Insect Conservation and Diversity

Insect Conservation and Diversity (2020) doi: 10.1111/icad.12437

Do single Pollard transects represent the local butterfly community? A case study from the Spitzberg near Tübingen, Germany

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Abstract. 1. Information on butterfly population size and distribution is a key tool for verifying species conservation status. Such data are rare and tend to be available on local rather than on regional scales. One important data source are monitoring schemes that have been implemented in several countries, e.g. the German butterfly monitoring scheme (TMD).

2. The main goal of the present study was to examine how representative single transects of the TMD are able to identify local or regional diversity patterns of butterflies. Total butterfly population size, density of individuals and species diversity pattern of a 624 ha large study area (Spitzberg) were recorded by intensive surveys.

3. Almost all butterfly species present at the Spitzberg were recorded by the TMD transects. For 22 species, local estimates based on records of the TMD transects ranged between 0 and 10% of the regional population size. Accordingly, the study demonstrates that population size changes of most of the species can potentially be identified.

4. Increasing cover of forest has a negative effect on species diversity and butterfly density, while the cover of nutrient-poor grassland and the diversity of biotope types has a positive impact on butterfly density and species diversity. Solar insolation has a positive effect on butterfly density.

5. Based on the results of the species–habitat relationships, the location of TMD transects could be optimised by aiming to cover the complete butterfly diversity of the study area. Additionally, monitoring of some of the species might be improved if winter surveys of eggs and larvae were implemented in the monitoring scheme.

Key words. Burnet moth, butterfly density, butterfly population, diversity of biotope types, solar insolation, species distribution, species diversity, Spitzberg, winter surveys.

Introduction

Data on butterfly population size and distribution provide important information for ecological studies to verify their conservation status and to develop conservation strategies to halt population declines. Although data on butterflies are readily available, surveys on butterflies are very time consuming when information on the whole butterfly community of larger study areas is needed. In many European countries, butterfly monitoring schemes (van Swaay *et al*., 2008) are the sole source of information on butterfly communities and their local population size. The advantages of these schemes are that they provide information on the number of individuals of all species during a complete season and that these data are typically collected for several years or even several decades. Another advantage is that year-to-year changes, so typical for insect populations (Roy *et al*., 2001; Mason *et al*., 2018), can be recorded by such long-term monitoring schemes.

The disadvantage is that monitoring data are restricted to a narrow transect, often 5 m in width and usually a few 100 m long. Extrapolating information obtained from such a transect to larger areas may be possible in homogeneous landscapes but is certainly limited in landscapes characterised by small-scale biotope changes. In such a case, trends detected may only be

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representative for the areas sampled, while their extrapolation to the whole region may produce biased results. Furthermore, data sets collected from such relatively short transects are usually too small to be used for species habitat analyses or to estimate factors controlling species presence or population size. Therefore, large-scale studies are needed. Such an approach was exemplarily conducted at the Spitzberg close to Tübingen, Germany, a study area of 623 ha in size. Within this area, two fixed transects (BW-7419-01 and BW-7419-02), 450 m and 600 m in size, were established on which butterflies and burnet moths have been recorded since 2015 and 2017, respectively. Both transects are part of the German butterfly monitoring scheme, referred to as TMD for "Tagfalter-Monitoring Deutschland" below (Kühn *et al*., 2008; Kühn *et al*., 2014). As is the case in most European countries, observers are free to choose the location of the transects (van Swaay *et al*., 2008). Hence, the transects do not record all habitats of a region and they are not chosen randomly or in a stratified random manner, as has been done, e.g. by the German common bird census (Sudfeldt *et al*., 2012) or the wider countryside butterfly survey (Brereton *et al*., 2011). The advantage of such schemes, where the location has been chosen at the discretion of the observers, is that they yield more data on rare butterflies, as they are typically located in areas of good quality habitat (van Swaay *et al*., 2008; Roy *et al*., 2015).

The main aim of the current study was to examine how representative single transects of TMD are able to identify regional diversity patterns of butterflies and to find out whether they have the potential to identify diversity changes. Here, diversity was used throughout to refer to species richness, i.e. the number of species observed. The results of the two transects were compared with results of systematic counts of butterflies and burnet moths within the whole Spitzberg area (624 ha). The aim of the study was to assess which species are not recorded by the monitoring scheme and to identify those species whose population sizes cannot be represented properly by the TMD. While monitoring schemes are aimed at identifying population changes, they hardly provide the data needed to analyse the causal relationships for such changes on a local or regional scale. Therefore, the aim of this study was also to identify factors controlling species diversity, the number of Red List species and the butterfly density (i.e. density of butterflies and burnet moths).

Material and methods

Study site

The Spitzberg in Baden-Württemberg (SW Germany) is located between the city of Tübingen in the east and Rottenburg-Wurmlingen in the west, an area of about 6 × 2 km (Gottschalk, 2019a). The highest point is the Kapellenberg near Wurmlingen with a height of 475 m. The Spitzberg consists of Keuper rocks, mainly gypsum-bearing shales, colourful marls and pebble sandstone and originates from the Triassic era about 149 million years ago. On the southern and western slopes of this old cultivated landscape, the forest has been almost completely cleared and replaced by a large number of terraces with dry stone-walls and nutrient-poor grassland and orchards (Table 1). The largest part is covered by woods, including the heights and the northerly slopes. The forest is characterised mainly by Scots pine (*Picea sylvestris*), oak (*Quercus* spec.) and beech (*Fagus sylvatica*). A total of 103 butterfly and burnet moth species have been reported from the Spitzberg since 1850, of which 69 species were still present in 2016 (Gottschalk & Komrowski, 2017). To analyse species–habitat relationships, the study area was divided into 128 raster cells 250 × 250 m in size (Fig. 1).

Species survey

Butterflies and burnet moths were counted using standardised line-transect counts (Pollard, 1991) in 2018. To ensure an equally distributed survey effort within the whole study area, the area was divided into 37 rasters 500 × 500 m maximum in size. Butterflies were recorded along transects of 5 m width covering all 37 raster cells. One complete survey of the study area was conducted per month between March and October 2018. Most species were identified directly in the field by observation, a few species by catching and using a field book (Settele *et al*., 2015) or by taking photographs (and determining the species based on these photographs afterwards). The sibling species *Leptidea sinapis* and *L. juvernica* and *Colias hyale* and *C. alfacariensis* were treated as one species, as they are virtually indistinguishable and can only be distinguished by analysing their caterpillars (*Colias*) or by morphometric analysis of their genitalia (*Leptidea*). All butterfly observations were logged using a GPS device (Garmin Oregon 700) to record the exact location of each observation. In addition, two transects of 400 and 650 m length were located in the south-west

Table 1. Percent cover of 19 biotope types within the 624 ha large study area and within a 2.5 m buffer around the two line-transects of the TMD.

	Biotope types	Study area (%)	TMD (%)
1	Arable fields	4.0	4.3
2	Lucerne	0.3	—
3	Boundary ridge	0.03	—
4	Wetland	0.01	—
5	Grassland	9.8	24.9
6	Nutrient-poor grassland	2.1	36.0
7	Vineyard	1.8	1.5
8	Orchards	11.9	1.3
9	Single tree, bush	0.2	1.8
10	Tree, bush	12.3	7.2
11	Deciduous forest	26.4	11.9
12	Deciduous forest along forest tracks	5.3	—
13	Mixed forest	14.7	0.4
14	Mixed forest along forest tracks	2.0	—
15	Coniferous forest	2.3	—
16	Coniferous forest along forest tracks	0.4	—
17	Forest edge	1.1	8.1
18	Roads	1.8	2.6
19	Urban area	3.3	0.04

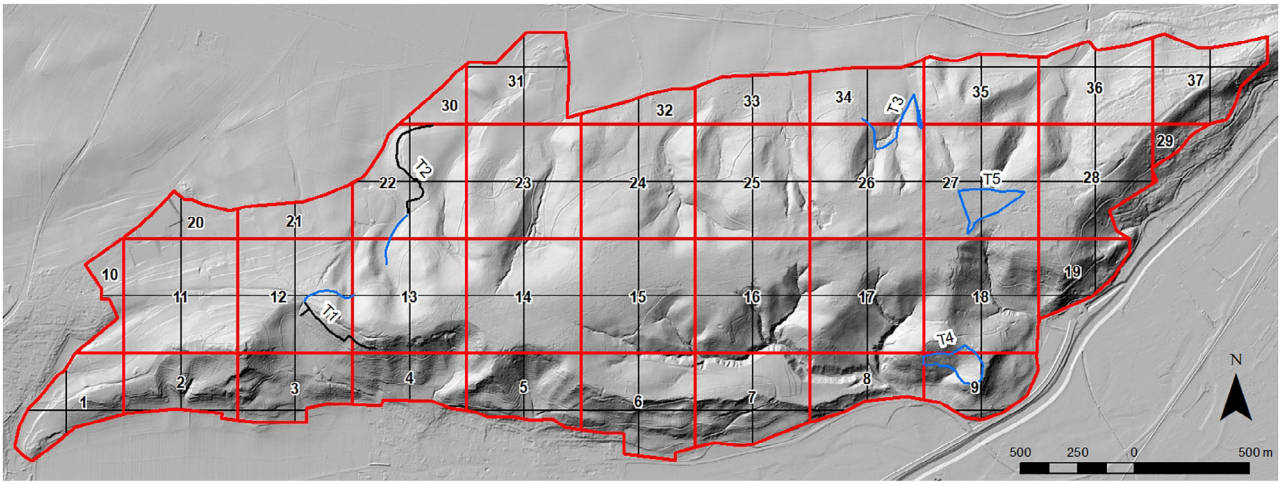

Fig 1. Topography of the Spitzberg, the location of the 37 raster cells (red lines) used to control sampling effort, the 128 raster cells (black and red lines) used for species habitat analyses and the location of the two transects T1 and T2 shown in black, where butterfly monitoring was conducted following the TMD standards. Transects shown in blue are potential additional transects to better represent butterfly population changes of the Spitzberg. [Color figure can be viewed at wileyonlinelibrary.com]

(T1) and north-west part (T2) of the Spitzberg (Fig. 1). The transects were sampled following the standards of the TMD scheme (Kühn *et al*., 2014). Butterflies and burnet moths were recorded once per week between 5 March and 26 October; accordingly, the total walked length on both transects was 27 km. In this study, the maximum number of individuals seen during one of the transect walks per raster was used for further analysis of butterfly density. This was done for pragmatic reasons, although other life-history traits (Nylin, 2009) for species survival and population stability are important (e.g. the number of generations per year, the number of individuals of the last generation or the generation length within a season). In addition, it was not possible to use distance sampling (DS) or capture-mark-recapture methods (Isaac et al., 2011; Pellet et al., 2012) to account for intraspecific variation in detectability and to reach absolute abundance estimates. DS could not be considered, as key assumptions were violated (randomly placed transects) and butterflies at the Spitzberg are too numerous and too quick to accurately estimate distance estimates (Isaac et al., 2011). Capture-mark-recapture methods require intense effort, which was not possible in view of the huge number of species involved in this study. As several species are known to be better detected using their preimaginal stages during the cold half of the year (Hermann, 2007), eggs and caterpillars of species of the genus *Apatura*, *Favonius*, *Limenitis*, *Satyrium* and *Thecla* were searched for in all 37 raster cells during the winters 2017/2018 and 2018/2019, following the recommendations of Hermann (2007). This survey was not conducted on the TMD transects. The total length of all transects walked within the study area in 2018 amounted to 650 km (Supporting Information Fig. S1).

Species–habitat analyses

Species–habitat relationships were analysed on 128 raster cells (Fig. 1). Cells with a size <1000 m^2 located at the edge of the study area were excluded from the analysis of species–habitat relationships. For each species, the total population size was estimated for (i) the whole study area and for (ii) the two TMD transects. The estimated population size of the two transects was based on the total number of counts. In order to estimate the population size for the whole study area, all walked transects were buffered with 2.5 m on each side using a GIS. Then, the maximum number of butterfly and burnet moth observations within this 2.5 m buffer were used to calculate the number of individuals of each species and biotope. These densities were used to estimate the population size for the complete study area and per cell. The estimates of the population sizes might be biased, e.g. by uncertainties in the biotope map which can be caused by an unclear boundary of two adjacent biotope types, uncertainties of the mapped GPS locations affected by atmospheric conditions and tree cover, or differences in the detection probabilities of species between biotopes. In order not to give a false sense of accuracy, the population size was rounded to the closest 100 for species estimated with more than 500 individuals and to the closest 10 for species estimated with less than 500 individuals.

Relationships between the number of individuals of all species per raster cell and seven different environmental variables were analysed using a generalised linear model (GLM), with a logarithmic link function and Poisson error distribution. To avoid multicolinearity, only variables that were not strongly correlated (i.e., $r < |0.7|$) were considered for modelling (Fielding & Haworth, 1995). From groups of correlated variables, only the variable with the most straightforward ecological interpretation was maintained. A second-order polynomial of all predictor variables was included to account for possible non-linear or humped responses. Variable selection followed the corrected Akaike information criterion (AICc) to ensure that models were exclusively built on meaningful information and to avoid overfitting (Vaughan & Ormerod, 2005). The models with the lower AICc

Table 2. Butterfly and burnet moth species recorded at the Spitzberg near Tübingen in 2018.

Scientific name	Individuals counted	Estimated population size	Abundance (%)	Raster frequency (%)	% TMD (%)	Red List status
Maniola jurtina	3457	11 500	19.6	100.0	20	
Melanargia galathea	2787	8200	14.0	57.8	28	
Polyommatus icarus	1573	3900	6.6	72.7	14	
Colias alfacariensis/ hyale	1101	1600	2.7	69.5	22	
Boloria dia	854	2100	3.6	47.7	22	
Pieris rapae	664	2200	3.7	75.0	7	
Lasiommata megera	646	1400	2.4	72.7	9	
Coenonympha pamphilus	572	2400	4.1	74.2	17	
Pieris napi	508	2800	4.8	100.0	6	
Argynnis paphia	500	2700	4.6	70.3	5	
Aphantopus hyperantus	351	2000	3.4	96.1	12	
Aglais io	345	1000	1.7	98.4	14	
Cupido argiades	313	900	1.5	71.9	26	
Polyommatus bellargus	309	500	0.9	41.4	40	3, 3
Coenonympha arcania	250	1100	1.9	46.9	19	
Ochlodes sylvanus	244	1100	1.9	93.0	5	
Gonepteryx rhamni	239	1000	1.7	97.7	16	
Zygaena filipendulae	216	800	1.4	70.3	41	
Anthocharis cardamines	205	1100	1.9	97.7	11	
Leptidea sinapis/ juvernica	203	1000	1.7	73.4	13	
Aglais urticae	179	500	0.9	86.7	41	
Brintesia circe	175	280	0.5	33.6	4	1, 3
Issoria lathonia	137	390	0.7	78.9	11	
Araschnia levana	133	700	1.2	90.6	2	
Thymelicus lineola	127	1000	1.7	65.6	20	
Polyommatus coridon	125	290	0.5	52.3	34	
Erynnis tages	115	340	0.6	63.3	23	
Polygonia c-album	108	500	0.9	91.4	17	
Celastrina argiolus	106	410	0.7	85.9	5	
Aricia agestis	105	270	0.5	61.7	31	
Lycaena phlaeas	92	190	0.3	59.4	18	
Papilio machaon	88	180	0.3	56.3	10	
Pieris mannii	86	230	0.4	52.3	2	
Limenitis camilla	84 (204)	200	0.3	77.3	8	
Vanessa atalanta	83	230	0.4	80.5	2	
Pararge aegeria	76	350	0.6	80.5	1	
Polyommatus semiargus	72	220	0.4	51.6	14	
Nymphalis polychloros	57	200	0.3	53.9	2	2, V
Pieris brassicae	47	220	0.4	78.1	19	
Thymelicus sylvestris	45	400	0.7	64.8	38	
Thymelicus acteon	40	230	0.4	26.6	20	V, 3
Vanessa cardui	36	130	0.2	46.9	31	
Argynnis adippe	32	70	0.1	28.1	19	3, 3
Zygaena viciae	25	30	0.1	3.1	52	
Polyommatus thersites	21	30	0.1	10.9	19	3, 3
Satyrium w-album	20 (28)	40	0.1	12.5	5	
Zygaena loti	20	30	0.1	4.7	60	V, 3
Satyrium pruni	16 (27)	50	0.1	7.8	38	
Carcharodus alceae	15 (60)	70	0.1	32.0	6	3, –
Satyrium acaciae	15 (23)	40	0.1	8.6	0	3, V
Favonius quercus	14 (110)	110	0.2	39.8	14	
Zygaena ephialtes	13	20	0.0	6.3	15	V, 3
Callophrys rubi	12	20	0.0	6.3	8	
Zygaena transalpina	12	20	0.0	1.6	75	3, 3

(continued)

Table 2. (continued)

Scientific name	Individuals counted	Estimated population size	Abundance (%)	Raster frequency (%)	% TMD (%)	Red List status
Apatura iris	11 (44)	20	0.0	17.2	9	
Thecla betulae	10 (304)	440	0.7	60.2	10	
Carterocephalus palaemon	9	10	0.0	6.3	67	
Colias crocea	7	10	0.0	4.7	0	
Lycaena tityrus	6	10	0.0	3.1	0	
Pyrgus malvae	6	10	0.0	5.5	17	
Cupido minimus	4	10	0.0	1.6	25	
Melitaea cinxia	4	10	0.0	5.5	50	2, 3
Apatura ilia	2	10	0.0	4.7	0	3, V
Aporia crataegi	1	0	0.0	0.0	0	
	17 728	58 700				

The number of individuals counted within the transects, the estimated population size and the relative abundance of each species for the total study area are shown. The numbers in brackets are the number of counted eggs (*C. alceae*, *F. quercus*, *S. acacia*, *S. pruni*, *S. w-album* and *T. betula*) or caterpillars (*L. camilla* and *A. iris*). Raster frequency shows the percentage of rasters in which the species were recorded. The column "% TMD" shows the proportion of individuals recorded at the two TMD transects compared to the total number of all individuals counted at the Spitzberg. Red list status on the national scale (first number) and at the state level (last number) is presented in the last column.

and the highest AICc weights were considered to be best (Burnham & Anderson, 2002). Additionally, competing models (i.e. ΔAICc <2) are presented in the Supporting Information Table S2.

Environmental information per raster cell included (i) altitude (mean), (ii) altitude (standard deviation), (iii) solar insolation (mean), (iv) number of biotope types, (v) percent cover of nutrient-poor grassland, (vi) percent cover of forest and (vii) percent cover of protected areas. Environmental variables 4, 5 and 6 are based on information on a biotope map, which was derived from 21 orthophotos taken on 6 May 2014. This map includes 19 biotope types (Table 1). Most butterfly species in forests occur along the lighter forest tracks but not deeper inside forests. To account for this, forest tracks were buffered 5 m along both sides and were separated from other forest types as an extra biotope type.

To account for autocorrelation (Dormann *et al*., 2007), a spatial auto-covariate was calculated using the "autocov_dist" function in R (neighbourhood radius was set to 500 m to include two neighbouring raster cells and the weighting scheme was set to "inverse") from the spdep package (Augustin *et al*., 1996; Bivand *et al*., 2013). The calculated autocovariate was involved in the GLM as an additional explanatory variable. To account for differences of transect length between rasters, we used the transect density per raster as a covariate in the GLM. All statistical analyses were conducted using the R version 3.5.2 (R Development Core Team 2018). The percentage deviance explained by each model (D^2) was used to quantify the overall model fit and was regarded as the explanatory power of the model.

In order to fill gaps of those species not recorded or underrepresented by the two current TMD transects, additional transects were considered. Therefore, species occurrence pattern as well as the estimated population size of each species of the Spitzberg were analysed. To do so, all butterfly and burnet moth observations recorded on transects that were walked within the complete study area in 2018 were analysed. Out of a myriad of potential transect locations, a small number of transects were chosen, exemplarily. These additional transects were selected by counting the number of species that were currently covered by less than 10% of the total butterfly and burnet moth population or by less than three individuals in TMD 1 and 2.

Results

Percent cover of biotope types differs between the total study area and the two transects (Table 1). While grassland, nutrient-poor grassland and forest edges are much more abundant, orchards and forests are much less abundant on both transects compared to the total study area.

Butterflies and burnet moth species

In total, 65 butterfly and burnet moth species were recorded, comprising 17 728 recorded and 58 700 estimated individuals for the whole study area (Table 2). Additionally, 800 eggs and caterpillars were found for eight species. These preimaginal stages found increased the number of records between 1.4 times for *Satyrium w-album* and up to a maximum of 30.4 times for *Thecla betula* (mean factor for eight species: 6.7). Butterfly density was highest on open habitats in the south and south-east and lowest in the central and northern part of the study area (Fig. 2a). Densities estimated per raster comprised 334 at the highest and 22 at the lowest individuals per ha.

The most abundant species were *Maniola jurtina* and *Melanargia galathea*, both accounting for more than 10% of the total butterfly population of the Spitzberg. The five species *Aglais io*, *Aphantopus hyperantus*, *Maniola jurtina*, *Melanargia galathea* and *Pieris napi* occurred in more than 120 rasters. Rare species were *Cupido minimus*, *Lycaena tityrus*, *Zygaena viciae* and *Zygaena transalpina*, recorded in five raster cells only. Species

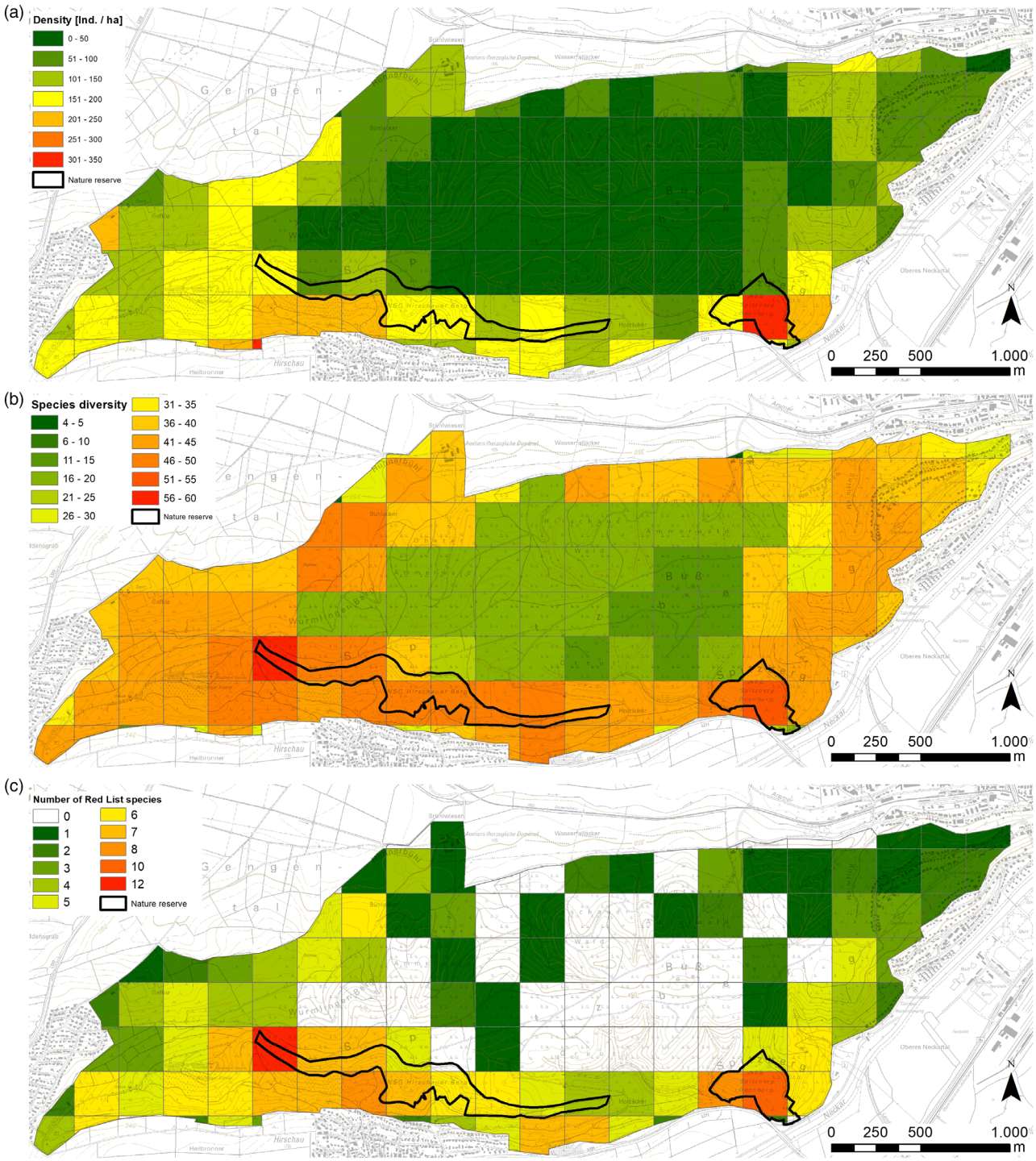

Fig 2. (a) Butterfly density, (b) species diversity and (c) number of Red List species at the Spitzberg near Tübingen, Germany. [Color figure can be viewed at wileyonlinelibrary.com]

richness showed a pattern similar to that of the butterfly density. Lowest numbers were recorded in the central part, comprising between 14 and 20 species. Highest numbers with more than 50 species were observed in the south-west and southern part of the study area (Fig. 2b). Species richness was also high in the west and in the north-west.

Thirteen species found are red-listed for Germany (Reinhardt & Bolz, 2011) and/or the state of Baden-

Table 3. Relative effects of variables on the three response variables analysed, calculated using a GLM. Estimates were obtained from the analysis of z-transformed data in order to make them comparable between predictors measured in different units.

	Number of species			Number of Red List species			Butterfly density		
	Estimate	Std. Error	*P*-value	Estimate	Std. Error	*P*-value	Estimate	Std. Error	*P*-value
Intercept	3.625	0.053	<0.001	0.852	0.218	<0.001	4.451	0.042	<0.001
Autocovariate	0.034	0.019	0.066	0.265	0.070	<0.001	0.147	0.012	<0.001
Solar insolation	Rejected			Rejected			0.074	0.012	<0.001
Altitude	Rejected			−0.182	0.091	0.045	−0.175	0.017	<0.001
Altitude (standard deviation)	0.051	0.017	0.003	0.204	0.066	0.002	0.046	0.013	<0.001
Number of biotope types	0.164	0.027	<0.001	0.336	0.103	<0.001	0.097	0.017	<0.001
Cover of protected areas (%)	0.028	0.046	0.541	0.126	0.161	0.432	0.131	0.032	<0.001
Cover of nutrient-poor grassland (%)	0.088	0.020	<0.001	0.198	0.053	<0.001	0.116	0.010	<0.001
Cover of forest (%)	−0.091	0.022	<0.001	−0.234	0.106	0.026	−0.324	0.018	<0.001
Altitude^2	Rejected			0.172	0.083	0.038	0.084	0.015	<0.001
Cover of protected areas (%)^2	−0.030	0.012	0.013	−0.071	0.040	0.077	−0.042	0.008	<0.001
Cover of nutrient-poor grassland (%)^2	Rejected			Rejected			Rejected		
Cover of forest (%)^2	−0.091	0.052	<0.001	−0.241	0.190	0.206	Rejected		
Transect density	Rejected			Rejected			0.352	0.107	0.001
Model accuracy, explained deviance (D^2):		72.6%			70.2%			84.8%	

Some predictor variables were not included among the AICc ranked models and therefore were marked as rejected.

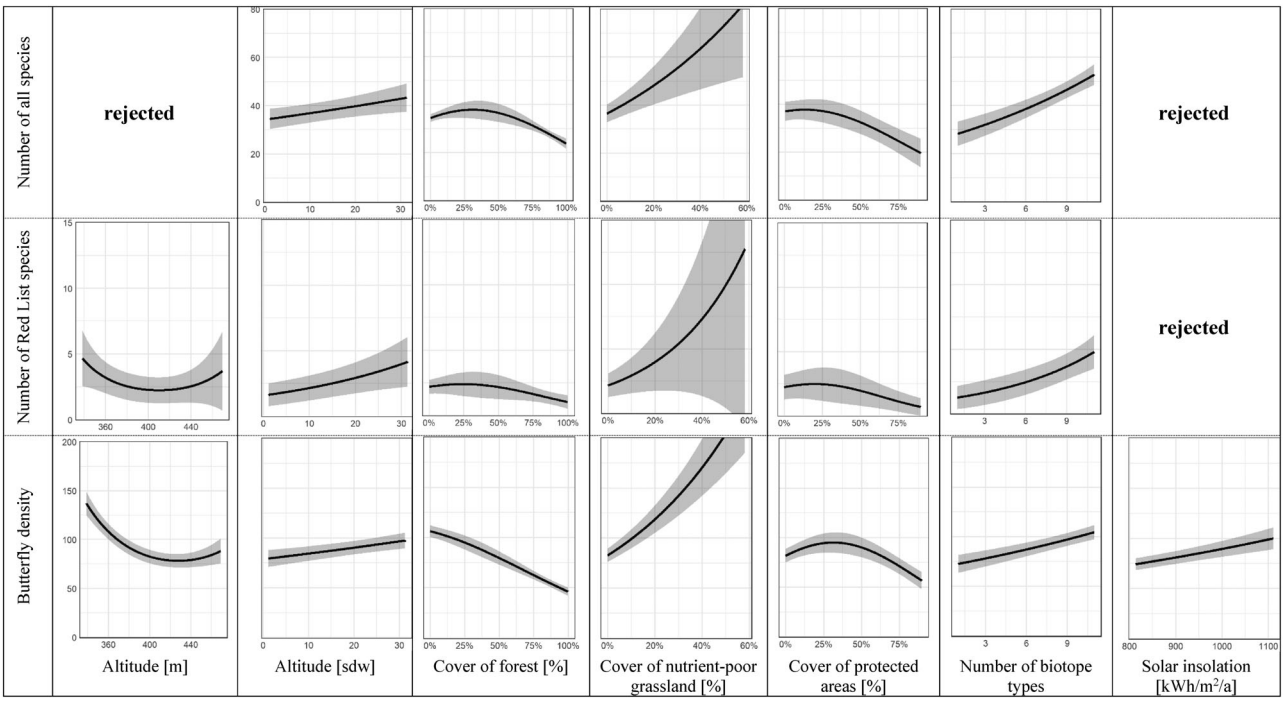

Fig 3. Relationship between number of all species, number of Red List species, butterfly density and environmental variables. Shown are the combined linear and polynomial effects based on the estimates calculated using a GLM.

Württemberg (Ebert et al., 2005). The population size of four Red List species (*Brintesia circe*, *Nymphalis polychloros*, *Polyommatus bellargus* and *Thymelicus acteon*) was estimated at 100 individuals or higher. Highest numbers of Red List species were found in the southern part of the Spitzberg, especially in some parts of the nature reserves. In the central and north-western part of the study area, zero to one Red List species was recorded.

About 92% of all butterfly and burnet moth species recorded at the Spitzberg were also sampled by the two TMD transects.

The TMD failed to record *Apatura ilia*, *Aporia crataegi, Colias crocea*, *Lycaena tityrus* and *Satyrium acaciae*. About 19% of the total butterfly population was recorded by the TMD. For 22 species, the number of individuals counted on the two transects covered less than 10% of their total population of the Spitzberg (Table 2).

TMD transects could be extended by an expansion of TMD transects T1 or T2 (additional length 250 m each) or using the additional transects T3 (length: 700 m), T4 (length: 700 m) or T5 (length: 800 m) (Fig. 1). An expansion of T1 and T2 would better represent butterfly population and species richness by seven and six species (Supporting Information Table S1). T3 and T5 would better represent butterfly population and species richness, as 9 and 10 species on each transect would be better represented, respectively. Nevertheless, the best option would be T4, as this transect would cover 16 of those species that were not properly represented by the current TMD transects.

Species response to environmental variables

Model accuracy depicted by percent deviance was quite high and amounted to 70.0 for the Red List species, 72.5 for all species and 84.8 for butterfly density (Table 3).

The response of butterfly density, number of species and number of Red List species to environmental variables showed quite similar patterns (Table 3; Fig. 3). An increase in the cover of forest had a negative effect on the number of species and the number of Red List species if the cover exceeded 40%. Butterfly density was strongly negatively affected without a peak at 40% forest cover. All response variables were positively associated with an increase in percent cover of nutrient poor grassland. Cover of protected areas showed a strong effect on the number of species. More than 20% cover was negative for the number of species and the number of Red List species, and more than 30% was negative for butterfly density. All three response variables showed a positive effect in response to an increase in the number of biotope types and an increase in standard deviation of the altitude. Solar insolation had a strong positive and altitude a negative effect on butterfly density.

Discussion

The present study documents that the two TMD scheme transects appear to be correctly placed, as they managed to capture 92% of species richness and 19% of the total butterfly population. This was achieved by 4.2% of the total sampling effort taken (27 km versus 650 km walked transects for the whole Spitzberg). Yet, for 22 species, the population size estimated on the two TMD transects covered less than 10% of the total butterfly and burnet moth population, or less than three individuals per species were observed. The TMD failed to detect five butterfly species that were recorded on other parts of the Spitzberg in 2018. This suggests that the selected transects of the TMD might not be able to detect all potential changes of butterfly populations for the Spitzberg. The species-specific reasons for the difference in species composition can be classified into three groups. One butterfly group comprising 11 species (*Apatura ilia*, *Apatura iris*, *Araschnia levana*, *Argynnis paphia*, *Celastrina argiolus*, *Limenitis camilla*, *Nymphalis polychloros*, *Ochlodes sylvanus*, *Pararge aegeria*, *Satyrium w-album* and *Vanessa atalanta*) is more closely associated with or is more abundant in forest habitats. The current transect locations touch but do not traverse forests. Furthermore, the occurrence of *Apatura ilia*, *Apatura iris*, *Limenitis camilla* and *Satyrium w-album*, as well as the non-forest species *Satyrium acaciae* is better recorded by searching for their eggs and larvae, as they have reasonably conspicuous egg or larval stages, which can be counted with greater success than flying adults (Hermann, 2007). The location of eggs and larvae might also be biologically more meaningful for species occurrence than that of adults (Nowicki *et al*., 2008). At the Spitzberg, the number of detections of these species was increased on average by a factor of 6.7 compared to the number of adults counted. Currently, the TMD design as well as most European butterfly schemes (van Swaay et al., 2008) do not involve winter surveys for butterflies. Winter surveys of butterflies could be included and standardised, as has been done for *Thecla betulae* in Britain (UK Butterfly Monitoring Scheme, 2020).

A second group of butterflies, including *Aporia crataegi*, *Brintesia circe*, *Callophrys rubi*, *Carcharodus alceae*, *Colias crocea*, *Lycaena tityrus*, *Pieris mannii* and *Satyrium w-album*, contains species that are less common at the Spitzberg or are restricted to specific and restricted habitats. For example, *Lycaena tityrus* is a rare species of the Spitzberg and has only been recorded at moist grasslands in the northern part, where *Rumex* spec., the host plant of the species, is more common. *Carcharodus alceae* and *Pieris mannii* are more common in private gardens in the southern part of the Spitzberg, where their host plants *Iberis* spec., *Eruca versicaria* and *Malva* spec. are present. Yet, as such gardens are usually fenced, it is difficult to include them in a regular TMD scheme. Rare species would be better recorded by species-specific surveys in which specific habitats or the larval host plant are searched for during the expected flight period. Most traditional butterfly monitoring schemes in Europe are not designed to cover these species (van Swaay et al., 2008), as recording of all rare species is time consuming and cannot be standardised. A third group, including *Lasiommata megera*, *Pieris napi* and *Pieris rapae*, reached reasonable numbers on the TMD transects, but these species are even more common at other sites of the Spitzberg. This is because the TMD transect routing in 2018 did not represent the same proportion of biotope types as are present in the total study area (see Table 1). This resulted in a different distribution of species and individuals. Biodiversity monitoring surveys can be flawed if they are not adjusted statistically before being initiated (Archaux & Bergès, 2008). To do so, the two characteristics sensitivity (absolute change detected) and blindness (failure to detect change in a species) can be optimised using the proper scale (Critchley & Poulton, 1998) and aiming to represent all biotope types of a region. Exemplarily, the results show how the current TMD transects could be optimised by additional transects to better represent the butterfly population and species richness.

Results on species–habitat relationships on a regional scale can show how strong environmental factors drive species distribution and butterfly density and can be used to reconsider transect locations. Number of biotope types, percent cover of forest, and nutrient-poor grassland are the most important drivers of butterfly diversity. More than 40% forest cover led to a decrease in the number of butterfly species. These findings are well known, as a huge number of butterfly species prefer open sunny habitats and are strongly influenced by increasing forest cover (Clench, 1966; Munguira *et al*., 2009; Herrando *et al*., 2016). Species associated with forest habitats usually prefer open woodland, glades, clearings, wide road verges or forest edges (Streitberger *et al*., 2012; Bubová *et al*., 2015). Seventy-five years ago, such habitat structures were common in the forest of the Spitzberg (Gottschalk, 2019b), but due to management changes 13 butterfly species have already been lost within these forests (Gottschalk & Komrowski, 2017). All response variables showed a positive response to nutrient-poor grassland. This confirms known responses of many insect species (Di Giulio *et al*., 2001; Dolek & Geyer, 2002; Bubová *et al*., 2015), including butterflies, which avoid fertilised grasslands (Öckinger *et al*., 2006). Fertilisers enhance the growth of annual grasses at the expense of annual forbs and can crowd out the larval host plants of butterflies (Weiss, 1999).

The number of species and the number of individuals show a negative response to an increasing cover of protected areas. The strong negative response between more than 20% and 30% cover of protected areas is reasonable, as the protected areas of the Spitzberg include 50% forest habitats and 7% bushland (Gottschalk, 2019b), which are both unsuitable to most butterfly species. This result indicates that the management of the protected areas should be revised, aiming towards a stronger promotion especially of Red List butterfly species. Yet, in the light of species conservation, this aspect urgently needs further investigation, including other study areas.

All response variables respond positively to an increase of biotope types. A high diversity of biotopes are known to support a high species diversity not only for butterflies but also for many insects, reptiles and birds (Weibull *et al*., 2000; Fuller *et al*., 2004; Diekötter *et al*., 2008). Density of butterflies does not show such a strong positive response to number of biotope types, which results from the fact that some species occur in large numbers in a small number of specific biotopes. In fact, 33% of all individuals recorded at the Spitzberg were contributed by *Maniola jurtina* and *Melanargia galathea*. Highest numbers of these two species were counted on a few grassland types.

All response variables showed a positive effect in response to an increasing standard deviation of the altitude. Higher values are displayed by areas with high topographic variability, which is a known estimator of plant species richness in hilly or mountainous landscapes (Hofer *et al*., 2008). Areas of high plant species richness might offer a higher number of nectar and host plants for butterflies (Steffan-Dewenter & Tscharntke, 1997). Butterfly density responds positively to solar insolation, which is a known driver of thermoregulation in butterflies (Wickmann, 2009). Number of species and number of Red List species do not show such a response. This can be explained by the fact that several species do not benefit from high solar insolation values. For example, *Anthocharis cardamines*, *Apatura ilia*, *Limenitis camilla*, *Nymphalis polychloros*, *Polygonia c-album*, *Polyommatus semiargus* and *Satyrium w-album* are known to be more common on less sunny or warm locations (Settele & Reinhardt, 1999).

Conclusion

The study provides evidence that percent cover of forest, number of biotope types and solar insolation are the most important drivers of butterfly diversity patterns in the focal area. Many species would benefit from an increase in open habitats and from a reduction of forest biotope types, especially on slopes exhibiting high solar radiation values. The study demonstrates that the current transects were able to detect most butterfly species of the study region and therefore are able to indicate possible regional biodiversity changes. In order to optimise the sensitivity, TMD transects should be relocated or augmented based on information on biotope type, solar radiation and topographic variability. TMD standards should be supplemented by including winter surveys of preimaginal stages in order to obtain data on elusive or low density species, which are often hard to count in their imago stage.

Acknowledgements

The author gratefully thank Heiko Hinneberg and Angelina Mattivi for statistical advice and Jana Niedermayer, Heiko Hinneberg, Thomas Bamann and Nora Magg for conducting the fieldwork on the TMD transects during the weeks in which I was not able to walk them. Three anonymous reviewers, Gregor Markl and Heiko Hinneberg provided very helpful comments on earlier versions of the manuscript. The permission to study the protected butterfly species within the two nature reserves was granted by the regional council of Tübingen in accordance with German law. Open access funding enabled and organized by Projekt DEAL.

Conflicts of interest

The author declare that he has no conflict of interest.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Walked transect to record butterflies and burnet moths at the Spitzberg between March and October 2018. All transects were tracked using a GPS (Garmin Oregon 700).

Table S1: Butterfly and burnet moth species recorded at the Spitzberg near Tübingen in descending order according to the number of individuals counted in the complete study area in 2018. The numbers of individuals counted on the two transects T1 and T2 in the years 2015–2019 are also shown. T2 was not

sampled in 2015 and 2016. The last five columns show the number of individuals on potential additional TMD transects. The numbers of individuals shown in these columns are lower compared to T1 and T2, as these transects were not visited on a weekly basis.

Table S2: Competitive models (ΔAICc <2), including degrees of freedom (Df), AICc, ΔAICc and model weights shown for number of species, number of Red List species and butterfly density.

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Accepted 7 July 2020