spini*. In each of the three species, the sample size was 11 data loggers. The values indicate the median and the range. Differences among species were analysed by Kruskal-Wallis *H* test and subsequent pair-wise comparisons using the Wilcoxon rank-sum test (for details see Section 2.3). n.s. = not significant.

Parameter	*Erebia medusa* (E)		*Melitaea aurelia* (M)		*Satyrium spini* (S)		Pairwise comparison
Air temperature (°C)							
Autumn	9.2	(7.7–10.1)	9.9	(8.3–11.0)	10.3	(9.1–10.9)	E < S
Winter	0.7	(0.2–1.3)	1.8	(0.7–2.3)	2.2	(1.8–2.6)	E < M, S
Spring	9.6	(8.7–10.0)	10.9	(10.0–11.7)	11.0	(10.3–11.8)	E < M, S
Summer	15.9	(15.0–16.5)	17.0	(16.1–17.6)	16.8	(16.4–17.8)	E < M, S
Relative air humidity (%)							
Autumn	91.3	(87.3–96.4)	89.4	(87.9–94.5)	88.0	(85.7–91.4)	n.s.
Winter	95.1	(94.2–95.8)	94.2	(93.3–96.6)	92.8	(91.4–95.1)	E > S
Spring	84.1	(82.8–85.4)	81.5	(79.5–83.1)	80.0	(77.8–82.9)	E > M, S
Summer	88.0	(83.3–94.3)	84.1	(81.1–85.6)	81.4	(80.3–83.1)	E, M > S

aurelia and *S. spini*, respectively. Step 2: A GLM was fitted to the data as described above. Steps 1 and 2 were repeated 100 times for each of the study species, and the coefficients of the 100 models per species were averaged to obtain the final climate niche model. The performance of the final models was evaluated by means of the area under the curve (AUC) of an ROC plot (Fielding and Bell, 1997).

Projections of the future climate in the study area with sufficiently fine spatial resolution, which we would have preferred to use for modelling possible future distributions, were not available. Therefore, we extrapolated the temperature values from the grid data until the year 2061 by means of the equation that describes the linear trend of annual mean temperature in the Upper Diemel Valley over the course of recent decades (cf. Table 2). Thus, the annual mean temperature in the Diemel Valley was assumed to increase by 0.22 °C per decade, resulting in a total increase of 1.10 °C until the year 2061. Annual precipitation was assumed to stay the same because no significant change was detected in climate data from the past (cf. Table 2). Finally, climatic suitability of the study area after 50 years of continued climate change was assessed by calculating the probability of occurrence of a species for all grid cells using the final climate niche models and the values of annual mean temperature and annual precipitation that were assumed for the year 2061. Grid cells with a probability of occurrence of 0–0.5 were considered as climatically unsuitable, those with values > 0.5–1.0 as suitable. Cells with probabilities > 0.5 under both current and projected future climates were considered as "stable". Cells with probabilities > 0.5 under current but ≤0.5 under future conditions were considered as "losses", those with probabilities ≤0.5 under current but > 0.5 under future conditions as "gains".

3. Results

3.1. Microclimate – temperature and humidity

3.1.1. Annual averages and seasonal variation

Throughout the year, the microclimate at the oviposition sites of *E. medusa* was significantly cooler than at the oviposition sites of *M. aurelia* and *S. spini* (Table 1, Fig. 2). The latter two species did not differ significantly from each other, although there was a slight tendency towards higher temperatures at the oviposition sites of *S. spini* in most seasons. Concerning relative air humidity, the annual and seasonal averages were highest, by a statistically significant margin, at the oviposition sites of *E. medusa* and lowest for *S. spini*. *M. aurelia* took an intermediate position.

The annual mean temperature at the oviposition sites of *E. medusa* (median = 8.8 °C) corresponded approximately to the annual mean air temperature (8.7 °C) at the reference weather station in Brilon in the Upper Diemel Valley (Fig. 2). The annual mean relative humidity at the oviposition sites (median = 89.2%), however, was considerably higher than at the reference station (79.2%). At the oviposition sites of *M. aurelia* and *S. spini*, both the annual mean temperature (median = 9.9 °C and 10.0 °C, respectively) and the annual mean relative humidity (median = 87.2% and 85.6%, respectively) were higher than at the reference station in Warburg (9.3 °C, 79.8%) in the Middle Diemel Valley.

3.1.2. Diurnal variation

In all seasons, the average temperature and humidity conditions at night were very similar to the general pattern described above on the basis of the seasonal averages, i.e., the microclimate of the oviposition sites of *E. medusa* was coolest and most humid and that of the oviposition sites of *S. spini* was warmest and driest (Figs. 3 and 4). During the day, the differences in temperature at the oviposition sites of the three species were generally much smaller than at night, especially in spring and autumn when no significant differences were found. Concerning relative humidity, the significant differences between *E. medusa* and *S. spini* that were observed at night persisted during the day in most seasons (except in autumn). The relative humidity at the oviposition sites of *M. aurelia*, which at night was almost as high as for *E. medusa*, decreased much more strongly during the day than in the case of *E. medusa*. Consequently, the conditions at the oviposition sites of *M. aurelia* were relatively humid (similar to those of *E. medusa*) at night, but relatively dry (similar to those of *S. spini*) during the day.

In summary, it can be stated that the differences between daytime and nighttime temperatures were considerably greater for *E. medusa* than for *M. aurelia* and *S. spini*. Concerning relative humidity, in contrast, *E. medusa* was the species with the smallest differences between daytime and nighttime.

3.2. Climate change in the study area

In the course of the past six decades, the annual mean air temperature increased significantly in both the Upper and the Middle Diemel Valley (Table 2). Concerning the seasonal mean temperatures, statistically significant increases were mainly found for the spring and summer seasons in both parts of the Valley. The strongest increase (on average +0.32 °C per decade) occurred in the Middle Diemel Valley in spring. In the other seasons, the air temperature did not increase significantly, except for the autumn period in the Middle Diemel Valley.

In contrast to the clear temperature trends, precipitation changed very little in the study area in the course of the past six decades. The only significant trend was found for the summer season in the Upper Diemel Valley, where precipitation decreased on average by 13.5 mm

Table 2

Temporal trends of several climatic parameters measured at two weather stations (Brilon and Borgentreich-Bühne) in the Diemel Valley from 1951 to 2011. The analyses were carried out as linear regressions (climatic parameter vs. year). SE_C = standard error of the regression coefficient, R^2 = percentage of explained variance, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, n.s. = not significant.

Parameter	Regression function	SE_C	R^2	Mean change	
				per decade	per 50 years
Brilon (Upper Diemel Valley)					
Mean temperature (°C)					
Year	y = 6.936 + 0.022 * x	0.005	0.23^{***}	+ 0.22 °C	+ 1.10 °C
Autumn	.	.	n.s.	.	.
Winter	.	.	n.s.	.	.
Spring	y = 6.039 + 0.029 * x	0.008	0.19^{***}	+ 0.29 °C	+ 1.45 °C
Summer	y = 14.198 + 0.026 * x	0.007	0.19^{***}	+ 0.26 °C	+ 1.30 °C
Mean relative humidity (%)					
Year	.	.	n.s.	.	.
Autumn	y = 82.457 + 0.054 * x	0.023	0.08^{*}	+ 0.54%	+ 2.7%
Winter	.	.	n.s.	.	.
Spring	.	.	n.s.	.	.
Summer	.	.	n.s.	.	.
Precipitation (mm)					
Year	.	.	n.s.	.	.
Autumn	.	.	n.s.	.	.
Winter	.	.	n.s.	.	.
Spring	.	.	n.s.	.	.
Summer	y = 332.609 − 1.351 * x	0.607	0.08^{*}	− 13.5 mm	− 67.6 mm
Snow cover > 5 cm (no. of days)	.	.	n.s.	.	.
Borgentreich (Middle Diemel Valley)					
Mean temperature (°C)					
Year	y = 7.780 + 0.027 * x	0.006	0.30^{***}	+ 0.27 °C	+ 1.35 °C
Autumn	y = 8.208 + 0.023 * x	0.010	0.11^{*}	+ 0.23 °C	+ 1.15 °C
Winter	.	.	n.s.	.	.
Spring	y = 7.156 + 0.032 * x	0.009	0.21^{**}	+ 0.32 °C	+ 1.60 °C
Summer	y = 15.543 + 0.029 * x	0.009	0.19^{**}	+ 0.29 °C	+ 1.45 °C
Mean relative humidity (%)					
Year	y = 83.477 − 0.096 * x	0.018	0.42^{***}	− 0.96%	− 4.8%
Autumn	.	.	n.s.	.	.
Winter	y = 87.613 − 0.056 * x	0.021	0.15^{*}	− 0.56%	− 2.8%
Spring	y = 80.211 − 0.124 * x	0.023	0.40^{***}	− 1.24%	− 6.2%
Summer	y = 80.629 − 0.156 * x	0.034	0.33^{***}	− 1.56%	− 7.8%
Precipitation (mm)					
Year	.	.	n.s.	.	.
Autumn	.	.	n.s.	.	.
Winter	.	.	n.s.	.	.
Spring	.	.	n.s.	.	.
Summer	.	.	n.s.	.	.
Snow cover > 5 cm (no. of days)	.	.	n.s.	.	.

per decade. The number of days with a snow depth > 5 cm did not change significantly either in the Upper or in the Middle Diemel Valley.

Concerning the relative air humidity, significant changes occurred mainly in the Middle Diemel Valley. Here, the relative humidity decreased in most seasons. The strongest decrease was found in summer (on average − 1.56% per decade). In the Upper Diemel Valley, the relative humidity showed a significant change only in autumn (on average + 0.54% per decade).

The long-term average (± standard deviation) of the temperature lapse rate in the study area and the adjacent low mountain range was estimated at − 0.58 (± 0.05) °C for a 100 m increase in elevation. This means that in the study area, species would have to move 171 m uphill to compensate for a 1 °C increase of the annual mean temperature.

3.3. Potential effects of climate change on species distributions

The climate niche models that relate the distribution of the study species and current climatic conditions had AUC values of 0.92 (*E. medusa*), 0.86 (*M. aurelia*) and 0.81 (*S. spini*), indicating excellent to outstanding model performance (Hosmer and Lemeshow, 2000). Thus, there is a high correlation between local climate and species distributions (for a visual comparison between current distributions and modelled probabilities of occurrence see Fig. A3a, c, d). The models indicate a positive relationship between the occurrence of *M. aurelia* and *S. spini* and annual mean temperature, and a negative one in the case of *E. medusa*. The occurrence of all three species is positively related to annual precipitation.

With respect to the future climate, the models predict that 79 (65.8%) of the 120 grid cells that were classified as suitable for *E. medusa* under current climatic conditions will become unsuitable by the

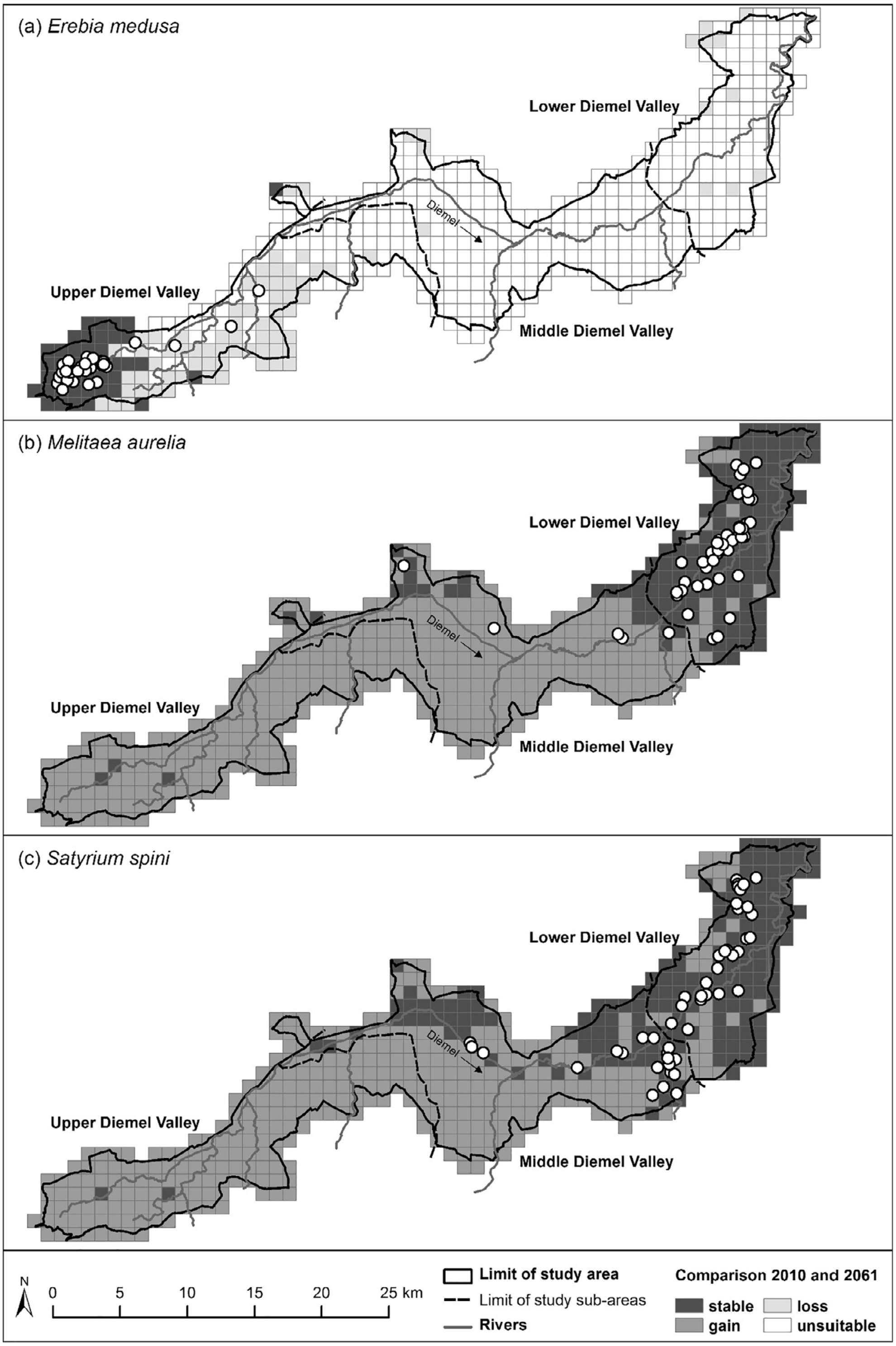

Fig. 5. Modelled climatic suitability of the Diemel Valley in the year 2061 with respect to (a) *Erebia medusa*, (b) *Melitaea aurelia* and (c) *Satyrium spini* under a scenario of moderate climate change. "Stable" grid cells had probabilities of occurrence > 0.5 under both current (year 2010) and projected future (year 2061) climates. "Losses" are cells with probabilities > 0.5 and ≤ 0.5 under current and future conditions, respectively. "Gains" are cells with probabilities ≤ 0.5 and > 0.5 under current and future conditions, respectively. Cells classified as "unsuitable" had probabilities ≤ 0.5 at both points in time. The white circles indicate the present distribution of the study species (cf. Fig. 1).

year 2061, the rest is predicted to remain suitable (Fig. 5). For *M. aurelia* and *S. spini*, in contrast, the climatically suitable area may dramatically increase. Under current climatic conditions, 147 grid cells were classified as suitable for *M. aurelia*, 173 for *S. spini*. Under the assumption of a 1.10 °C increase in annual mean temperature and no change in annual precipitation, all 535 grid cells (i.e., the entire study area) are predicted to become suitable for both species by the year 2061. This is equivalent to an increase in climatically suitable area by

264% in the case of *M. aurelia* and 209% in the case of *S. spini*.

4. Discussion

4.1. Microclimate

The microclimatic measurements at the oviposition sites of *E. medusa*, *M. aurelia* and *S. spini* in the Diemel Valley revealed significant interspecific differences. These differences roughly reflect the overall distribution of the three species along the climatic gradient in the study area. Regarding annual and seasonal averages, the oviposition sites of *E. medusa* (a species that is restricted to the mountainous Upper Diemel Valley), are cooler and more humid than those of *M. aurelia* and *S. spini* (species that occur only in the Middle and Lower Diemel Valley). In terms of mean values, the microclimates of the oviposition sites of the latter two species are largely similar to each other.

Interestingly, the interspecific differences in annual and seasonal mean temperatures were mainly due to differences in nighttime temperatures, because at night the oviposition sites of *E. medusa* in the Upper Diemel Valley were clearly cooler than those of *M. aurelia* and *S. spini* in the Middle and Lower Diemel Valley in all seasons. During the day, however, the heating of the near-ground air layer due to absorption of solar radiation by the ground seemed to be the dominant factor that determined the temperature at the oviposition sites, thus compensating for the generally cooler climate of the Upper Diemel Valley (cf. Stoutjesdijk and Barkmann, 1992). As a result, the daytime temperatures at the oviposition sites of *E. medusa* closely resembled those at the oviposition sites of *M. aurelia* and *S. spini* in spring, summer and autumn, although the daytime readings of the weather station in the Upper Diemel Valley were generally lower than those of the station in the Middle Diemel Valley. During the winter, when the angle of incidence of solar radiation was low and the sky mostly clouded, the effect of radiative heating was marginal (cf. Stoutjesdijk and Barkmann, 1992). Consequently, the night- and daytime patterns of the temperature were very similar to each other in winter.

The apparent tolerance of *E. medusa* towards high daytime temperatures from spring to autumn suggests that the sensitivity of this continental-montane species to climate change, which various authors assume (Caspari, 2008; Fartmann and Hermann, 2006; Schulte et al., 2007; Settele et al., 2008; Stuhldreher et al., 2014), is related to factors other than warm growing seasons. High winter temperatures, which in a laboratory experiment decreased the survival rates of the overwintering larvae and the vitality of the subsequent life-stages (Stuhldreher et al., 2014), are probably more detrimental. Moreover, the results of the microclimatic measurements hint at the humidity of the air being another important factor. Although *E. medusa* showed the strongest diurnal temperature variation, the differences between night- and daytime relative humidity were the smallest of the three species. While the nighttime values were similarly high in all three species, the humidity of the air at the oviposition sites of *E. medusa* decreased less strongly during the day than was the case for *M. aurelia* and *S. spini*. Consequently, the daytime values for *E. medusa* were considerably higher than those for *M. aurelia* and *S. spini*, especially in spring and summer. This is probably due to the fact that the vegetation is higher and soils are deeper in the habitats of *E. medusa* than in the habitats of the other species (Fartmann, 2004; pers. obs.). Moreover, the larval habitats of *E. medusa* are characterised by thick layers of litter (Stuhldreher and Fartmann, 2015, 2014) which retain dew and rain and hereby probably act as a humidity buffer during the day. The importance of relatively humid conditions may be explained by a low desiccation resistance of the eggs. Among the butterflies from the subfamily Satyrinae, there are great differences concerning the desiccation resistance of the eggs (Bergman, 1999; Karlsson and Wiklund, 1985). Species that deposit their eggs in relatively dry microhabitats (e.g., *Lasiommata* sp.) have drought-resistant eggs, whereas the mortality of eggs from species living in more humid habitats can be very high when the ambient air is dry. Other life-cycle stages of *E. medusa* could be equally sensitive to a lack of humidity and thus explain the apparent dependence on humidity, but there are no studies relating to this.

In summary, it can be stated that all three study species reproduce at sites that provide warm microclimatic conditions throughout the growing season. At these sites, the daytime temperature of the air far exceeds that of “average” locations. The importance of warm microclimates for grassland butterflies, especially for threatened species, is a well-documented fact (Fartmann, 2006b; Settele et al., 2009; Thomas, 1993; WallisDeVries and van Swaay, 2006). The continued existence of particularly warm conditions is usually linked to some kind of repeated mechanical disturbance such as regular mowing or grazing and tramping by animals which counteracts succession by destroying plant biomass and thereby maintains early seral stages where the near-ground air layer heats up faster and more strongly than in dense vegetation. Therefore, the successful conservation of grassland butterflies, including *E. medusa*, *M. aurelia* and *S. spini*, and many other thermophilous insects necessitates that the traditional forms of land-use that created and shaped the semi-natural open landscapes of Europe are continued or re-introduced (Bonari et al., 2017). However, there is no universal “recipe” concerning type, intensity and timing of disturbance that is equally suited for all butterfly species, which is why conservation measures should always be designed according to the specific needs of the target species (Eichel and Fartmann, 2008; Loeffler et al., 2013; Stuhldreher and Fartmann, 2014; WallisDeVries et al., 2016).

4.2. Climate change in the study area

Since the middle of the 20th century, strong increases of the mean temperature have occurred throughout the Diemel Valley, particularly in spring and summer. Additionally, the relative air humidity decreased significantly in the Middle Diemel Valley, whereas it remained largely the same in the Upper Diemel Valley. With respect to precipitation, there were no significant changes, except for the summer season in the Upper Diemel Valley for which precipitation decreased. In the following, the possible effects of these climatic changes on the distribution of the three threatened study species will be discussed, focussing on the possible effects of rising temperatures as temperature is the parameter that changed most strongly during recent decades.

In the Diemel Valley, all three study species reach the current northwestern distribution boundary in Europe (Fartmann, 2004; Kudrna et al., 2011). In addition, *E. medusa* reaches its current lower elevational limit within the region. There are strong indications that these boundaries are at least partly due to climatic constraints. Firstly, the xerothermophilous species *M. aurelia* and *S. spini* have never been recorded either in the Upper Diemel Valley or anywhere far northwest of their current range. Moreover, *M. aurelia* colonised the Diemel Valley only in the 1990s. Secondly, all populations of *E. medusa* in the Middle and Lower Diemel Valley, where the species had occurred locally until the 1980s, became extinct (Stuhldreher and Fartmann, 2014). The causes of these extinctions could not be unambiguously determined (Stuhldreher and Fartmann, 2014), but large-scale distribution modelling showed that the occurrence of *E. medusa* can be well explained by climatic variables and that large parts of its current range are likely to become unsuitable due to climate change (Settele et al., 2008).

As the current distribution pattern of the study species in the Diemel Valley is very likely shaped by climatic constraints, it may change significantly if global warming continues. Within 50 years from now, the annual mean temperature may increase by 1.10 °C in the Upper Diemel Valley and 1.35 °C in the Middle Diemel Valley if climate warming in the study area continues at the same rate as in the past (i.e., at the rate determined by the analyses of climatic changes since the middle of the 20th century). These are conservative estimates as they are based on linear trends over the period from 1951 to 2011, although the rate of warming has generally increased in Germany since the beginning of the 1990s (DWD, 2016). Moreover, regional projections of climatic changes in North Rhine-Westphalia predict an increase of the annual mean temperature of 1.4–2.3 °C for the period 2031–2060 under emission scenario A1B, depending on the climate model used (Kropp et al., 2009). Even the conservative estimates of future warming (+1.10 °C and +1.35 °C in the Upper and Middle Diemel Valley, respectively) are of similar magnitude as the observed differences in annual and seasonal mean temperatures in the larval habitats of *E. medusa* on the one hand and *M. aurelia* and *S. spini* on the other (cf. Table 1). Hence, we conclude that by the middle of the century, the larval habitats of *E. medusa* in the Upper Diemel Valley may become as warm as those of *M. aurelia* and *S. spini* in the Middle and Lower Diemel Valley currently are—even when a relatively low rate of future climate warming is assumed. Consequently, *M. aurelia* and *S. spini* may be able to expand their ranges to higher altitudes and colonize the Upper Diemel Valley, where calcareous grasslands with sufficient amounts of the host plants exist (Fartmann, 2004; pers. obs.). We assume that both species will not be negatively affected by further decreases of the air humidity because both are known to occur in even hotter and drier habitats than the calcareous grasslands of the Diemel Valley (Ebert and Rennwald, 1991a, 1991b; Hermann, 2007). In contrast, *E. medusa* may incur severe population declines. Given the regional lapse rate of the air temperature of −0.58 °C per 100 m (which is very similar to the value of −0.6 °C used by Franco et al. (2006) in a study on range shifts of butterflies in Britain), the species would have to move 188 m uphill to track an increase in the mean annual temperature of 1.1 °C. As *E. medusa* is already restricted to elevations between 300 and 500 m a.s.l., there is little margin for moving uphill because within the study area there are very few grasslands at elevations > 500 m a.s.l. (Fartmann, 2004; pers. obs.; cf. Streitberger et al., 2016). In the long term, *E. medusa* may therefore become restricted to the Rothaar Mountains southwest of the study area. This holds true even if—as discussed above—winter temperatures are more important than spring and summer temperatures, because the increase in the mean winter temperature was equal to that of the annual mean temperature, both in the Upper and Middle Diemel Valley. Alternatively, the species could move to microclimatically cooler habitats within its current range, such as grasslands on north-facing slopes. However, very few of such habitats exist as most of the north-facing slopes of the Diemel Valley are forested (Fartmann, 2006a; pers. obs.). Modelling the possible future distribution of the three species in the Diemel Valley under a scenario of moderate climate change supported the conclusions derived from the comparison of microclimatic preferences with long-term trends of the regional climate.

However, there are some uncertainties as to whether the three species will react to future climate change in the way described above. Firstly, it is not clear whether mesoclimatic changes will entail identical changes in the microclimatic conditions of the larval habitats of butterflies. It has been suggested that global warming can lead to microclimatic cooling in spring by advancing the onset of plant growth in spring, especially in combination with high inputs of nitrogen through atmospheric deposition (WallisDeVries and van Swaay, 2006). However, current nitrogen deposition rates of 10–20 kg ha^{-1} y^{-1} in the study area are comparatively low (Wichink Kruit et al., 2014) and are, at most, at the lower end of the critical loads for calcareous (15–25 kg ha^{-1} y^{-1}) and mesic grasslands (20–30 kg ha^{-1} y^{-1}) (Achermann and Bobbink, 2003). Secondly, *M. aurelia* and *S. spini* will be able to expand their ranges only if the mobility of both species is high enough to cope with the lower density of extant calcareous grasslands in the western half of the study area. However, single migrating individuals of *M. aurelia* have repeatedly been observed in calcareous grasslands around the city of Marsberg in the eastern part of the Upper Diemel Valley since 2005, about 15 km away from the next population (W. Schubert, pers. comm.; pers. obs.). This suggests that at least this relatively mobile species may be able to expand its range in the Diemel Valley in response to climate warming.

4.3. Implications for conservation

If northern and montane species cannot shift their ranges to higher latitudes or elevations, either because habitats that are both climatically and structurally suitable simply do not exist or they are inaccessible due to fragmentation, the populations at the "warm" margins are under strong evolutionary pressure to develop physiological and ecological adaptations to climate change. Local evolutionary responses to climate change have indeed been documented for many species (Parmesan, 2006). However, the available evidence suggests that these adaptations have typically involved shifts in seasonality, rather than increases in absolute thermal tolerance which would be necessary to allow species to survive under previously unsuitable climatic regimes and thereby conserve their geographic distribution in the face of climate change (Bridle and Vines, 2007; Parmesan, 2006). This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in the contraction of species' ranges at these warm boundaries (Parmesan, 2006; for case studies on butterflies see Dieker et al., 2011, Franco et al., 2006, Konvicka et al., 2003, Merrill et al., 2008, Wilson et al., 2005; Wilson et al., 2007).

Based on the results of this and other studies on the ecology of *E. medusa*, *M. aurelia* and *S. spini*, we conclude that there is one potential "climate change loser" (*E. medusa*) and two potential "winners" (*M. aurelia* and *S. spini*). The range of *E. medusa* within the study area is likely to contract, whereas *M. aurelia* and *S. spini* may become more widely distributed while persisting in the warmest parts of the region.

As all three species are highly relevant to nature conservation in both North Rhine-Westphalia and Hesse, conservation managers should try to slow down the decline of *E. medusa* and enable *M. aurelia* and *S. spini* to track climate change. To this end, two complementary measures should be taken:

1. Broaden the spectrum of available habitats by preserving or creating heterogeneous vegetation structures within existing patches and restoring nutrient-poor grasslands at north- and east-facing slopes (cf. Fartmann, 2006a; Streitberger et al., 2016). This would enable the species to accommodate extreme weather conditions, at least up to a certain degree, without having to move to other habitat patches (cf. Ackerly et al., 2010; Shafer, 1999; Thomas et al., 1999).
2. Enhance habitat connectivity at the landscape level to facilitate the colonisation of previously unoccupied habitat patches within the study area and beyond.

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Declaration of interest statement

None.

Appendix

See Figs. A1–A3

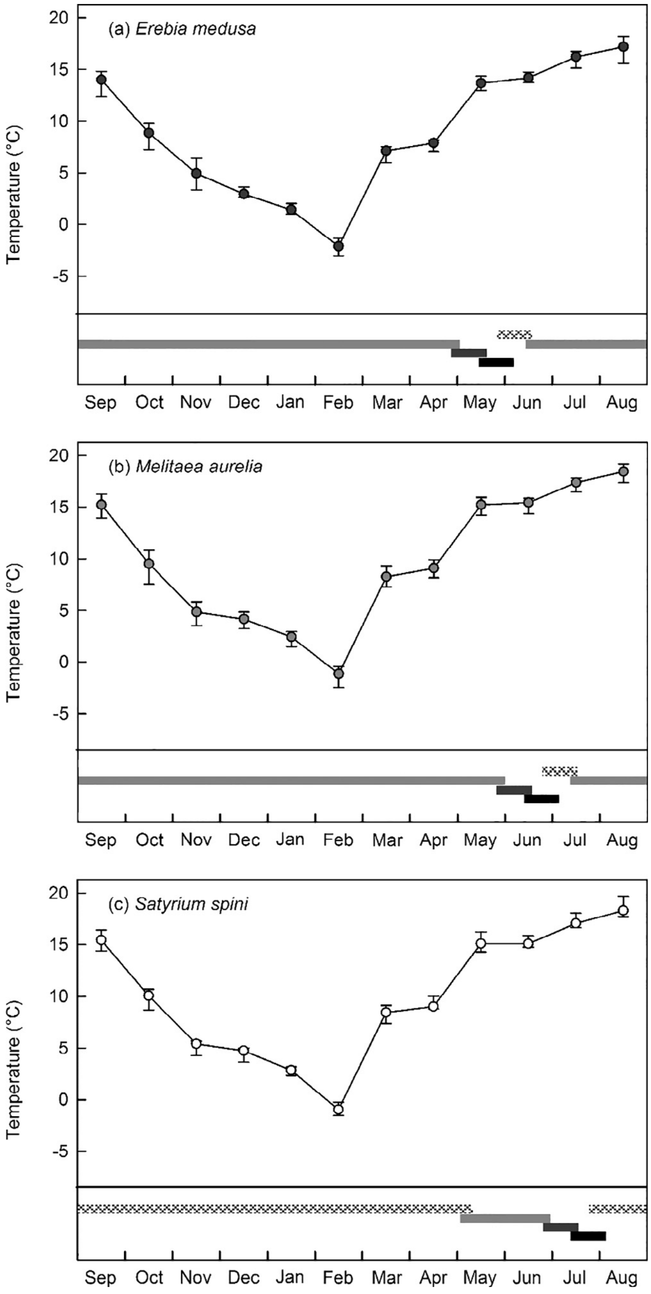

Fig. A1. Monthly mean air temperature at the oviposition sites of (a) *Erebia medusa*, (b) *Melitaea aurelia* and (c) *Satyrium spini*. In each of the three species, the sample size is 11 data loggers. The points represent the median, and the bars indicate the range of values. The bars at the bottom of the diagrams indicate the approximate timing and duration of the different stages within the species' life-cycle in the Diemel Valley (▨ egg, ░ larva, ▓ pupa, █ adult).

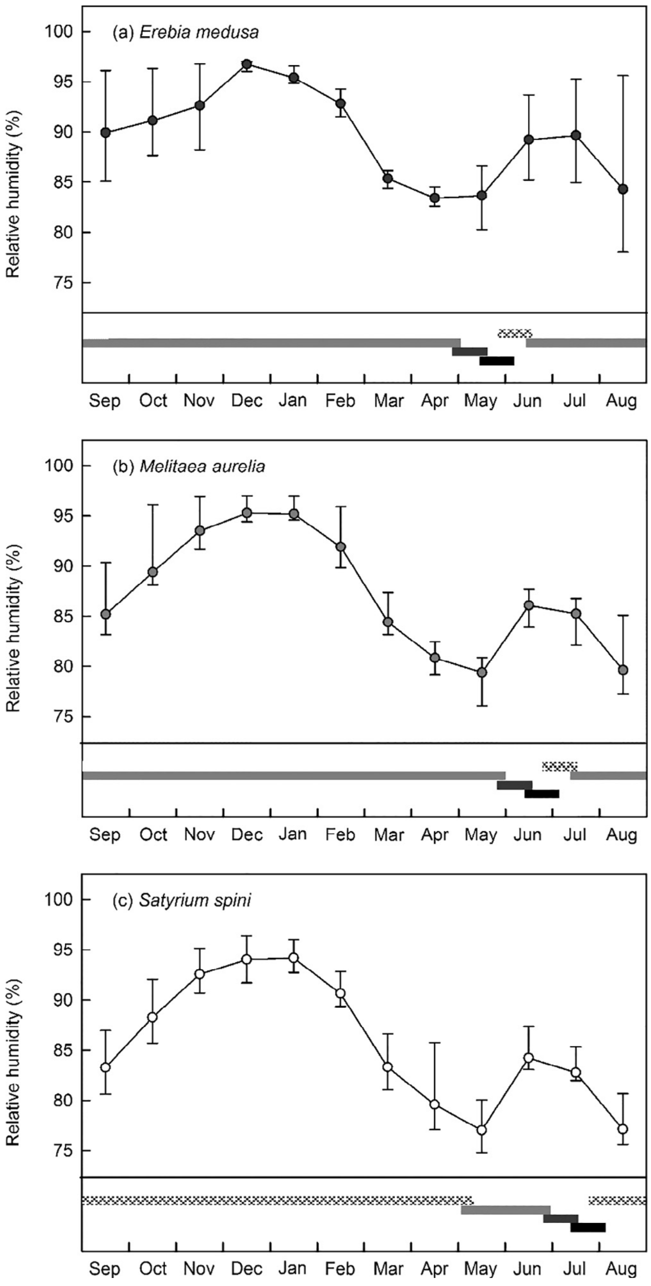

Fig. A2. Monthly average of the relative air humidity at the oviposition sites of (a) *Erebia medusa*, (b) *Melitaea aurelia* and (c) *Satyrium spini*. In each of the three species, the sample size is 11 data loggers. The points represent the median, and the bars indicate the range of values. The bars at the bottom of the diagrams indicate the approximate timing and duration of the different stages within the species' life-cycle in the Diemel Valley (▨ egg, ▬ larva, ▬ pupa, ▬ adult).

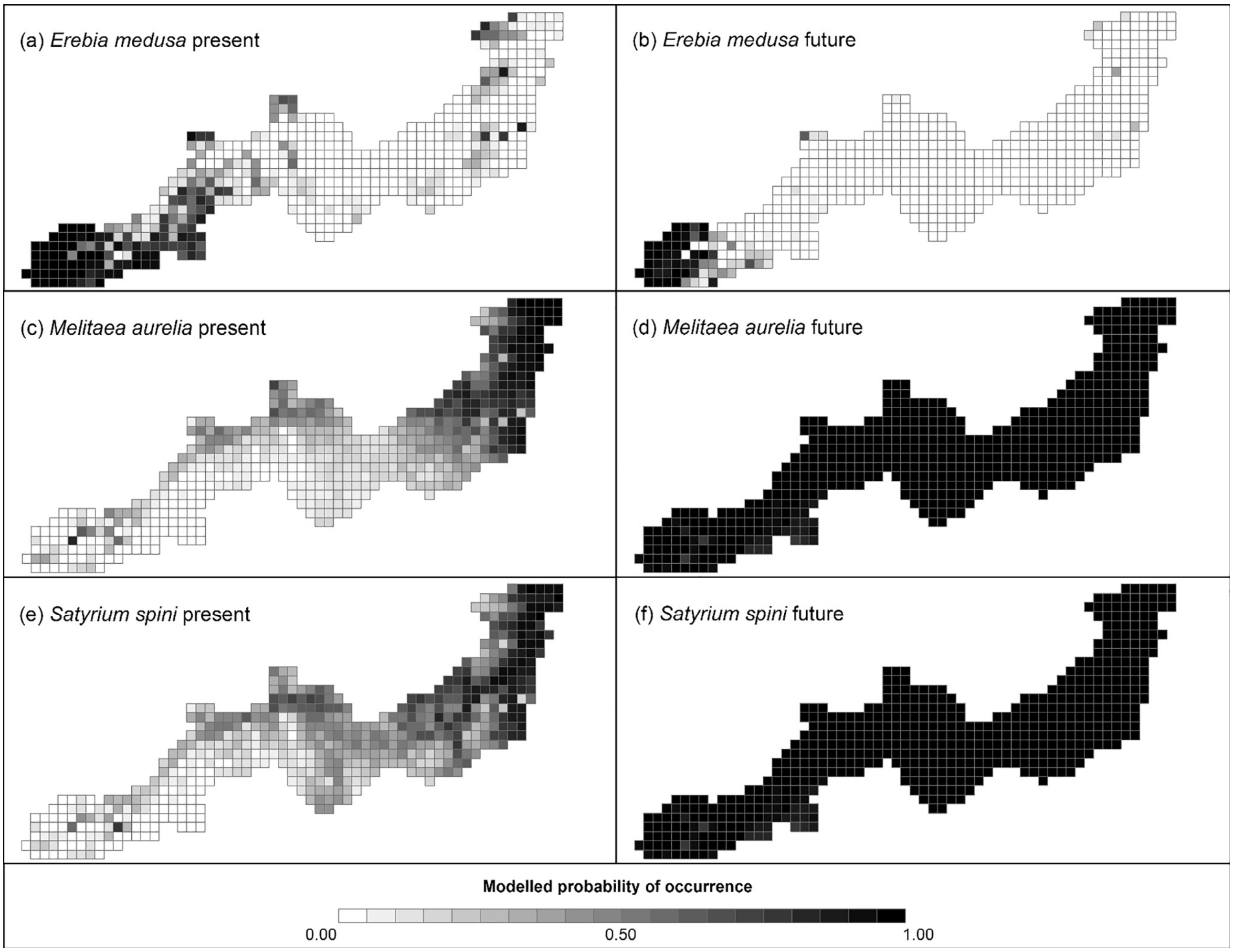

Fig. A3. Probabilities of occurrence of *Erebia medusa* (a, b), *Melitaea aurelia* (c, d) and *Satyrium spini* (e, f) in the Diemel Valley as predicted by climate niche models with annual mean temperature and annual precipitation as predictors. The maps on the left (a, c, e) show the probabilities under current (year 2010) climatic conditions, the maps on the right (b, d, f) show the probabilities that are predicted by the models for the year 2061, based on an assumed increase of the annual mean temperature of 0.22 °C per decade (the annual precipitation is assumed to stay the same).

References

Achermann, B., Bobbink, R., 2003. Empirical critical loads for nitrogen. Proceedings of an Expert Workshop, 11–13 November 2002, Berne. Environmental Documentation No. 164. Swiss Agency for the Environment, Forests and Landscape.

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Divers. Distrib. 16 (3), 476–487. http://dx.doi.org/10.1111/j.1472-4642.2010.00654.x.

Anthes, N., Fartmann, T., Hermann, G., Kaule, G., 2003. Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine *Euphydryas aurinia* colonies. J. Insect Conserv. 7 (3), 175–185. http://dx.doi.org/10.1023/a:1027330422958.

Ashton, S., Gutierrez, D., Wilson, R.J., 2009. Effects of temperature and elevation on habitat use by a rare mountain butterfly: implications for species responses to climate change. Ecol. Entomol. 34 (4), 437–446. http://dx.doi.org/10.1111/j.1365-2311.2008.01068.x.

Bergman, K.O., 1999. Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biol. Conserv. 88 (1), 69–74. http://dx.doi.org/10.1016/s0006-3207(98)00088-3.

Boggs, C.L., Inouye, D.W., 2012. A single climate driver has direct and indirect effects on insect population dynamics. Ecol. Lett. 15 (5), 502–508. http://dx.doi.org/10.1111/j.1461-0248.2012.01766.x.

Bonari, G., Fajmon, K., Malenovsky, I., Zeleny, D., Holusa, J., Jongepierova, I., Kocarek, P., Konvicka, O., Uricar, J., Chytry, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: the importance of heterogeneity and tradition. Agric. Ecosyst. Environ. 246, 243–252. http://dx.doi.org/10.1016/j.agee.2017.06.010.

Bridle, J.R., Vines, T.H., 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends Ecol. Evol. 22 (3), 140–147. http://dx.doi.org/10.1016/j.tree.2006.11.002.

Caspari, S., 2008. Bestandssituation des Rundaugen-Mohrenfalters *Erebia medusa* ([Denis & Schiffermüller], 1775) (Lepidoptera, Satyrinae) im Saarland, Teil 1: Kalkgebiete. Abh. Delattinia 34, 111-126.

Dennis, R.L.H., 2010. A Resource-based Habitat View for Conservation: Butterflies in the British Landscape. Wiley-Blackwell, Oxford (UK).

Development Core Team, R., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Devictor, V., van Swaay, C.A.M., Brereton, T., Brotons, L., Chamberlain, D., Heliola, J., Herrando, S., Julliard, R., Kuussaari, M., Lindstrom, A., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M.F., Wynhoff, I., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Change 2 (2), 121–124. http://dx.doi.org/10.1038/nclimate1347.

Dieker, P., Drees, C., Assmann, T., 2011. Two high-mountain burnet moth species (Lepidoptera, Zygaenidae) react differently to the global change drivers climate and land-use. Biol. Conserv. 144 (12), 2810–2818. http://dx.doi.org/10.1016/j.biocon.2011.07.018.

DWD (Deutscher Wetterdienst), Zeitreihen und Trends http://www.dwd.de/DE/leistungen/zeitreihenundtrends/zeitreihenundtrends.html?nn=16102#buehneTop, 2016 (accessed 17.08.16).

DWD (Deutscher Wetterdienst), 2018. CDC FTP-Server Rasterdaten, ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/multi_annual/air_temperature_mean/8110/ and ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/multi_annual/precipitation/8110/ (accessed 26.03.18).

DWD (Deutscher Wetterdienst), 2015. WebWerdis (Weather Request and Distribution System), https://werdis.dwd.de/werdis/toSearch.do.

Ebert, G., Rennwald, E., 1991a. Die Schmetterlinge Baden-Württembergs. Band 1, Tagfalter I. Eugen Ulmer, Stuttgart (Germany).

Ebert, G., Rennwald, E., 1991b. Die Schmetterlinge Baden-Württembergs. Band 2, Tagfalter II. Eugen Ulmer, Stuttgart (Germany).

Eichel, S., Fartmann, T., 2008. Management of calcareous grasslands for Nickerl's Fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. J. Insect Conserv. 12 (6), 677–688. http://dx.doi.org/10.1007/s10841-007-9110-9.

Fartmann, T., 2006a. Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. Ann. Zool. Fenn. 43 (4), 335–347.

Fartmann, T., Hermann, G., 2006. Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa – von den Anfängen bis heute. In: Fartmann, T., Hermann, G. (Eds), Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa, Abh. Westf. Mus. Naturkde., vol. 68 (3/4), pp 11–57, Münster (Germany).

Fartmann, T., 2004. Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales – Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. Abh. Westf. Mus. Naturkde., vol. 66 (1), pp. 1–256, Münster (Germany).

Fartmann, T., 2006. Welche Rolle spielen Störungen für Tagfalter und Widderchen? In: Fartmann, T., Hermann, G. (Eds), Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa, Abh. Westf. Mus. Naturkde., vol. 68 (3/4), pp. 259–270, Münster (Germany).

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24 (1), 38–49. http://dx.doi.org/10.1017/s0376892997000088.

Franco, A.M.A., Hill, J.K., Kitschke, C., Collingham, Y.C., Roy, D.B., Fox, R., Huntley, B., Thomas, C.D., 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Glob. Change Biol. 12 (8), 1545–1553. http://dx.doi.org/10.1111/j.1365-2486.2006.01180.x.

Garcia-Barros, E., Fartmann, T., 2009. Butterfly oviposition: sites, behaviour and modes. In: Settele, J., Shreeve, T., Konvicka, M., Van Dyck, H. (Eds.), Ecology of Butterflies in Europe. Cambridge University Press, Cambridge (UK), pp. 29–42.

Giraudoux, P., 2013. pgirmess: Data analysis in ecology. R package version 1.5.7.

Helbing, F., Cornils, N., Stuhldreher, G., Fartmann, T., 2015. Populations of a shrub-feeding butterfly thrive after introduction of restorative shrub cutting on formerly abandoned calcareous grassland. J. Insect Conserv. 1–8. http://dx.doi.org/10.1007/s10841-015-9766-5.

Hermann, G., 2007. Tagfalter suchen im Winter – Zipfelfalter, Schillerfalter und Eisvögel [Searching for butterflies in winter – hairstreaks, purple emperors, poplar admirals and white admirals]. Books on Demand GmbH, Norderstedt (Germany).

Hill, J.K., Thomas, C.D., Huntley, B., 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 266 (1425), 1197–1206. http://dx.doi.org/10.1098/rspb.1999.0763.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J., Huntley, B., 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 269 (1505), 2163–2171. http://dx.doi.org/10.1098/rspb.2002.2134.

HMUELV (Hessisches Ministerium für Umwelt, Energie, Landwirtschaft und Verbraucherschutz) (Ed), 2009. Rote Liste (Gefährdungsabschätzung) der Tagfalter (Lepidoptera: Rhopalocera) Hessens, 3. Fassung. Wiesbaden (Germany).

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. Wiley, New York (USA).

Karlsson, B., Wiklund, C., 1985. Egg weight variation in relation to egg mortality and starvation endurance of newly hatched larvae in some satyrid butterflies. Ecol. Entomol. 10 (2), 205–211. http://dx.doi.org/10.1111/j.1365-2311.1985.tb00549.x.

Kennedy, A.D., 1997. Bridging the gap between general circulation model (GCM) output and biological microenvironments. Int. J. Biometeorol. 40 (2), 119–122. http://dx.doi.org/10.1007/s004840050031.

King, G., Zeng, L., 2001. Logistic regression in rare events data. Political Anal. 9 (2), 137–163.

Kolbeck, H., 2013. Kreuzdorn-Zipfelfalter *Satyrium spini* ([Denis & Schiffermüller], 1775). In: Braeu, M., Bolz, R., Kolbeck, H., Nummer, A., Voith, J., Wolf, W. (Eds.), Tagfalter in Bayern. Eugen Ulmer, Stuttgart (Germany), pp. 224–226.

Konvicka, M., Maradova, M., Benes, J., Fric, Z., Kepka, P., 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. Glob. Ecol. Biogeogr. 12 (5), 403–410. http://dx.doi.org/10.1046/j.1466-822X.2003.00053.x.

Kraemer, B., Kaempf, I., Enderle, J., Poniatowski, D., Fartmann, T., 2012. Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. J. Insect Conserv. 16 (6), 857–865. http://dx.doi.org/10.1007/s10841-012-9473-4.

Kropp, J., Holsten, A., Lissner, T., Roithmeier, O., Hattermann, F., Huang, S., Rock, J., Wechsung, F., Luettger, A., Pompe, S., Kuehn, I., Costa, L., Steinhaeuser, M., Walther, C., Klaus, M., Ritchie, S., Metzger, M., 2009. Klimawandel in Nordrhein-Westfalen – regionale Abschätzung der Anfälligkeit ausgewählter Sektoren. Abschlussbericht des Potsdam-Instituts für Klimafolgenforschung (PIK) für das Ministerium für Umwelt und Naturschutz, Landwirtschaft und Verbraucherschutz Nordrhein-Westfalen (MUNLV), https://www.pik-potsdam.de/research/climate-impacts-and-vulnerabilities/research/rd2-flagship-projects/CCD/ccd/studies/anfaelligkeitsstudie_nrw_lowres (accessed 17.08.16).

Kudrna, O., Harpke, A., Lux, K., Pennerstorfer, J., Schweiger, O., Settele, J., Wiemers, M., 2011. Distribution Atlas of Butterflies in Europe. Gesellschaft für Schmetterlingsschutz, Halle (Germany).

LANUV NRW (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen) (Ed), 2011. Rote Liste und Artenverzeichnis der Schmetterlinge (Lepidoptera) – Tagfalter (Diurna) – in Nordrhein-Westfalen. Recklinghausen (Germany).

Loeffler, F., Stuhldreher, G., Fartmann, T., 2013. How much care does a shrub-feeding hairstreak butterfly, *Satyrium spini* (Lepidoptera: Lycaenidae), need in calcareous grasslands? Eur. J. Entomol. 110 (1), 145–152. http://dx.doi.org/10.14411/eje.2013.020.

Maes, D., Jacobs, I., Segers, N., Vanreusel, W., Van Daele, T., Laurijssens, G., Van Dyck, H., 2014. A resource-based conservation approach for an endangered ecotone species: the Ilex Hairstreak (*Satyrium ilicis*) in Flanders (north Belgium). J. Insect Conserv. 18 (5), 939–950. http://dx.doi.org/10.1007/s10841-014-9702-0.

Merrill, R.M., Gutierrez, D., Lewis, O.T., Gutierrez, J., Diez, S.B., Wilson, R.J., 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. J. Anim. Ecol. 77 (1), 145–155. http://dx.doi.org/10.1111/j.1365-2656.2007.01303.x.

Mueller-Wille, W., 1981. Westfalen. Landschaftliche Ordnung und Bindung eines Landes (2. Aufl.). Aschendorfsche Verlagsbuchhandlung, Münster, Germany.

Parmesan, C., 2003. Butterflies as bio-indicators of climate change impacts. In: Boggs, C.L., Watt, W.B., Ehrlich, P.R. (Eds.), Evolution and Ecology Taking Flight: Butterflies as Model Systems. The University of Chicago Press, Chicago (USA), pp. 541–560.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Reinhardt, R., Bolz, R., 2011. Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands – Bearbeitungsstand: 4. Fassung. Natursch. Biol. Vielfalt, vol. 3, pp 167–194, Bonn-Bad Godesberg (Germany).

Rockstroem, J., Steffen, W., Noone, K., Persson, A., Chapin III, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sorlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. Nature 461 (7263), 472–475. http://dx.doi.org/10.1038/461472a.

Roy, D.B., Sparks, T.H., 2000. Phenology of British butterflies and climate change. Glob. Change Biol. 6 (4), 407–416. http://dx.doi.org/10.1046/j.1365-2486.2000.00322.x.

Roy, D.B., Thomas, J.A., 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. Oecologia 134 (3), 439–444. http://dx.doi.org/10.1007/s00442-002-1121-3.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287 (5459), 1770–1774. http://dx.doi.org/10.1126/science.287.5459.1770.

Schraml, E., Fartmann, T., 2013. Frühlings-Mohrenfalter *Erebia medusa* ([Denis & Schiffermüller], 1775). In: Braeu, M., Bolz, R., Kolbeck, H., Nummer, A., Voith, J., Wolf, W. (Eds.), Tagfalter in Bayern. Eugen Ulmer, Stuttgart (Germany), pp. 504–506.

Schulte, T., Eller, O., Niehuis, M., Rennwald, E., 2007. Die Tagfalter der Pfalz. Fauna und Flora in Rheinland-Pfalz, vol. 37, 1–340.

Settele, J., Dover, J., Dolek, M., Konvicka, M., 2009. Butterflies of European ecosystems: impact of land use and options for conservation management. In: Settele, J., Shreeve, T., Konvicka, M., Van Dyck, H. (Eds.), Ecology of Butterflies in Europe. Cambridge University Press, Cambridge (UK), pp. 353–370.

Settele, J., Kudrna, O., Harpke, A., Kuehn, I., van Swaay, C.A.M., Verovnik, R., Warren, M., Wiemers, M., Hanspach, J., Hickler, T., Kuehn, E., Van Halder, I., Veling, K., Vliegenthart, A., Wynhoff, I., Schweiger, O., 2008. Climatic risk atlas of European butterflies. BioRisk, vol. 1, 1–710.

Shafer, C.L., 1999. National park and reserve planning to protect biological diversity: some basic elements. Landsc. Urban Plan. 44 (2–3), 123–153. http://dx.doi.org/10.1016/s0169-2046(98)00115-7.

Siegel, S., Castellan, N.J., 1988. Nonparametric Statistics for the Behavioral Sciences, 2nd ed. McGraw-Hill, New York.

Stoutjesdijk, P., Barkmann, J.J., 1992. Microclimate, Vegetation and Fauna. Opulus Press, Uppsala.

Streitberger, M., Jedicke, E., Fartmann, T., 2016. Auswirkungen des rezenten Klimawandels auf die Biodiversität in Mittelgebirgen – eine Literaturstudie zu Arten und Lebensräumen. Natursch. Landschaftsplan. 48 (2), 37–45.

Stuhldreher, G., Fartmann, T., 2014. When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. J. Insect Conserv. 18 (5), 965–979. http://dx.doi.org/10.1007/s10841-014-9704-y.

Stuhldreher, G., Fartmann, T., 2015. Oviposition-site preferences of a declining butterfly *Erebia medusa* (Lepidoptera: Satyrinae) in nutrient-poor grasslands. Eur. J. Entomol. 112 (3), 493–499. http://dx.doi.org/10.14411/eje.2015.067.

Stuhldreher, G., Hermann, G., Fartmann, T., 2014. Cold-adapted species in a warming world – an explorative study on the impact of high winter temperatures on a continental butterfly. Entomol. Exp. Appl. 151 (3), 270–279. http://dx.doi.org/10.1111/eea.12193.

Systat Software, 2011. SigmaPlot for Windows Version 12.5.

Thomas, J.A., 1993. Holocene climate changes and warm man-made refugia may explain why a 6th of British butterflies possess unnatural early-successional habitats. Ecography 16 (3), 278–284. http://dx.doi.org/10.1111/j.1600-0587.1993.tb00217.x.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conradt, L., 2001a. Ecological and evolutionary processes at expanding range margins. Nature 411 (6837), 577–581. http://dx.doi.org/10.1038/35079066.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., Goodger, B., 2001b. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 268 (1478), 1791–1796. http://dx.doi.org/10.1098/rspb.2001.1693.

Thomas, J.A., Thomas, C.D., Simcox, D.J., Clarke, R.T., 1986. Ecology and declining status of the Silver-spotted Skipper butterfly (*Hesperia comma*) in Britain. J. Appl. Ecol. 23 (2), 365–380. http://dx.doi.org/10.2307/2404023.

Thomas, J.A., Simcox, D.J., Wardlaw, J.C., Elmes, G.W., Hochberg, M.E., Clarke, R.T., 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. J. Insect Conserv. 2 (1), 39–46. http://dx.doi.org/10.1023/a:1009640706218.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D., Webb, N.R., 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Funct. Ecol. 13, 55–64. http://dx.doi.org/10.1046/j.1365-2435.1999.00008.x.

Thomas, J.A., Simcox, D.J., Hovestadt, T., 2011. Evidence based conservation of butterflies. J. Insect Conserv. 15 (1–2), 241–258. http://dx.doi.org/10.1007/s10841-010-9341-z.

Thomas, J.A., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 360 (1454), 339–357. http://dx.doi.org/10.1098/rstb.2004.1585.

Turlure, C., Choutt, J., Baguette, M., Van Dyck, H., 2010. Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. Glob. Change Biol. 16 (6), 1883–1893. http://dx.doi.org/10.1111/j.1365-2486.2009.02133.x.

Turlure, C., Radchuk, V., Baguette, M., Van Dyck, H., Schtickzelle, N., 2011. On the significance of structural vegetation elements for caterpillar thermoregulation in two peat bog butterflies: *Boloria eunomia* and *B. aquilonaris*. J. Therm. Biol 36 (3), 173–180. http://dx.doi.org/10.1016/j.jtherbio.2011.02.001.

Van Dyck, H., Bonte, D., Puls, R., Gotthard, K., Maes, D., 2015. The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? Oikos 124 (1), 54–61. http://dx.doi.org/10.1111/oik.02066.

van Swaay, C.A.M., Warren, M., 2003. Prime Butterfly Areas in Europe: Priority Sites for Conservation. National Reference Centre for Agriculture Nature Management and Fisheries, Wageningen (Netherlands) (Germany).

WallisDeVries, M.F., van Swaay, C.A.M., 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Glob. Change Biol. 12 (9), 1620–1626. http://dx.doi.org/10.1111/j.1365-2486.2006.01202.x.

WallisDeVries, M.F., Noordijk, J., Colijn, E.O., Smit, J.T., Veling, K., 2016. Contrasting responses of insect communities to grazing intensity in lowland heathlands. Agric. Ecosyst. Environ. 234, 72–80. http://dx.doi.org/10.1016/j.agee.2016.04.012.

WallisDeVries, M.F., 2006. Larval habitat quality and its significance for the conservation of Melitaea cinxia in northwestern Europe. In: Fartmann, T., Hermann, G. (Eds), Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa, Abh. Westf. Mus. Naturkde., vol. 68 (3/4), pp 281–294, Münster (Germany).

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414 (6859), 65–69. http://dx.doi.org/10.1038/35102054.

Wichink Kruit, R., Schaap, M., Segers, A., Heslinga, D., Builtjes, P., Banzhaf, S., Scheuschner, T., 2014. Modelling and mapping of atmospheric nitrogen and sulphur deposition and critical loads for ecosystem specific assessment of threats to biodiversity in Germany – PINETI (Pollutant INput andEcosysTemImpact). Substudy Report 1. Texte Umweltbundesamt 60, 1–160.

Williams, E.H., 1981. Thermal influences on oviposition in the montane butterfly *Euphydryas gillettii*. Oecologia 50, 342–346. http://dx.doi.org/10.1007/bf00344974.

Wilson, R.J., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R., Monserrat, V.J., 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecol. Lett. 8 (11), 1138–1146. http://dx.doi.org/10.1111/j.1461-0248.2005.00824.x.

Wilson, R.J., Gutierrez, D., Gutierrez, J., Monserrat, V.J., 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Glob. Change Biol. 13 (9), 1873–1887. http://dx.doi.org/10.1111/j.1365-2486.2007.01418.x.