

When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly

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Abstract The conservation of most temperate grassland habitats and their characteristic fauna and flora requires regular low-intensive forms of land-use to counteract natural succession. Although many species tolerate moderate disturbance regimes, some are known to be susceptible to grazing or mowing, thereby causing a management dilemma. One of these species is the Woodland Ringlet butterfly, *Erebia medusa*. In this study, we analysed which environmental factors determine the occurrence of *E. medusa* in the Diemel Valley (Central Germany). Furthermore, we conducted microclimatic measurements during the winter months to investigate the role of the litter layer as a microclimatic buffer. Patch occupancy in the Diemel Valley was well explained by the amount of litter present in a patch and connectivity to other inhabited patches. The role of local climatic conditions could not be clarified, due to inter-correlations with connectivity. During the winter, the air temperature inside the litter layer was significantly less variable than above it. We conclude that the current distribution of *E. medusa* in the Diemel Valley is caused by the combined effect of habitat quality and connectivity, and perhaps also by climatic factors. The importance of the litter layer reflects the dependence of *E. medusa* on low-intensive or absent land-use. In addition,

the litter layer possibly constitutes an essential habitat element, as it buffers temperature fluctuations and thus probably reduces the energy consumption of overwintering larvae. Given the species' preference for abandoned grasslands, the conservation of *E. medusa* requires a low-intensity habitat management, for example, by rotational grazing or mowing of small parts of the sites. On the landscape level, the preservation of well-connected habitat networks is important.

Keywords Connectivity · *Erebia medusa* · Global change · Litter · Microclimatic buffer · Range retraction · Vegetation structure

Introduction

The transition from traditional to modern agriculture, which in Central Europe mainly occurred in the twentieth century, has led to major changes in land-use (Ellenberg and Leuschner 2010). Agricultural intensification on the one hand and land abandonment on the other, have caused great losses of semi-natural habitats, especially in grassland ecosystems (Vitousek 1994; Stoate et al. 2001). Consequently, specialised species that vitally depend on open habitats with low land-use intensity have suffered severe population declines (Robinson and Sutherland 2002; Van Swaay et al. 2009). More recently, global warming has become another important driver of change and contributes to the alteration of the environmental conditions of organisms (Walther et al. 2002; Parmesan and Yohe 2003). Thus, optimal management of the remaining semi-natural habitats is crucial to the preservation of wild biota in the face of global change (Dawson et al. 2011).

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The answer to the question concerning which type and intensity of land-use are optimal in terms of nature conservation is closely linked to the habitat requirements of the focal species. Since habitat preferences vary greatly among species, different target species require different conservation strategies. This is especially true for butterflies, many of which are highly specialised organisms with very specific habitat requirements (García-Barros and Fartmann 2009; Munguira et al. 2009; Dennis 2010).

Traditional low-intensity grazing or mowing have proven to be beneficial for many butterflies of calcareous grasslands (Erhardt and Thomas 1991; Dover et al. 2011), but some species prefer particularly high- or low-disturbance regimes. Whereas some butterflies depend on frequent grazing that leads to low-growing swards interspersed with patches of bare ground, e.g. *Hesperia comma* (Thomas et al. 1986) and *Maculinea arion* (Thomas et al. 1998) at the northern parts of their range, others tolerate only low grazing or mowing intensities and prefer a closed vegetation cover, e.g. *Hamearis lucina* (Fartmann 2006) and *Melitaea aurelia* (Eichel and Fartmann 2008). A species for which a strong preference for abandoned grasslands is assumed (Schmitt 1993; Fartmann 2004), but has never been systematically investigated so far, is the Woodland Ringlet (*Erebia medusa*).

In several countries at *E. medusa*'s western (Atlantic) range margin, the species has declined, e.g. in Belgium, France and Luxembourg (Van Swaay and Warren 1999). Similarly, population declines have been observed for many regions of Germany (Bolz and Geyer 2003; Lobenstein 2003; Fartmann 2004; Reinhardt et al. 2007; Schulte et al. 2007) and for Switzerland (Sonderegger 2005). In contrast, comparable population collapses have not been observed in more continental countries. Habitat loss is considered an important driver of *E. medusa*'s range retraction, but the species probably also suffers from climate change (Fartmann and Hermann 2006; Schulte et al. 2007; Settele et al. 2008). However, quantifying the relative importance of these drivers is difficult. This is because in Europe, the gradient of decreasing land-use intensity, which stretches from the north-west to the south-east of the continent (IVM 2013; Smit et al. 2008), is roughly paralleled by a climatic gradient of increasing continentality (Krähenmann et al. 2011). Moreover, lowland regions, where the negative effects of global warming—if they truly exist—should be more severe than at higher altitudes, have suffered from agricultural intensification (and subsequent habitat degradation and fragmentation) more severely than mountain ranges (MacDonald et al. 2000). Hence, disentangling the impacts of possible drivers of extinction requires a detailed comparison of current environmental conditions of sites where the species once occurred but is

absent today, with the conditions of sites that are still inhabited.

In the face of the double threat of land-use and climate change, the preservation of the Central European populations of *E. medusa* (and other species with a similar ecology) will require special conservation efforts. However, detailed knowledge of *E. medusa*'s habitat requirements is scarce (Fartmann and Hermann 2006). In this paper, we present a detailed study of the distribution and the habitats of this species at its current north-western range margin in Germany, the Diemel Valley.

The study aims to:

1. compare *E. medusa*'s current and past distribution in the Diemel Valley,
2. analyse its habitat preferences,
3. identify possible causes for the extinction of lowland populations of *E. medusa* in the study area,
4. derive recommendations for the appropriate management of habitats of *E. medusa*.

Materials and methods

Study species

The woodland ringlet (*E. medusa* Fabricius 1787) is a nymphalid butterfly that occurs widely from central and south-eastern Europe eastwards to East Asia. Its altitudinal range extends from the lowlands to the subalpine level (Ebert and Rennwald 1991; Settele et al. 2008). Except in high mountain regions, *E. medusa* is univoltine (Sonderegger 2005). In our study area, it is on the wing for about 4 weeks, usually between the start of May and mid-June (Fartmann 2004, pers. obs.). However, the time of adult emergence varies with weather conditions in spring. The preferred biotopes of *E. medusa* are nutrient-poor grasslands and woodland glades with a low land-use intensity (Ebert and Rennwald 1991; Schraml and Fartmann 2013). Various grass species, namely *Agrostis capillaris*, *Bromus erectus*, *Deschampsia cespitosa*, *Deschampsia flexuosa*, *Festuca ovina* agg., *Festuca rubra* agg., *Molinia caerulea* and *Nardus stricta*, have been reported to serve as larval host plants (Schmitt 1993; Sonderegger 2005; Schraml and Fartmann 2013); however, only *Festuca ovina* agg. and *F. rubra* agg. have been verified to be systematically used for oviposition (Fartmann 2004). *E. medusa* overwinters as the third larval instar on the bases of grass tussocks or in the litter layer (Sonderegger 2005; pers. obs.). Currently, the species is regarded as “near threatened” in Germany (Reinhardt and Bolz 2011).

Study area

The study area, the Diemel Valley, covers an area of about 460 km² in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse. It is the largest area of calcareous grassland in the northern half of Germany (Fartmann 2004) and the northernmost German Prime Butterfly Area (Van Swaay and Warren 2003). The climate is suboceanic (Müller-Wille 1981) and varies greatly with altitude. The Upper Diemel Valley (ca. 200–600 m a.s.l.) is the coolest (annual mean temperature 7.6 °C) and wettest (mean annual precipitation 814 mm) part of the study area (all meteorological values were derived from 1-km² grid datasets from Germany's National Meteorological Service, pers. comm.). The Middle Diemel Valley comprises elevations between ca. 140 and 380 m a.s.l. Here, precipitation is lower (703 mm) and mean temperature is higher (8.2 °C). The Lower Diemel Valley (ca. 100–375 m a.s.l.) is similarly warm (8.3 °C), but precipitation (756 mm) is higher, due to orographic rainfall caused by the eastwardly adjacent elevations of the Rheinhardswald and Solling.

Sampling design

Patch occupancy

An extensive study of the butterfly fauna in the Diemel Valley in the late 1990s (Fartmann 2004) showed that all previously known populations of *E. medusa* in the Middle and Lower Diemel Valley became extinct, whereas the species was still relatively widespread in the western part of the Upper Diemel Valley. Consequently, we restricted our systematic search for extant populations to the Upper Diemel Valley, but all locations with historic records were also surveyed. Data on historic observations of *E. medusa* were taken from Fartmann (2004) and Pähler and Dudler (2010), who compiled information from historic literature covering the study area and local entomologists' unpublished data.

During the flight period of *E. medusa* in 2010, all potentially suitable habitat patches in the Upper Diemel Valley were checked at least twice to assess the presence or absence of the species. All low-intensively used and abandoned grasslands that contained at least one of the grass species that had previously been reported as larval host plants were considered as potentially suitable. Furthermore, we surveyed all patches with historic records in the Middle and Lower Diemel Valley and their surroundings within a 2-km radius. Populations of *E. medusa* were regarded as discrete local subpopulations of the regional metapopulation if they were separated from each other by

more than 50 m of improved grassland, arable fields or forest.

Adult habitats

Based on the patch occupancy survey in 2010, randomly chosen subsets of 20 currently occupied and 20 vacant patches in the Upper Diemel Valley were subjected to a detailed assessment of the habitat characteristics during the flight period of *E. medusa* in 2011. Additionally, all 12 currently unoccupied patches for which historic observations are reported in the literature were analysed in the same way. In each patch, the height and cover of the vegetation layers, abundance of the potential host plants, slope, aspect and the annual mean of the potential duration of daily sunshine were recorded in three plots of 1 m² which were randomly placed in the predominant vegetation structures. Sunshine duration was recorded using a horizonscope (Tonne 1954). Slope and aspect were measured using a compass with an inclinometer. Together with the latitude of the study area (51.5°N), slope and aspect served to calculate the heat-load index of the plots (using equation 3 on p. 605 in McCune and Keon 2002). In statistical analyses, the mean values of the three plots were used. In the field, we noted the dominant vegetation type [nutrient-poor (calcareous or siliceous) or mesic grassland] of the patches and whether they were managed (grazed or mown) or abandoned. The altitude (m a.s.l.) of the patches was derived from topographic maps. Characteristics of the local climate of each patch (mean annual temperature, mean number of frost days per year and mean annual precipitation) were derived from 1-km² grid datasets of Germany's National Meteorological Service, which contain 30-year (1961–1990) mean values. The area of the patches and their distance to neighbouring populations of *E. medusa* were determined on the basis of aerial photographs using ESRI ArcGIS 10.0.

Microclimatic measurements

As the patch occupancy analysis revealed the accumulation of litter as a key factor for the presence of *E. medusa*, we investigated the potential role of the litter layer as a microclimatic buffer (Möllenbeck et al. 2009; Weking et al. 2013) for diapausing larvae during the winter 2012/2013. Pairs of temperature data loggers (Maxim iButton®) were placed in 15 habitat patches with populations of *E. medusa*. In each case, one of the loggers was placed within the litter layer and the other one, above it. The data loggers measured the air temperature hourly with an accuracy of 0.5 °C for 78 days from 26 November 2012 until 11 February 2013. To prevent the logger above the litter layer from being affected by direct sunlight—which would have led to

unreasonably high temperature recordings—a white plastic lid was installed 3 cm above it.

Data analysis

Significance tests

For metric parameters, the habitat characteristics of occupied, unoccupied and extinct patches were compared by ANOVA if the data were normally distributed (Shapiro–Wilk test) with equal variances (Levene test), otherwise by Kruskal–Wallis H tests. We used Dunnett’s and Wilcoxon rank-sum tests as post hoc procedures to carry out planned comparisons (occupied patches vs. unoccupied and extinct patches). Concerning the categorical variables land-use and vegetation type, differences between groups of patches were analysed by Fisher’s exact test. As the shares of grazed and mown patches were highly uneven (20 vs. 4, respectively), we pooled mown and grazed patches into the category “managed grassland” and compared them with abandoned ones. Similarly, we pooled 13 calcareous and six siliceous grasslands in the category “nutrient-poor grassland” and compared them with mesic grasslands.

In the analysis of the microclimatic measurements, differences in the means and the standard deviations of the temperature recordings within and above the litter layer were tested using paired t or Wilcoxon signed rank tests. Periods with a snow cover of 5–20 cm (19 days) and periods without snow (59 days) were analysed separately. Snow-cover data came from a weather station of Germany’s National Meteorological Service in Brilon–Thülen (0.8 km north of the north-western boundary of the study area at 457 m a.s.l.).

Connectivity index

To assess the isolation of the habitat patches, we used the connectivity index proposed by Hanski (1999), with the equation:

$$CI_i = \sum_{j \neq i} \exp(-\alpha \times d_{ij}) \times A_j^b$$

where CI_i denotes the connectivity of patch i , the parameter α is a measure of the dispersal ability (1/average migration distance in km), d_{ij} is the edge-to-edge distance (in km) from all other occupied patches to patch i , A_j is the size (in m^2) of neighbouring occupied patches, and b is a parameter that scales the size of the surrounding habitat patches; this was set to 0.5 according to the assumptions of Moilanen and Nieminen (2002), who suggested that the ratio of patch edge to patch area decreases with $A^{0.5}$ when patch area increases.

As there is no reliable information concerning the average migration distance of *E. medusa*, we empirically searched for the value of α at which the fit (measured as McFadden’s Pseudo R^2) of a simple logistic regression model with presence/absence as the response and habitat connectivity as the explanatory variable, was best. The model fit was best when an average migration distance of 0.8 km was assumed. Consequently, we set $\alpha = 1.25$.

For the extinct patches outside of the exhaustively surveyed Upper Diemel Valley, we were not able to calculate precise connectivity values, as the surroundings of these patches were surveyed only within a 2-km radius. To estimate approximate connectivity values for these patches, we assumed that one neighbouring population of *E. medusa* inhabits an average-sized habitat patch just on the border of the surveyed area (i.e. at a distance of 2 km from the extinct patch). Considering the absence of *E. medusa* from the Middle and Lower Diemel Valley documented by Fartmann (2004), this assumption is very optimistic and thus, most probably over-estimates the connectivity of the extinct patches.

Habitat models

For a more detailed analysis of the habitat characteristics of occupied, unoccupied and extinct patches, we fitted two different sets of binomial Generalised Linear Models (GLMs), both of them containing the presence/absence of the species as the response variable and a logit link function. The first set of GLMs analysed the association of environmental parameters with the patch occupancy (occupied/unoccupied) of *E. medusa* within the current range of the species in the Diemel Valley (Table 3). The second set of GLMs contrasted the occupied patches with the extinct patches (Table 4). The modelling procedure described hereafter was identical in both sets of GLMs.

To avoid overfitting, we fitted three different models, each containing a different set of environmental factors (vegetation, climate and landscape characteristics; GLMs 1–3 in Tables 3, 4) (cf. Heikkinen et al. 2005). Land-use and altitude, which were highly inter-correlated with vegetation and climate variables, respectively, were not used in the habitat models. All explanatory variables were checked for inter-correlations using Spearman’s correlation coefficient before being entered into the models. Principal components were calculated and entered into the models for variables with correlation coefficients >0.71 . For the moss and litter layer, however, we multiplied height by cover and thus, in both cases, obtained a single variable that indicates the volume of moss/litter present in a habitat patch. If graphical inspection of the raw data suggested unimodal rather than linear relationships between the presence of the species and environmental variables, the

centred and squared values of the variables were entered into the full model in addition to the untransformed ones.

In each GLM, non-significant predictors were excluded from the final model by backward elimination based on likelihood ratio tests (type III tests). Only explanatory variables significant at the 5 % level were retained in the final models. The significant variables from GLMs 1–3 were then entered together in a model and a hierarchical variance partitioning (Chevan and Sutherland 1991) was carried out to determine the magnitude of their independent and joint effects. This method allows the identification of predictors whose independent correlation with the response variable is strong, in contrast to predictors that have little independent effect, but have a high correlation with the response resulting from joint correlation with at least one of the other predictors.

As we aimed to find the minimum adequate model to predict the occurrence of *E. medusa*, a backward elimination of non-significant predictors was again carried out for the synthesis model in the first set of GLMs (GLM 4 in Table 3).

As model performance criteria, we used McFadden's Pseudo R^2 , which can be interpreted as a goodness-of-fit measure (Menard 2000) and the area under the curve (AUC) of an ROC plot (Fielding and Bell 1997), which is a threshold-independent measure of the overall discriminative ability of logistic regression models. According to Hosmer and Lemeshow (2000), models with AUC values >0.7 are acceptable, >0.8 are excellent and >0.9 are outstanding.

When assessing the performance of the GLMs in terms of AUC values, we used the approach of internal validation via bootstrapping, proposed by Schröder et al. (2009). We generated 2,000 bootstrap samples, which served as training data and re-fitted our final models to each of them. Each time, the model was then applied to the original dataset (which thus functioned as test data). We calculated the AUC value for both the training and the test dataset and the difference between both values. This difference indicates the over-optimism of the “naive” assessment of the model performance on the training data. Finally, we calculated the mean over-optimism over all replicates and subtracted it from the naive AUC value of the final model. Thereby, we obtained a realistic estimate of the model's ability to discriminate locations where *E. medusa* is present, from locations where it is absent.

To compare observations with model predictions for individual patches, we converted the occurrence probabilities predicted by the GLMs into presence-absence data. The optimal threshold above which a given probability was classified as a presence was determined by maximising Cohen's Kappa (Cohen 1960), a widely used measure for the proportion of correctly classified cases after accounting

for chance effects (Freeman and Moisen 2008). As measures of classification success, we used Cohen's Kappa and the percentage of correctly classified patches. Hence, the Kappa statistic was used both as a criterion for threshold level selection and as a performance measure (c.f. Segurado and Araujo 2004; Settele et al. 2008). According to Landis and Koch (1977), values of kappa >0.6 indicate substantial agreement, and values >0.8 suggest almost perfect agreement, between observations and model predictions.

All statistical analyses were conducted with R 2.14.1 (R Development Core Team 2011) and the packages *pgirmess* (Giraudeau 2013) and *pROC* (Robin et al. 2011), except for the Kappa-maximising procedure, which was run in the Delphi program ROC_AUC (Schröder 2006).

Results

Patch occupancy

Altogether, we found 32 populations of *E. medusa*, all of which were located in the Upper Diemel Valley, with a clear concentration in the westernmost part of the study area (Fig. 1a). Seven currently unoccupied patches from which the species was previously reported are situated in the Middle and Lower Diemel Valley, and another five in the Upper Diemel Valley. Most of the historic records date back to the 1960s, 1970s and 1980s, except for three patches in the Upper Diemel Valley, where *E. medusa* was observed for the last time in 1993, 1999 and 2010, respectively. Potentially suitable habitats where *E. medusa* has never been observed are scattered over the whole study area.

Adult habitats

Habitat patches with the presence of *E. medusa* were situated at significantly higher altitudes, received more precipitation, had a thicker litter layer, a lower cover of mosses and lichens and were better connected to neighbouring populations of *E. medusa* than both unoccupied and extinct patches (Table 1). Moreover, occupied patches were characterised by a significantly cooler local climate (mean annual temperature, mean number of frost days), a higher cover of *Festuca rubra* agg., a lower cover of *F. ovina* agg. and a higher total host plant cover than extinct patches.

The majority (70 %) of the occupied patches were abandoned grasslands, whereas only 45 % of the unoccupied and 42 % of the extinct patches were not used (Table 2). Concerning the vegetation type, the frequency of mesic grasslands on the one hand and nutrient-poor semi-

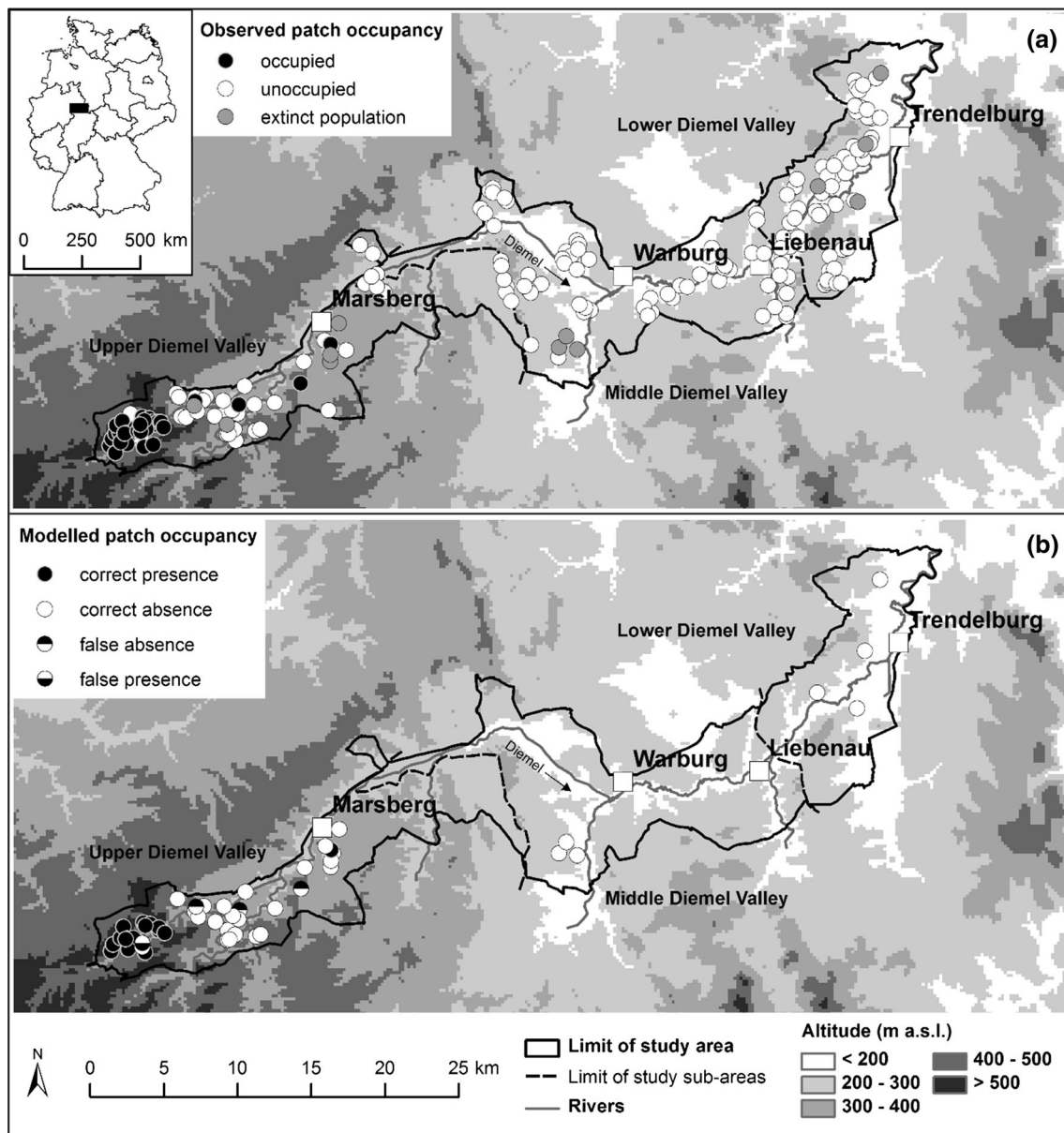


Fig. 1 Observed and modelled distribution of *E. medusa* in the Diemel Valley in Central Germany. **a** Patch occupancy in 2010; **b** modelled patch occupancy of the study sites based on the occurrence probabilities predicted by the synthesis model (GLM 4 in Table 3)

dry calcareous or siliceous grassland on the other, differed significantly among the three groups of habitat patches. Mesic grasslands accounted for 85 % of the occupied patches and 15 % were semi-dry calcareous or siliceous grasslands. Among the unoccupied and extinct patches, the proportions of mesic and semi-dry grasslands were roughly equal.

The results of the GLM analysis of occupied and unoccupied patches in the Upper Diemel Valley indicated positive correlations between the presence of *E. medusa* and the amount of litter, the total cover of bare ground (GLM 1), the heat-load index, mean annual precipitation

(GLM 2) and the connectivity of the patches with neighbouring populations (GLM 3) (Table 3). Hierarchical partitioning of these five variables showed that the amount of litter had the greatest independent contribution to the explained variance, followed by habitat connectivity (Fig. 2a). In agreement with the results of the hierarchical partitioning, only the amount of litter and habitat connectivity remained in the final version of the synthesis model (GLM 4).

The final version of the synthesis model is well calibrated (McFadden's Pseudo $R^2 = 0.45$) and has an excellent discriminative ability (AUC corrected = 0.90). This in

Table 1 Mean values \pm SD of all numerical environmental parameters in the habitat patches of *Erebria medusa* in the Diemel Valley

Parameter	Habitat patches			P (test)	Pairwise comparisons
	Occupied (N = 20)	Unoccupied (N = 20)	Extinct (N = 12)		
<i>Vegetation characteristics</i>					
Height (cm)					
Small shrubs (<0.5 m)	0.0 ± 0.0	0.8 ± 2.8	6.3 ± 10.6	*KW	n.s.
Herb layer	21.5 ± 7.8	20.5 ± 9.8	22.1 ± 14.5	n.s. ^{AV}	n.s.
Mosses/lichens	1.5 ± 1.2	2.1 ± 1.4	1.2 ± 0.7	n.s. ^{KW}	n.s.
Litter	4.1 ± 1.4	2.1 ± 1.5	2.0 ± 1.0	***KW	O > U; O > E
Cover (%) ¹					
Small shrubs (<0.5 m)	0.0 ± 0.0	0.6 ± 2.0	1.5 ± 3.4	*KW	n.s.
Herb layer	70.2 ± 13.2	63.6 ± 16.6	72.5 ± 14.4	n.s. ^{AV}	n.s.
Mosses/lichens	32.3 ± 28.9	54.0 ± 27.4	61.5 ± 23.1	*KW	O < U; O < E
Litter	76.9 ± 13.2	65.0 ± 25.6	52.7 ± 29.6	n.s. ^{KW}	n.s.
<i>Festuca rubra</i> agg.	21.5 ± 15.1	15.2 ± 11.9	4.0 ± 7.1	***KW	O > E
<i>Festuca ovina</i> agg.	1.3 ± 3.0	6.0 ± 11.2	5.3 ± 5.6	*KW	O < E
Total cover of host plants	23.9 ± 15.7	21.2 ± 13.3	10.0 ± 11.8	*KW	O > E
Total cover of bare ground	2.3 ± 3.3	1.9 ± 2.4	3.7 ± 4.2	n.s. ^{KW}	n.s.
<i>Climate characteristics</i>					
Altitude (m a.s.l.)	428.5 ± 48.8	365.9 ± 57.5	273.1 ± 59.1	***AV	O > U; O > E
Heat load index (unitless)	0.83 ± 0.05	0.79 ± 0.06	0.83 ± 0.05	*AV	n.s.
Mean potential duration of					
Daily sunshine (h)	9.0 ± 1.4	8.0 ± 2.0	9.2 ± 1.2	n.s. ^{AV}	n.s.
Mean annual temperature (°C)	7.5 ± 0.3	7.6 ± 0.3	8.1 ± 0.3	***KW	O < E
Mean no. of frost days/a	93.3 ± 5.5	91.5 ± 5.9	85.3 ± 5.3	**KW	O > E
Mean annual precipitation (mm)	909.0 ± 81.5	828.6 ± 76.7	740.5 ± 54.0	***KW	O > U; O > E
<i>Landscape characteristics</i>					
Patch area (ha)	1.4 ± 1.7	2.7 ± 5.2	2.1 ± 1.9	n.s. ^{KW}	n.s.
Connectivity (unitless)	543.8 ± 308.3	140.4 ± 229.5	27.8 ± 35.2	***KW	O > U; O > E

Differences between occupied, unoccupied and extinct patches were analysed by ANOVA (AV) or the Kruskal–Wallis test (KW). Dunnett's and Wilcoxon-rank-sum tests served as post hoc procedures to compare unoccupied and extinct patches against currently occupied patches. Significant differences between groups of patches are highlighted by bold type

n.s. Not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

¹ All potential host plant species other than *Festuca rubra* agg. and *Festuca ovina* agg. had a low abundance and occurred in <10 % of the patches and therefore were excluded from statistical analyses

line with the results of the threshold-dependent approach, which yielded a high value of the Kappa statistic (0.80) and a high correct classification rate (90 %). Moreover, the spatial pattern of predicted presences and absences matches the actual distribution of *E. medusa* in the study area (Fig. 1b).

The second set of GLMs (Table 4), which contrasted the occupied with the extinct patches, yielded similar results to those of the first set of GLMs. Again, the amount of litter, mean annual precipitation and habitat connectivity were the predictors with the strongest independent effects (Fig. 2b). In contrast to the first set of GLMs, however, the height of the herb layer was significantly related to the presence of *E. medusa*, whereas the head-load index had no influence. The negative valency of the estimate of the

centred and squared values of the height of the herb layer indicates that the occupied patches had an intermediate vegetation height, whereas some of the extinct patches had a herb layer that was either too low or too high. The model that contained only vegetation parameters correctly predicted 11 out of the 12 extinct patches as unoccupied. The models containing only climatic or landscape variables, respectively, correctly predicted the absence of *E. medusa* for all extinct patches.

Microclimatic measurements

The data-logger recordings in the *E. medusa* habitats revealed significant differences between the temperature conditions within and above the litter layer. Within the

Table 2 Absolute and relative frequencies of the categorical variables land-use and vegetation type

Parameter	Habitat patches						<i>P</i> (test)
	Occupied (N = 20)		Unoccupied (N = 20)		Extinct (N = 12)		
	N	%	N	%	N	%	
Land-use							n.s.
Managed grassland	6	30.0	11	55.0	7	58.3	
Abandoned grassland	14	70.0	9	45.0	5	41.7	
Vegetation type							<0.05
Nutrient-poor grassland	3	15.0	9	45.0	7	58.3	
Mesic grassland	17	85.0	11	55.0	5	41.7	

Differences between the three groups of patches were analysed with Fisher's exact test

litter layer, the mean air temperature was significantly higher and less variable than directly above it, regardless of whether the ground was covered by snow or not (Fig. 3). On average, the mean temperature inside the litter layer was 0.95 °C higher than outside during periods with a snow cover and 0.93 °C higher during periods without snow cover. The mean differences in the standard deviations of the temperature recordings were 0.28 and 0.83 °C in periods with and without a snow cover, respectively.

Discussion

Drivers of the current distribution

Relative importance of different environmental factors

The spatial distribution of butterfly populations in cultivated landscapes is mainly determined by three factors: habitat quality within patches, patch area and patch isolation (Dennis and Eales 1997; Anthes et al. 2003; Eichel and Fartmann 2008). The relative importance of these factors varies from species to species. In our study, the occurrence of *E. medusa* within its current range in the Diemel Valley was explained well by the combined effect of habitat quality and isolation, whereas patch area was not important. Habitat quality primarily depended on the amount of litter, as the host plants were sufficiently abundant in all studied patches. The significant but weak correlations between the presence of the species and the amount of bare ground and the heat-load index, respectively, indicate that the vegetation cover should not be too dense and that *E. medusa* prefers south-facing slopes, which provide a warmer microclimate than flat or even north-facing slopes. The

second most important factor, habitat connectivity (i.e. the degree of isolation from neighbouring populations), showed a high joint contribution to the explained variance. This was most probably caused by its relatively strong inter-correlation with the mean annual precipitation ($r_s = 0.66$, $P < 0.001$), which also showed high joint effects. Thus, it was not possible to completely disentangle the effects of habitat connectivity and the precipitation regime.

Habitat quality

The importance of large amounts of litter for the presence of *E. medusa* can be interpreted in two different, but not mutually exclusive ways: firstly, as a mere result of very low or absent land-use, and secondly, in terms of an essential habitat element that is required by the species at one or more stages of its life cycle. The first interpretation would mean that there is a direct deleterious effect of grazing or mowing, most likely by damaging the eggs and young larvae. Because the females of *E. medusa* mostly attach their eggs between 7 and 14 cm above ground to the exterior parts of the host plants (Fartmann 2004; pers. obs.) this appears plausible, but remains to be tested experimentally. Dover et al. (2010) assume that even adult butterflies are often directly killed by mowing and hay harvesting if these activities are carried out early in the morning when the ambient temperature is still too low to allow escape by flight. On the other hand, the results of the microclimatic measurements show that the litter layer acts as a microclimatic buffer during the winter by significantly reducing temperature fluctuations. Overwintering larvae might benefit from this, in terms of energy consumption. Due to the exponential relationship between the ambient temperature and the metabolic rate of ectothermic animals, constant temperatures are energetically less demanding than strongly fluctuating regimes with the same mean temperature (Ruel and Ayres 1999). Common garden experiments with larvae of the *Propertius* Duskywing (*Erynnis propertius*), indeed demonstrated that a thermally variable environment is more energy-demanding than a stable one (Williams et al. 2012).

Even in periods with a thin snow cover, the buffering effect of the litter remains significant. Clearly, much thicker snow covers than those that occurred during the microclimatic measurements are necessary to achieve an equally strong buffering effect as that of thick layers of litter. Hence, the dependency of *E. medusa* on litter accumulation should be less pronounced in regions with thick and long-lasting snow covers—an hypothesis that remains to be tested in field studies that encompass long climatic or altitudinal gradients.

Table 3 Results of the generalised linear model analyses on the association of several environmental parameters (metric predictor variables) with the patch occupancy of *Erebia medusa* (binary response variable) within the current range of the species in the Diemel Valley

GLM	Variables	Estimate	SE	P	R ² _{MF}	AUC _{naive}	CI(AUC _{naive})	AUC _{cor}	Cut-off	Kappa	CCR (%)
1	Vegetation characteristics				0.29	0.86	0.73–0.96	0.83	0.3125	0.65	82.5
	Intercept	−3.413	1.149								
	Amount of litter ²	0.011	0.003	<0.001							
	Total cover of bare ground	0.304	0.168	<0.05							
	Not significant: small shrubs (<0.5 m) ¹ , height of herb layer, height of herb layer (centred and squared values), cover of herb layer, amount of mosses/lichens ² , total cover of host plants ³										
2	Climate characteristics				0.26	0.87	0.74–0.97	0.85	0.595	0.60	80.0
	Intercept	−27.096	10.486								
	Heat-load index	18.038	9.395	<0.05							
	Mean annual precipitation	0.014	0.005	<0.01							
	Not significant: mean potential duration of daily sunshine, temperature factor ⁴										
3	Landscape characteristics				0.29	0.77	0.58–0.92	0.77	0.4175	0.65	82.5
	Intercept	−1.460	0.555								
	Connectivity	0.004	0.001	<0.001							
	Not significant: patch area										
4	Synthesis model				0.45	0.92	0.81–0.99	0.90	0.67	0.80	90.0
	Intercept	−3.794	1.240								
	Amount of litter ²	0.009	0.003	<0.01							
	Connectivity	0.005	0.001	<0.001							
	Not significant: total cover of bare ground, heat load index, mean annual precipitation										

Sample size: 20 occupied and 20 unoccupied habitat patches. Non-significant predictors were excluded from the final models by backward elimination (P value of likelihood ratio test >0.05). R^2_{MF} = McFadden's Pseudo R^2 ; AUC_{naive} = The area under the curve of a receiver operating characteristics plot of the original dataset; $CI(AUC_{naive})$ = range of the 95 % confidence interval of the naive AUC values (calculated on 2,000 bootstrap replicates with the bootstrap percentile method); AUC_{cor} = AUC values corrected for over-optimism by internal model validation via bootstrapping; cut-off = the cut-off value that was used to classify the predicted occurrence probabilities into predicted presences and absences; Kappa = Cohen's Kappa statistic; CCR = correct classification rate

¹ Synthetic variable (principal component of height and cover values)

² Synthetic variable (height \times cover)

³ Synthetic variable (sum of the cover values of all potential host plants that were present in a patch)

⁴ Synthetic variable (principal component of mean annual temperature and mean number of frost days per year). High values of the temperature factor indicate high temperatures and few frost days

Consistent with the assumption that the litter layer plays an important role as a microclimatic buffer, Hermann (pers. comm.) reports that populations of *E. medusa* in litter-poor, low-intensively used pastures or meadows mown once a year have been declining for approximately the last 10 years in the Heckengäu region (federal state of Baden-Wuerttemberg, South-west Germany, 450–500 m a.s.l.). In contrast, populations that inhabit litter-rich abandoned grasslands in the same region, are relatively stable.

Litter accumulation is also a striking characteristic of the habitats and oviposition sites of *Erebia aethiops*, a sibling species of *E. medusa* that inhabits open woodlands (Leopold 2006; Slamova et al. 2013), and some other satyrine species such as *Coenonympha hero* (Bräu and Dolek 2013) and *C. oedippus* (Bräu et al. 2010; Örvössy et al. 2013).

Land-use and vegetation type

Assessing the direct effects of land-use and vegetation type is difficult, as these variables are strongly inter-correlated with the vegetation structure. Moreover, differences in the grazing and mowing intensities of the used patches exist, but it was not possible to reliably assess their exact intensities. Therefore, we consider that the amount of litter (whose role was discussed above) reflects the land-use intensity more precisely than the rough distinction between grazing/mowing versus abandonment. This explains why the proportions of used and abandoned grasslands did not differ significantly between occupied, unoccupied and extinct patches, although the patch dynamics of *E. medusa* in the Upper Diemel Valley clearly hint at a direct effect of land-use on *E. medusa*'s occurrence: at an abandoned mesic grassland patch where *E. medusa* had been present

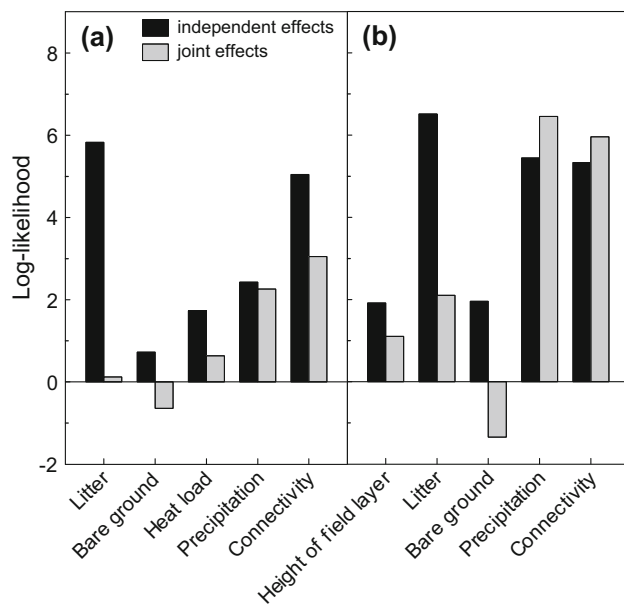


Fig. 2 Results of hierarchical partitioning of the variables that were identified as significant predictors of the occurrence of *E. medusa* by the GLM analyses of **a** occupied versus unoccupied patches within the current range of *E. medusa* (c.f. GLMs 1–3 in Table 3) and **b** occupied versus extinct patches (c.f. GLMs 1–3 in Table 4). The distribution of independent effects indicates the relative contribution of each predictor to the total amount of explained variance in the model (the sum of the independent effects equals the log-likelihood of the intercept-only model minus the log-likelihood of the full model). The joint effects indicate the degree to which each predictor is inter-correlated with at least one of the other predictors. Negative joint variance indicates that this predictor acts as a suppressor of other predictors (Chevan and Sutherland 1991)

for the last 10 years (pers. obs.), no individuals were observed during repeated visits in 2011 after cattle grazing had been re-introduced during the species' flight period in 2010. The historic records from two calcareous grasslands south of the city of Marsberg date back to a time when these sites were not grazed (W. Schubert, pers. comm.). After re-introduction of grazing, *E. medusa* disappeared from the surroundings of Marsberg at the end of the 1990s (Fartmann 2004). However, in 2007, a small population had newly colonised a mesic grassland after grazing had ceased there in 2005 (pers. obs.). It cannot be deduced from our dataset whether the significant effect of vegetation type suggests a preference for more humid conditions, or whether this is simply due to the inter-correlation with the vegetation structure (e.g. the amounts of litter were higher in mesic than in semi-dry grasslands).

Patch connectivity

The strong positive correlation between habitat connectivity and the occurrence probability of *E. medusa*, which is probably at least partly a direct effect of isolation, suggests

that *E. medusa* has a low capacity to colonise remote patches. This interpretation is supported by the fact that *E. medusa* is assumed to be a relatively sedentary species, whose dispersal is constrained especially by forests (Schmitt et al. 2000). In addition, the importance of a dense network of neighbouring populations might indicate that isolated populations of *E. medusa* cannot persist in the long term, but we have no direct evidence for this. In general, isolated butterfly populations often suffer from several adverse phenomena (Hanski 1998; Thomas 2000; Schtickzelle and Baguette 2009): demographic stochasticity (which has a real impact only in very small populations), genetic stochasticity (which leads to decreased fitness and/or adaptive potential due to inbreeding effects and random genetic drift), environmental stochasticity (direct deleterious effects of occasional variation in the environmental conditions such as particularly bad weather conditions) and migrating individuals “getting lost” when the surroundings are unsuitable for successful reproduction. The latter point is especially problematic for species with intermediate mobility, which leave their natal habitats more readily than species with low mobility, but at the same time fail to reach neighbouring patches more often than highly mobile ones (Thomas 2000). According to our field observations in two successive years, we consider *E. medusa* to be such a species with intermediate mobility, as we occasionally observed migrating individuals at 0.1–2.0 km (median = 1.0 km) from the next occupied patch, but not in large numbers (18 individuals in total).

Local climate

Finally, our modelling results suggest that the local climate, especially annual precipitation, might be one of the drivers of the current distribution of *E. medusa* in the Diemel Valley. At the European scale, *E. medusa*'s present distribution can be explained well by climatic variables, and modelling the species' future distribution under various climatic scenarios revealed a high climate-change risk (Settele et al. 2008). An experimental study on the effects of winter temperatures on *E. medusa* indeed showed that higher overwintering temperatures increase larval mortality and potentially decrease adult fitness (Stuhldreher et al. 2014). The climate-niche model for *E. medusa* established by Settele et al. (2008) suggests that the species' occurrence is related to the soil water content of the upper soil horizon, which the authors interpret as “a realistic measure of water availability and near surface microclimate” (p. 21), and to accumulated growing degree days until August, which is described as being “highly representative for general temperature gradients across Europe”. High values of the soil water content and low-to-medium values of

Table 4 Results of the generalised linear model analyses on the association of several environmental parameters (metric predictor variables) with the patch occupancy of *Erebia medusa* (binary response variable) in occupied (N = 20) and extinct (N = 12) patches in the Diemel Valley

GLM	Variables	Estimate	SE	P	R^2_{MF}	AUC _{naive}	CI(AUC _{naive})	AUC _{cor}	Cut-off	Kappa	CCR (%)
1	Vegetation characteristics				0.63	0.95	0.86–1.00	0.92	0.6325	0.80	90.6
	Intercept	−5.658	2.850								
	Height of herb layer (centred and squared values)	−0.021	0.015	<0.01							
	Amount of litter ²	0.029	0.012	<0.001							
	Total cover of bare ground	0.492	0.339	<0.05							
	Not significant: small shrubs (<0.5 m) ¹ , height of herb layer, cover of herb layer, amount of mosses/lichens ² , total cover of host plants ³										
2	Climate characteristics				0.56	0.95	0.85–1.0	0.95	0.705	0.87	93.8
	Intercept	22.714	8.057								
	Mean annual precipitation	0.028	0.010	<0.001							
	Not significant: heat load index, mean potential duration of daily sunshine, temperature factor ⁴										
3	Landscape characteristics				0.53	0.85	0.69–0.98	0.85	0.7	0.75	87.5
	Intercept	−1.297	0.618								
	Connectivity	0.010	0.005	<0.001							
	Not significant: patch area										

The presence samples used in this analysis are the same as in Table 3. Non-significant predictors were excluded from the final models by backward elimination (P value of likelihood ratio test >0.05). R^2_{MF} = McFadden's Pseudo R^2 ; AUC_{naive} = the area under the curve of a receiver operating characteristics plot of the original dataset; $CI(AUC_{naive})$ = range of the 95 % confidence interval of the naive AUC values (calculated on 2,000 bootstrap replicates with the bootstrap percentile method); AUC_{cor} = AUC values corrected for over-optimism by internal model validation via bootstrapping; cut-off = the cut-off value that was used to classify the predicted occurrence probabilities into predicted presences and absences; Kappa = Cohen's Kappa statistic; CCR = correct classification rate

¹ Synthetic variable (principal component of height and cover values)

² Synthetic variable (height × cover)

³ Synthetic variable (sum of the cover values of all potential host plants that were present in a patch)

⁴ Synthetic variable (principal component of mean annual temperature and mean number of frost days per year). High values of the temperature factor indicate high temperatures and few frost days

growing degree days appear to favour the presence of *E. medusa* at the European scale. Similarly, occupied patches in the Diemel generally receive significantly more precipitation than unoccupied patches. The beneficial effects of higher precipitation might consist of a lower desiccation risk of the immature stages and a better insulation of the overwintering larvae due to thicker snow cover.

Reasons for the local extinctions

Currently, *E. medusa* is restricted to the mountainous westernmost part of the Diemel Valley. Historic records from the literature indicate that in the second half of the twentieth century, the species was also present in the Middle and Lower Diemel Valley. Thus, there has been a substantial contraction of the range of *E. medusa* within the study area and a slight upslope shift of its low-elevation range boundary. Compared to the large number of potentially suitable habitats in the Middle and Lower Diemel Valley, however, the number of historic records is low,

indicating that *E. medusa* was never common in the lowlands of the Diemel Valley.

The relative importance of deteriorating habitat quality, increasing isolation and climate change for the extinction of the lowland populations of *E. medusa* in the Diemel Valley cannot be unambiguously determined. This is because the habitat patches where the species has become extinct differ greatly from the patches that are still occupied, with respect to vegetation structure, connectivity and local climate. Nevertheless, we suggest that unsuitable vegetation structure (the amount of litter in particular) is one of the reasons for the current absence of *E. medusa* from the formerly occupied patches. Litter is the predictor with the highest independent effect on patch occupancy within the current range of the species (Fig. 2a), as well as when the currently occupied patches are compared to the extinct patches (Fig. 2b). Increasing isolation and/or climatic factors, however, probably also contributed to the observed extinctions, but distinguishing the effects of these two predictors is impossible as they are inter-correlated and consequently, both show high joint contributions to the

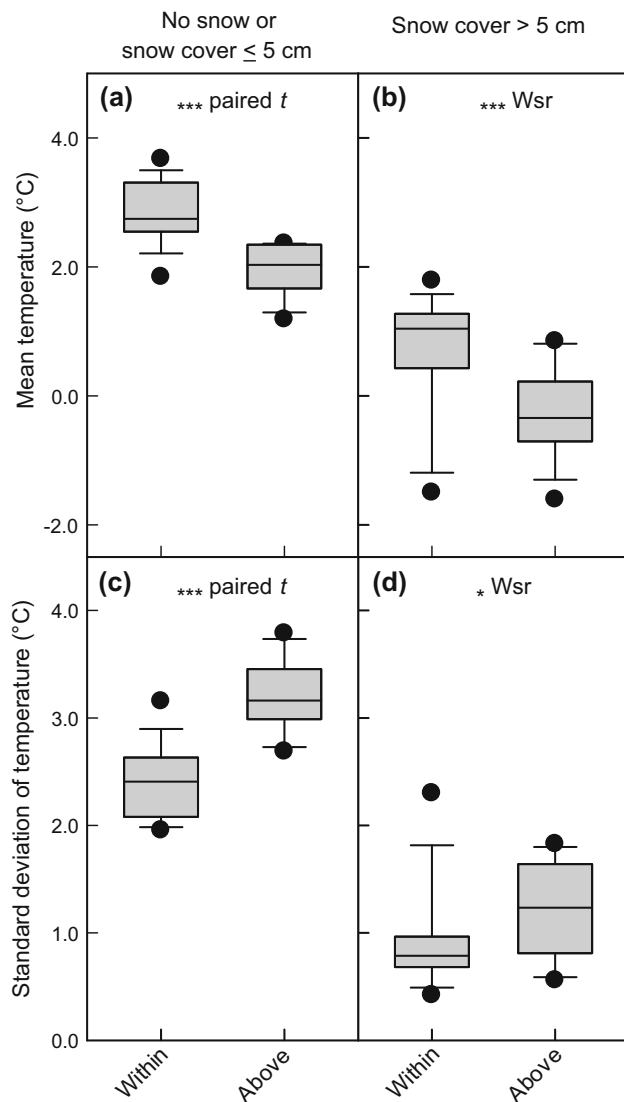


Fig. 3 Air temperature and its variability within and above the litter layer in habitats of *E. medusa* during the winter months, measured by 15 pairs of data loggers in 15 different habitat patches. Differences were analysed using paired *t* or Wilcoxon signed rank tests. Within the litter layer, the mean temperature is significantly higher than outside during periods with little or no snow cover (**a** $t = 9.055$, $P < 0.001$), as well as during periods with more than 5 cm of snow (**b** $Z = -3.067$, $P < 0.001$). The litter layer significantly reduces temperature fluctuations regardless of whether there is a snow cover (**d** $Z = 2.272$, $P < 0.05$) or not (**c** $t = -7.434$, $P < 0.001$)

explained variance (Fig. 2b). Possibly, the climatic conditions in the relatively warm and dry lowlands of the Diemel Valley were already marginal when *E. medusa* was still present there. The climatic changes that have occurred in recent decades might have rendered these locations even less suitable. Because *E. medusa* has always been quite rare in the Middle and Lower Diemel Valley, isolation might also have contributed to the species' decline in these regions, via the mechanisms discussed above.

Implications for conservation

The habitat requirements of many species cannot be defined in terms of land-use types alone (Van Dyck 2012). Instead, a realistic definition of what comprises a suitable habitat must take into account crucial species-specific resources, conditions and movements and thus focus on functional rather than structural habitats (Vanreusel and Van Dyck 2007; Turlure et al. 2010; Van Dyck 2012). Our study species is a good example of the usefulness of this resource-based (or functional) habitat concept proposed by Dennis et al. (2003), as the occurrence of *E. medusa* is closely related to the presence of a non-consumable resource (litter) and to the configuration of the landscape (dense network of local populations). Moreover, the case of *E. medusa* shows that conservation management schemes should be based on a careful evaluation of the components of the functional habitat of the target species. Otherwise, even well-intended measures can have undesired outcomes, as demonstrated for other target butterfly species (Johst et al. 2006; Konvicka et al. 2008; Goffart et al. 2010). For *E. medusa*, the re-introduction of grazing or mowing in abandoned grasslands has the potential to drive entire populations to extinction.

The outcome of our study on the habitat preferences and patch occupancy of *E. medusa* in the Diemel Valley indicates that conservation measures to promote this species should consider both the habitat and the landscape level. Maintaining a suitable vegetation structure in the species' habitats, as well as avoiding intensive grazing and frequent mowing are most important. In the short-to-medium term, the complete absence of any grazing or mowing is most favourable, as this eliminates the risk of reducing the litter layer, which appears to be an essential habitat element, and of damaging the immature stages. However, refraining from any kind of land-use activities will in the long term lead to a grass-dominated vegetation with a low plant diversity and thus cause a management dilemma between the requirements of *E. medusa* and those of plant and other invertebrate species. Moreover, even in very nutrient-poor grasslands, succession will continue slowly, and eventually render sites unsuitable for *E. medusa*, due to the dominance of tall grasses and forbs and shrub encroachment. Solutions to this dilemma might include rotational grazing or mowing, if sufficiently large parts of the habitats are excluded every year. Similar recommendations have been provided for other management-sensitive butterfly and moth species (e.g. Balmer and Erhardt 2000; Waring 2001; Goffart et al. 2010; Slamova et al. 2013).

Based on our observations in the Diemel Valley, we recommend that any management measures in the habitats of *E. medusa* should be scheduled as late in the year as possible. For example, one of the study sites here is

mulched every year in August, and yet *E. medusa* had been present there for the last 10 years (pers. obs.). Consistent with this, Schmitt (1993) recorded *E. medusa* in some meadows in the Saarland (South-west Germany) that were mown in mid-July or later, although in much lower numbers than in abandoned grasslands.

On the landscape level, maintaining a network of well-connected habitat patches appears to be crucial. In our study, patch area was not a limiting factor for the occurrence of *E. medusa*. Therefore, we conclude that even small patches can contribute to providing an overall habitat area that is large enough to sustain a regional metapopulation if the patches are situated close to each other.

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