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Disentangling the effects of host resources, local, and landscape variables on the occurrence pattern of the dusky large blue butterfly (*Phengaris nausithous*) in upland grasslands

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Abstract

Determining the effects of local and landscape drivers on endangered species and predicting potential suitable habitats for their persistence is crucial for effective conservation management. Here, we applied a multi-scale approach to disentangle the effects of host resources, local, and landscape variables on the occurrence pattern of *Phengaris* (=*Maculinea*) *nausithous* in semi-natural upland grasslands. Our approach comprised the assessment of host parameters (plant cover, density, height, flower heads density, ant nest density, ant colony size), local grassland management (pasture, meadow), site conditions (area, shape, terrain attributes), and landscape variables (landscape composition, connectivity). We used ensemble of small models based on bivariate generalized linear models for explaining and predicting the butterfly occurrence pattern. Bivariate models revealed that host ant nest density, plant cover and height, local grassland management type (pasture), slope and eastness, landscape forest cover and grassland connectivity had a positive effect on the occurrence of *P. nausithous* (average explained deviance 20.5%). Host ant density, host plant cover, and local grassland management were the most influential factors on the ensemble predictions. The presence of *P. nausithous* in upland grasslands is not only determined by host resources, but also by local and landscape factors. Such factors proved to be relevant for identifying and predicting suitable grassland sites for this endangered species. Consequently, we recommend that conservation actions should include a landscape perspective to promote connectivity by facilitating coherent grazing networks enabling dispersal between semi-natural upland grasslands and thus species persistence.

Keywords Butterfly conservation · Connectivity · Ensemble of small models · Grazing · Land use · Site occupancy

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Introduction

Semi-natural grasslands have a high nature conservation value and provide key habitats for biodiversity in European agricultural landscapes (Habel et al. 2013; Bengtsson et al. 2019). Their persistence is entirely or partially dependent on the maintenance of low-intensity farming practices such as livestock grazing and hay cutting (Halada et al. 2011). During the last century, about 90% of the semi-natural grasslands have been lost in Northern and Western Europe as a consequence of intensification of agricultural land use or land abandonment (Plieninger et al. 2006; Bengtsson et al. 2019). Both processes have led to habitat loss and consequent habitat fragmentation at the landscape scale along with the deterioration of habitat quality at the local scale, thereby threatening the long-term survival of general biodiversity including insect species (Krauss et al. 2010; Öckinger et al. 2012).

Several butterfly species are considered flagship species for insect conservation and have been widely used as model organisms over the last decades for studying the effects of habitat loss, fragmentation and degradation at multiple spatial scales (Settele and Kühn 2009; Dover and Settele 2009; Barua et al. 2012). In agricultural landscapes, species richness and population densities of butterflies have frequently been related to variations in habitat area and isolation as proxies for habitat loss and fragmentation, respectively (Krauss et al. 2003; Öckinger and Smith 2006; Binzenhöfer et al. 2008; Dover and Settele 2009). As more than 40% of the grassland butterflies occur as metapopulations (Ranius et al. 2011), their persistence and dynamics are greatly influenced by variations in habitat area and connectivity (Thomas and Hanski 1997; Dover and Settele 2009). Likewise, landscape characteristics such as matrix composition may affect butterfly species distribution and community composition by providing additional resources, depending on the quality of the matrix and the species-specific needs (Öckinger et al. 2012). Furthermore, there is consensus that degradation of local habitat quality plays an important role in determining butterflies occurrence (Thomas et al. 2001; Mortelliti et al. 2010). Many studies have shown that butterfly species are negatively affected by the alteration of specific local conditions such as microclimate, nectar resources or host plant availability (Thomas et al. 2001; Binzenhöfer et al. 2005; Curtis et al. 2015). Investigating the combined effect of local and landscape variables on butterflies inhabiting semi-natural grasslands has recently gained more attention (Krämer et al. 2012; Villemey et al. 2015). For example, Binzenhöfer et al. (2008) found that the negative effect of low habitat quality (high shrub cover) on the occurrence of the Small Blue butterfly (*Cupidus minimus*) may be compensated by higher connectivity between host plant patches in agricultural landscapes; and Poniatowski et al. (2018) showed that habitat quality is the most important factor determining the occurrence of specialist species in calcareous grasslands, although the persistence of some species depended on the degree of habitat connectivity.

Large Blue butterflies of the genus *Phengaris* (= *Maculinea*) are one of the most sensitive grassland specialist insects in Europe (van Swaay et al. 2012). The dusky large blue *Phengaris nausithous* (Bergstässer, 1779) is a myrmecophilus specialist associated to humid grasslands across Central Europe (Munguira and Martín 1999). This species is cataloged by the IUCN Red List as near to threatened in Europe, and is strictly protected and listed in Annexes II and IV of the Habitats Directive (Council Directive 92/43/EEC) and the Annex II of the Bern Convention (van Swaay et al. 2012). The complex life cycle of this univoltine species involves the great burnet *Sanguisorba officinalis* (Linneus, 1773) and the red ant *Myrmica rubra* (Linnaeus, 1758) as major food source and larval host (Witek et al. 2008; Tartally et al. 2019), making it especially vulnerable to any factor that adversely affects the persistence of its host resources at both local and landscape scale (Thomas 1984; Munguira and Martín 1999). The host plant *S. officinalis* is a perennial and hydrophilic species sensitive to changes in grassland management and fragmentation (Loritz and Settele 2005; Musche and Settele 2005; Winter et al. 2008); while the presence and abundance of the host ant *M. rubra* is highly determined by vegetation cover and soil moisture (Dauber and Wolters 2004; Wynhoff et al. 2011). An increase in cutting frequency or grazing intensity leads to a loss of structural heterogeneity in grasslands thereby indirectly affecting the phenology of the host plant and microhabitat of the host ant (Dauber and Wolters 2004; Johst et al. 2006; Settele and Henle 2009; Pérez-Sánchez et al. 2018). Mowing events or livestock trampling further directly influence *P. nausithous* through egg and larval destruction on the flower heads (Johst et al. 2006; Settele and Henle 2009). Likewise, abandonment of grassland management accompanied by shrub encroachment may benefit the host ant, but decreases the abundance of the host plant in the long run (Smith et al. 2002; Pérez-Sánchez et al. 2018). Hence, local grassland management plays a key role in the conservation of the endangered dusky large blue butterfly in Europe (Settele and Henle 2009; van Swaay et al. 2012).

The dusky large blue butterfly is a well-studied species within the *Phengaris* genus in terms of host specificity (Tartally et al. 2019), habitat preferences (Thomas 1984; Batáry et al. 2009; Kőrösi et al. 2012), resource requirements (Anton et al. 2008; Dierks and Fischer 2009), grassland management (Johst et al. 2006; Settele and Henle 2009), and (meta)population dynamics at local (Nowicki 2017; Vrabec et al. 2017) and landscape scale (Nowicki and Vrabec 2011; Kajzer-Bonk et al. 2013; Nowicki et al. 2015). However, to improve the conservation of this highly specialized butterfly there is an urgent need to analyze simultaneously the influence of host resources, local site conditions including grassland management, and landscape variables (see Loritz and Settele 2005; Kajzer-Bonk et al. 2016). To gain a better understanding, this study aims at disentangling the effects of host resources (plant and ant), local (type of grassland management and environmental site conditions) and landscape variables (landscape composition and connectivity) on the occurrence pattern of *P. nausithous* in extensively managed upland grasslands. We specifically aimed to (*i*) explain the occurrence of *P. nausithous* in relation to host resources, local grassland management and environmental conditions, and landscape variables, and (*ii*) predict and map potential suitable grassland habitats. Based on our findings, we identify key parameters for the conservation of this highly specialized butterfly in semi-natural upland grasslands.

Materials and methods

Study area and selection of grassland sites

The study area was situated in the vicinity of the city of Zella-Mehlis in the Thuringian Forest, Central Germany (Fig. 1). The area is characterized by a short but steep elevation gradient ranging from 450 m (Zella-Mehlis) to *c.* 900 m above sea level (highest mountain peak). Mean annual temperature is 5 °C and mean annual precipitation is 1100 mm (Deutscher Wetterdienst 2017). The landscape is dominated by spruce forest (65%), followed by built-up areas (15%), extensively managed grasslands (11%) and small fragments of arable fields (3%). Within the forest-dominated landscape, grasslands are predominantly located in the surrounding of the city or along mountain valleys on steep slopes (Fig. 1). Some grassland sites are isolated from each other by forests and have been traditionally used for haymaking, while others are connected by rotational grazing to allow moving livestock from one pasture to the next. The presence of *P. nausithous* has recently been reported in the study region, although up-to-date

estimations about potential or current population size do not exist (TLUG 2009).

We conducted a pre-study by analyzing detailed land cover data and carrying out a visual inspection of grasslands in 2016 to check host plant availability. Land owners were asked for permission to access their grassland sites and consulted for background information on grassland management. A total of 32 grassland sites along an elevational gradient were selected according to differences in management type, grassland isolation, and landscape composition (Fig. 1; Fig. 1 in Online Appendix 1). The selected sites were either extensively grazed by cattle (pasture, $n = 20$) at low to moderate stocking rate (0.6 livestock units per hectare) or traditionally mown with light machines (meadow, $n = 12$). Extensive pastures were managed by means of rotational grazing that involves rotating a small number of cattle over several grassland sites along the elevational gradient from late-May to late-August. The extensively managed meadows were mown once a year in late summer (between mid and end of August). All selected grassland sites have not experienced any history of either management intensification (increased livestock density or mowing rate, mineral fertilizer or pesticide use) or land abandonment (woody plant encroachment) in the last decades. In addition, all selected
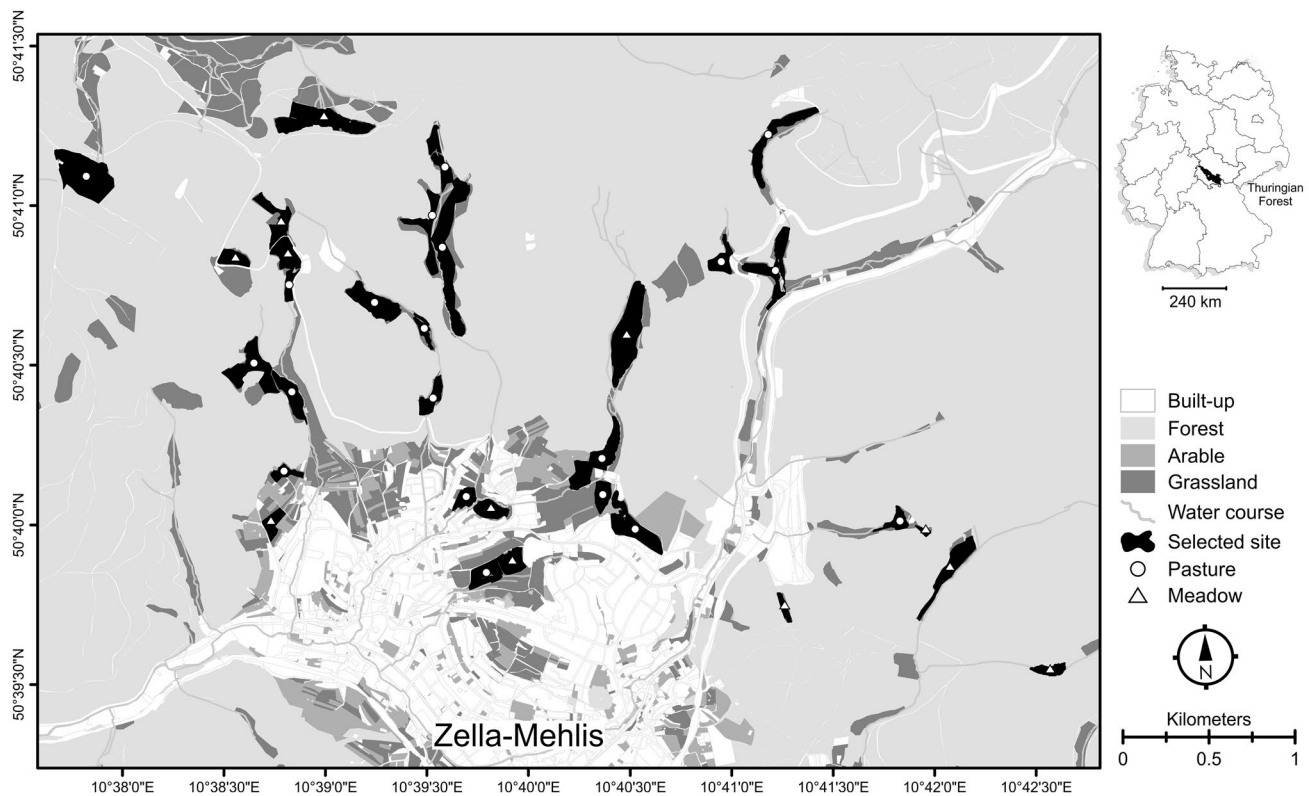
Fig. 1 Study area in the Thuringian Forest, Central Germany. The map shows the distribution of the 32 selected grassland sites (black) within the grassland complexes (dark gray) and forest matrix (light grey). Topographical distance between selected grassland sites is 2.1 ± 0.6 km (mean $\pm$ SE)

grassland sites were covered by agri-environment scheme (AES) agreements that have been implemented as part of the European Common Agricultural Policy to provide funding to farmers to undertake environmentally friendly farming practices to restore and maintain biodiversity in agricultural landscapes (Science for Environment Policy 2017).

Data collection

Sampling of the host plant, butterfly, and host ant was performed in three chronological steps according to each species' phenology, and data from every sampling step were pooled at grassland site level. First, the distribution of the host plant *S. officinalis* was mapped at each grassland site in late June 2017. To assess the distribution of *S. officinalis*, we performed transect walks (of 10 m width) per grassland site using a modified Braun-Blanquet cover-abundance scale (Wikun and Shanholtzer 1978). Since *S. officinalis* was heterogeneously distributed within the selected grassland sites, four cover-classes were used to assess the host plant abundance and cover: "absent" (area without host plant), "present" (area with less than 5 individuals representing less than 1% of the vegetation cover), "sparse" (area with up to 49 individuals occurring scattered and representing 2–12% of the vegetation cover), and "dense" (area with more than 50 individuals of host plant occurring aggregated and representing more than 50% of the vegetation cover). The area occupied by each discrete cover-class within the grassland sites was digitized and mapped using a Getac F110 G2 device (GPS: SiRFstarIV).

Second, the occurrence of *P. nausithous* was sampled three times at each grassland site during the flight period (mid-July, July–August, and late-August 2017). We used a modified version of Pollard's standardized counts on 5 m × 50 m transects covering the entire grassland site (Pollard transects; Pollard and Yates 1993). All adult individuals in flight or perched on *S. officinalis* flower heads within 5 m in front of (and above), and 2.5 m right and left of the observer were counted during a slow walk along the Pollard transect (*c*. 5 min). Surveys were conducted under stable weather conditions (no rain, temperatures > 17 °C) between 10:00 and 17:00 h local time. Depending on the grassland area, five to 18 Pollard transects were completed per site. To complement the host plant assessment, the number of *S. officinalis* individuals, flower heads, and plant height were recorded in five plots (1 m × 1 m) randomly distributed along each Pollard transect after the butterfly recording.

Third, *M. rubra* nest density was determined following Seifert's (2017) method for non-arboreal species survey (late-August). Nests were directly located within a spatially nested approach covering three levels of search effort: an intensive scrutiny (*S*) search performed on ground and vegetation within a smaller area (*S* sampling area = 64 m²

quadrat); a quick (*Q*) search on soil performed within a larger area (*Q* sampling area = 400 m² quadrat); and a spot inspection (*SI*) in the most promising nest habitats in a variable area adjacent to the *Q*-areas (Seifert 2017). Although *S* sampling area aims to detect small species with hidden nests and *Q* sampling area reflects realistic nest densities of larger species (Seifert 2017), all sampling levels (*S*, *Q*-, and *SI*) are sensitive to detect *M. rubra* nests. The combination of the three sampling areas, hereafter Seifert-plot, allows the calculation of integrated species-specific density in 100 m² (Seifert 2017). We additionally calculated the colony size of *M. rubra* within each Seifert-plot using the non-destructive procedure proposed by Skórka et al. (2006). One to three Seifert-plots were conducted per grassland site depending on its size. All ant specimens collected individually and per nest were fixed on ethanol 90% and determined to species level in the laboratory following Seifert (2018). Detailed information about the host ant sampling methods is provided in Box 1 in Online Appendix 1.

Host species parameters

To characterize parameters related to the host plant resource per grassland site, we calculated the total *S. officinalis* density (m⁻²), the total area (m²) occupied by the "dense" and "sparse" cover-classes as proxies of the so-called foodplant patches (sensu Nowicki et al. 2007; Anton et al. 2008), and the evenness among all cover-classes based on the weighted areas (%) as a measure of the host plant heterogeneity per site. We additionally considered the mean flower heads density (m⁻²) and mean plant height (cm) within the "dense" cover-class per grassland site. Regarding the host ant resource, *M. rubra* nest density (100 m⁻²) and mean colony size (number of workers) per grassland site were used as a surrogate of nest availability and foraging intensity of workers (i.e. a measure of probability of larvae adoption; Kempe et al. 2016).

Local variables

Management type as either pasture or meadow was treated as a local variable (categorical). In addition, a set of continuous variables characterizing local abiotic conditions were measured for each grassland site. Total area (ha) and compactness index were calculated per grassland site as a proxy of grassland size and shape respectively (Gillman 2002). Mean elevation, slope, aspect, SAGA Wetness Index (SWI), and solar radiation (SRD) were calculated per grassland site using a digital elevation model derived from LiDAR data with a spatial resolution of 10 m (German Office for Surveying and Geoinformation). Slope was calculated as mean inclination degree of the grassland surface, while aspect was measured as the exposure of the mean slope per grassland

site transformed by means of eastness [sine (aspect° · π/180°)] and Beers' index [cos((45°− aspect°) · π/180) + 1]. Eastness values vary from − 1 to + 1 indicating grasslands facing west to east respectively; while Beers' index generate aspect values with maximum at northeast (2.0) and minimum at southwest (0.0), assigning positive values to intermediate aspects descending from 2.00 to 0.00 according to the sine of the azimuth (Beers et al. 1966). SWI and SRD were used as proxies for soil moisture and temperature, respectively. SWI was calculated using the System for Automated Geoscientific Analyses (SAGA 2.3.2) module in QGIS version 2.18.16, and SRD was calculated using the Area Solar Radiation tool in ArcGIS 10.5.1.

Landscape variables

Landscape composition was calculated using digital thematic maps (German Real Estate Cadastre Information system, ALKIS) at a fine spatial resolution (1:5000). The percentage cover of forest, grassland, arable land and built-up area (i.e. roads, urban, and industrial areas) were calculated within a geodesic buffer of 250 m (edge to edge) for each grassland site. Such buffer size provides an adequate spatial scale for evaluating the effect of landscape composition on grassland specialist butterflies, including the lower limit of the mean dispersal range of *P. nausithous* (Hovestadt et al. 2011; Krämer et al. 2012; Nowicki et al. 2014).

Grassland connectivity was measured in terms of structural and functional connectivity. We used Hanski's connectivity index modified by Moilanen and Nieminen (2002) as a structural connectivity index taking into account all neighboring grasslands within a distance of 250 m from the edge of the focal grassland site (*i*):

$$S_i = \sum_{j \neq i} exp\left(-\alpha \cdot d_{ij}\right) \cdot A_j^b$$

where A_j is the size (m²) of neighboring grassland *j*, and d_{ij} is the distance (km) between the focal grassland site *i* and neighboring grassland *j* (Moilanen and Nieminen 2002). Parameter *α* scales the effect of distance to migration (1/*α* is the average migration distance of a species), while *b* scales the emigration as a function of the area (Moilanen and Nieminen 2002). Since we focused on the structural connectivity per grassland site within a fixed surrounding range, an average migration distance of 250 m (*α* = 4) without emigration parametrization (*b* = 1) was set in order to be consistent with the spatial scale. In addition, circuit theory was used to calculate an effective resistance maps for *P. nausithous* potential movement between grassland sites as a proxy of functional connectivity (McRae et al. 2008). Circuit theory approach allows predicting expected routes that an animal with preference for low-resistance habitat will use to move

through a landscape (McRae et al. 2008). A landscape resistance matrix with 10 m cell size was derived from ALKIS land cover data by assigning six levels of resistance according to the habitat requirements of *P. nausithous* (Table 1 in Online Appendix 1). An effective resistance value per grassland site was computed using the "one to all" option within CIRCUITSCAPE 4.0.5 software (McRae et al. 2013).

Statistical analysis

Pairwise Spearman rank coefficients (r_s) were calculated to evaluate collinearity among an initial set of 24 predictor variables, and highly correlated variables ($|r_s| > 0.7$) were excluded (Schröder et al. 2009; Dormann et al. 2013). A final set of 15 variables was selected for further analysis based on their ecological relevance for the studied butterfly (Table 1). More information about variable selection is provided in Box 2 in Online Appendix 1.

We adopted the ensemble of small models (ESM; Breiner et al. 2015) approach to analyze the occurrence pattern (true presence/absence data) of *P. nausithous* across grassland sites in response to host resources, local and landscape variables (Table 1). This approach has been successfully applied to model the occurrence and ecological niche of rare species with very few presences within small data sets (Breiner et al. 2015; Della Rocca et al. 2017; Beukema et al. 2018). The ESM approach combines sets of "small" models (e.g. bivariate) into an ensemble, weighted by each "small" model performance and thereby avoiding overfitting without losing explanatory power (Breiner et al. 2015). Generalized linear models (GLM; binomial distribution) were used as modelling technique due to their robust performance and computation time (Schröder et al. 2009; Breiner et al. 2015). Bivariate combinations that include either host ant nest density (*Mrub_density*; Table 1) or area covered by the host plant "dense" class (*Soff_dense*; Table 1) were selected as potential pool of "small" models to account for the parasite-host relationship between *P. nausithous, S. officinalis,* and *M. rubra*. Twenty-seven bivariate GLMs were fitted using the number of Pollard transects per grassland site as weights. Bivariate GLMs were estimated on the full data set (*n* = 32) and AIC was used for model selection (model with smallest AIC), potentially reducing the models to univariate. To obtain realistic model performance measures for selecting bivariate models to be included in the ensemble, we used leave-two-out internal cross-validation (LTOCV; stratified: 1 presence, 1 absence). Models with an explained deviance (median of LTOCV runs) > 15% were included in the ensemble. We used the median instead of the mean of explained deviance since it is unaffected by outliers that frequently occur in leave-two-out cross-validation (see Online Appendix 2).

Table 1 Variables (with minimum, median, and maximum values) used as potential predictors of *P. nausithous* occurrence in managed upland grasslands ($n = 32$)

Variable	Description	Values		
		Min	Median	Max
Host species parameters				
Soff_dense	Area (m^2) occupied by the host plant cover-class "dense" (vegetation cover dominated by *S. officinalis*). A $\log_{10}$- transformation was applied to achieve approximate normality	0	3.75	4.73
Soff_sparse	Area (m^2) occupied by the host plant cover-class "sparse" (*S. officinalis* representing 2–12% of the vegetation cover). A $\log_{10}$- transformation was applied to achieve approximated normality	0	3.26	4.41
Soff_evenness	Variance ($\ln[x + 1]$ transformed) among weighted areas (%) of each cover-class as a measure of host plant heterogeneity. Values ranges from 0 to 3.25 and reflects higher or lower level of evenness in host plant cover-class per grassland site	0.31	2.32	3.26
Soff_height	Mean height (cm) of the host plant (*S. officinalis*) within the "dense" cover-class	0	41.5	73.6
Mrub_density	Integrated density estimation of *M. rubra* (nests/100 m^2) following Seifert ([2017])	0	0.14	8.01
Local variables				
Mtyp	Management type of grassland sites (pasture: $n = 20$; meadow: $n = 12$)	–	–	–
Size	Area of grassland site (ha)	0.21	1.79	6.31
Shape	Compactness index as a proxy of grassland shape, values ranges from 0 (irregular shape) to 1 (circular shape) as maximum compactness (Gillman [2002])	0.01	0.35	0.71
Eastness	Grassland aspect transformed into "eastness" [sine (aspect° $\cdot$ $\pi/180$)]. Values ranges from -1 (west) to $+1$ (east) representing grasslands facing west to east respectively	-1.00	0.27	0.99
Slope	Mean slope of grassland site (°)	2.44	8.08	12.4
SWI	Mean SAGA wetness index of grassland site based on local topography as a proxy of soil moisture	7.09	8.99	13.5
SRD	Mean monthly solar radiation (kWh/m^2/day) of grassland site as a proxy of soil temperature	4.91	5.25	5.46
Landscape variables				
%Forest	Percentage cover (%) of forest surrounding each grassland site (geodesic buffer of 250 m from the edge)	0	75.89	96.1
Connectivity	Hanski's (1990) connectivity index modified by Moilanen and Nieminen ([2002]) as proxy of structural connectivity per grassland site ($\alpha = 4$, $b = 1$). Larger values indicate higher connectivity	1733	50,099	176,645
LS_resistance	Effective landscape resistance to movement of *P. nausithous* between grassland sites as a proxy of functional connectivity. Higher values indicate more isolated grassland sites	0.05	0.69	2.79

Ensemble predictions were then obtained by averaging the predicted values of the selected bivariate GLMs, using the LTOCV-derived median explained deviances as weight. The relative influence of each predictor variable in the ensemble predictions was quantified by permutation tests (see Online Appendix 2). To identify grassland sites of high habitat suitability within the study area, the predicted occurrence probabilities P of *P. nausithous* were mapped. As a critical threshold (P_{crit}) for discriminating between suitable ($P > P_{crit}$) and unsuitable ($P < P_{crit}$) grassland habitats, we chose the probability at which the predicted and observed prevalence were the same (P_{fair} in Schröder and Richter [2000]). All data analyses were performed using the statistical program R 3.5 (R Development core team 2018). ESM analysis was performed using Biomod2 (Thuiller et al. [2019]) and Ecospat (Broenniman et al. [2018]) packages. Modifications of Ecospat functions, a comparison with the approach used by Breiner et al. ([2015]) and a template script for the ESM analysis are provided in Online Appendix 2.

Results

A total of 13 grassland sites were occupied by *P. nausithous* (13 presences vs. 19 absences) representing 41% of the grassland sites surveyed. Overall, 47 *P. nausithous* individuals were detected with 1.47 ± 0.82 (mean $\pm$ 95% CI) individuals per site (min $= 1$, max $= 9$). The host plant occurred on 94% of the grassland sites, with a mean density of 2.82 ± 0.72 individuals m^{-2}. Host plant cover-classes were relatively evenly distributed in 47% of the surveyed grassland sites, while the "dense" cover-class dominated in most of the remaining sites (Fig. 1 in Online Appendix 3). The mean density of flower heads within the "dense" cover-class was 6.16 ± 2.13 flowers m^{-2}. A total of 63 nests of *M. rubra* were recorded in 17 grassland sites, with densities ranging from 0.11 to 8.01 nests 100 m^{-2} (Fig. 1 in Online Appendix 3). The mean colony size per site was 377.4 ± 139.51 workers (min $= 215.6$,

max = 1104.1 workers). Landscape results are summarized in Table 1 and Fig. 2 in Online Appendix 3.

Thirteen out of 27 fitted bivariate GLMs were above the selection threshold for the ESM, with an average explained deviance of 20.5% per model (Table 2; Table 2 in Online Appendix 3). All bivariate GLMs within the ESM showed a robust cross-validated performance based on the explained deviance (median of 247 runs from 13 presences × 19 absences; Table 2). Four parameters characterizing host resources, three local variables related to grassland management and site conditions and two landscape variables explained the occurrence of *P. nausithous* in the ESM (Table 2). According to the resulting model, the occurrence of *P. nausithous* was related to high host ant nest density (*Mrub_density*), large areas covered by the host plant (*Soff_dense, Soff_sparse*), high plant height (*Soff_height*), steep slopes (*Slope*), and east-southeastern exposure (*Eastness*; Fig. 2). Moreover, about 85% of butterfly presences were detected in pastures, and according to the bivariate models this grassland management type (*MtypPasture*) positively affected its occurrence (Table 2, Fig. 2). A high percentage cover of forest (*%Forest*) in the surrounding landscape matrix positively affected the occurrence of the butterfly, while a higher *P. nausithous* occurrence was detected in connected but spatially clustered grassland sites (low values of *Connectivity*; Fig. 2, Table 2). Bivariate GLMs containing *Soff_evenness*, *Size*, *Shape*, *SWI*, *SRD,* and *LS_resistance*

factors did not surpass the threshold criterion for the ESM or were reduced to univariate models by AIC selection (Table 2 in Online Appendix 3).

The ESM outperformed each of the bivariate models yielding a higher explained deviance (except *Biva$_{18}$* and *Biva$_1$*; Table 2). This performance was confirmed through other commonly used measures for model performance such as the Area-Under the Curve (AUC = 0.91 ± 0.05) and Total Sum of Squares (TSS = 0.82 ± 0.03; Schröder et al. 2009). The most important predictors in the ensemble predictions were *Soff_dense, Mtyp,* and *Mrub_density*, representing together about 60% of the difference in explained deviance (Fig. 3). Of the remaining predictors, *Soff_height* and *Soff_sparse* were most influential (Fig. 3). Response curves for the main predictors indicate that *P. nausithous* is more likely to occur in grassland sites with *M. rubra* densities higher than 1.46 nests per 100 m^2 (Fig. 4a), grasslands with *S. officinalis* covering densely areas > 5000 m^2 (Fig. 4b), and grassland sites managed as pastures rather than meadows (Fig. 4). Ensemble predictions of *P. nausithous* occurrence probability varied between 0.14 and 0.87 per grassland site (Fig. 5). Fourteen out of 32 grassland sites were considered suitable habitats for the butterfly according to the P_{crit} threshold ($P > 0.51$). Eleven of these sites were occupied by the butterfly while the remaining three were unoccupied (Fig. 5). Two grassland sites, where *P. nausithous* was observed, had rather low predicted probabilities of occurrence (Fig. 5).

Table 2 Characteristics of the bivariate models in the ensemble

	Models	Bivariate combinations		Coefficients ± SE			Evaluation		AIC
		Predictor 1	Predictor 2	Intercept	Predictor 1	Predictor 2	Training exp dev	Testing exp dev	
1	Biva$_{18}$	Soff_dense	Mtyp (Pasture)	−6.81 ± 1.12	1.38 ± 0.27	2.54 ± 0.35	32.8	40.8	261.9
2	Biva$_1$	Mrub_density	Soff_dense	−7.10 ± 1.37	0.85 ± 0.16	1.66 ± 0.33	29.8	28.4	274.7
3	Biva$_{26}$	Soff_dense	Connectivity	−4.38 ± 1.0	1.48 ± 0.81	≪ −0.01	23.3	22.7	300.8
4	Biva$_2$	Mrub_density	Soff_sparse	−3.05 ± 0.53	0.85 ± 0.16	0.72 ± 0.14	22.0	18.9	306.1
5	Biva$_5$	Mrub_density	Mtyp (Pasture)	−1.71 ± 0.27	0.44 ± 0.12	1.18 ± 0.32	21.8	18.5	305.3
6	Biva$_{22}$	Soff_dense	Slope	−6.48 ± 1.20	1.12 ± 0.25	0.28 ± 0.06	21.4	15.5	309.3
7	Biva$_{21}$	Soff_dense	Eastness	−4.34 ± 0.96	1.11 ± 0.24	0.84 ± 0.22	19.7	15.9	313.3
8	Biva$_4$	Mrub_density	Soff_height	−1.90 ± 0.32	0.54 ± 0.11	0.03 ± 0.01	18.7	31.3	316.2
9	Biva$_{12}$	Mrub_density	%Forest	−2.42 ± 0.48	0.77 ± 0.15	0.02 ± 0.01	18.1	16.6	321.1
10	Biva$_9$	Mrub_density	Slope	−2.76 ± 0.54	0.53 ± 0.12	0.27 ± 0.06	17.2	25.8	322.2
11	Biva$_8$	Mrub_density	Eastness	−0.72 ± 0.16	0.57 ± 0.11	0.74 ± 0.20	15.3	27.8	328.8
12	Biva$_{13}$	Mrub_density	Connectivity	−0.28 ± 0.02	0.61 ± 0.12	≪ −0.01	13.2	16.2	338.5
13	Biva$_{11}$	Mrub_density	[a]	−0.66 ± 0.16	0.63 ± 012	–	12.5	15.3	340.6
	ESM	All combinations					29.6		310.7

The performance of each model was evaluated by leave-two-out internal cross-validation (LTOCV; stratified: 1 presence, 1 absence) resulting in 247 runs (13 presences × 19 absences). Only models with an explained deviance > 15% (median of 247 LTOCV runs) were included in the ensemble. Models in the table are ordered by their training data performance. This table output can be accessed using the function model.characteristics.runs provided in Online Appendix 2

[a]Bivariate model reduced to univariate model by the AIC selection procedure
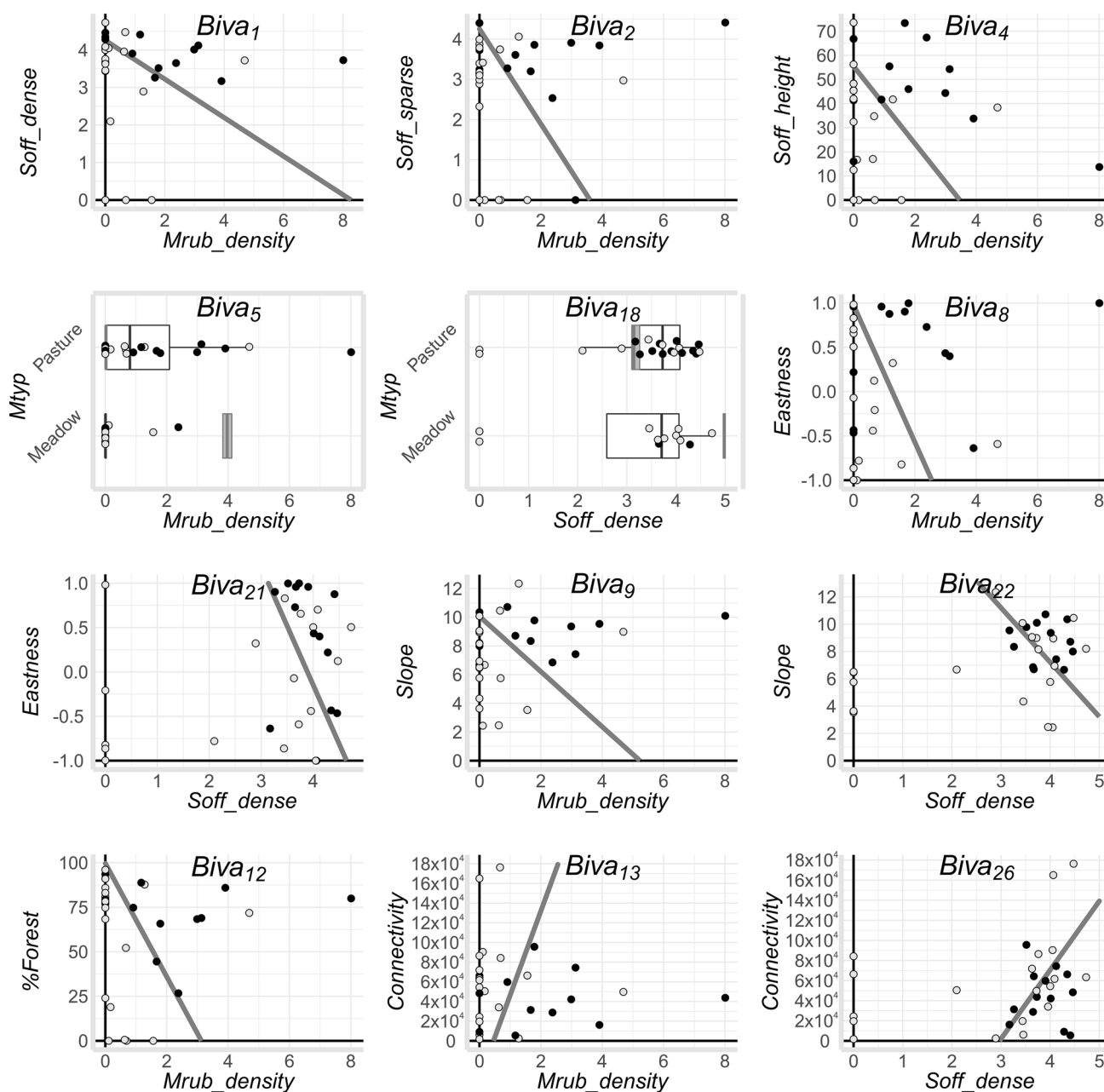
Fig. 2 Effects of predictor variables on the occurrence pattern of *P. nausithous*. Each bivariate combination corresponds to the model fitted within the ensemble (see Table 2). Models with the categorical predictor management type (*Mtyp*) are represented as jittered boxplots (*Biva₅* and *Biva₁₈*). Dots represent observations per grassland site, color-coded by the presence (filled dot) and absence (empty dot) of the butterfly. Solid lines (grey) denote 50% probability of occurrence of *P. nausithous* according to each model (*Biva_n*; Table 2). A description of predictor variables is given in Table 1

Discussion

In this study we found that the occurrence pattern of *Phengaris nausithous* in upland grasslands is not only explained by host resources, but also by local and landscape variables. Still, host resources namely nest density of *M. rubra*, area covered by *S. officinalis,* and host plant height, were the most important drivers of *P. nausithous* site occupancy. Several

studies highlighted that the abundance of the host ant is the main factor limiting the occurrence of *P. nausithous,* if suitable host plants are present (Anton et al. 2008; Dierks and Fischer 2009; Jansen et al. 2012; Kempe et al. 2016). Our results are in line with this, since nest density of *M. rubra* was the most frequent predictor in the ESM, even as a univariate model. However, we observed *P. nausithous* in four grasslands sites where *M. rubra* was absent (Fig. 1 in Online
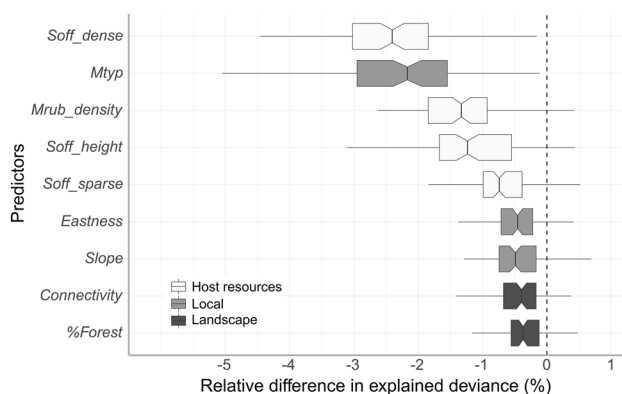
Fig. 3 Predictor contribution to the ensemble predictions. The contribution of a predictor is derived from the difference in explained deviance between models applied to the original predictor (i.e. in its original observed order) and to the randomly permuted predictor (all other predictors remain unchanged), divided by the frequency of the predictor in the ensemble. The larger the difference in model performance, the more important is the predictor. Predictor contribution can be accessed through the function permutation.test.esm provided in Online Appendix 2

Appendix 3). These findings might appear contradictory, but can be attributed to complementary causes, (i) short-distance movement between grassland sites, (ii) exploitation of an alternative host ant, or (iii) *M. rubra* nests undersampling. It seems likely that those *P. nausithous* individuals observed in grassland sites without *M. rubra* belong to neighboring populations where the host ant occurs, and that they explored close-by habitats in search of favorable conditions for mating (e.g. G3, G200; Fig. 1 in Online Appendix 3). Although the

inter-habitat mobility is low for *P. nausithous* (100–200 m; Nowicki et al. 2014), imagos are able to move larger distances between host plant areas in landscapes dominated by forest (> 500 m; Hovestadt et al. 2011; Nowicki et al. 2014). In more isolated sites where inter-grassland movement may be limited, it might be possible that *P. nausithous* completes its life cycle by exploiting an alternative host ant like *M. scabrinodis* or *M. ruginodis* for instance (Witek et al. 2008; Jansen et al. 2012). Although both *Myrmica* species were recorded in such isolated grassland sites, the alternative host explanation might seems unlikely since reports of *P. nausithous* infesting other *Myrmica* species nest are rather seldom along Central Europe (Tartally et al. 2019). Thus, a more feasible explanation is that *M. rubra* nests most likely occurred in such grassland sites but at very low densities, and therefore have probably been overlooked despite our robust sampling effort.

The broad distribution and dominance of *S. officinalis* in the grassland sites suggest that host plant cover may not be a limiting factor in the study region (Fig. 1 in Online Appendix 3). However, two host plant cover-classes and host plant height were relevant factors explaining and predicting the butterfly occurrence. In general, *P. nausithous* tends to occur with higher frequency and density in small areas covered by *S. officinalis* rather than in larger ones (Thomas 1984; Anton et al. 2005; Loritz and Settele 2005), although this pattern may be scale-dependent and vary geographically. In well-established metapopulations in Poland, for instance, the area covered by the host plant affects the spatial occurrence positively but population density negatively (Nowicki et al. 2007). In any case, host
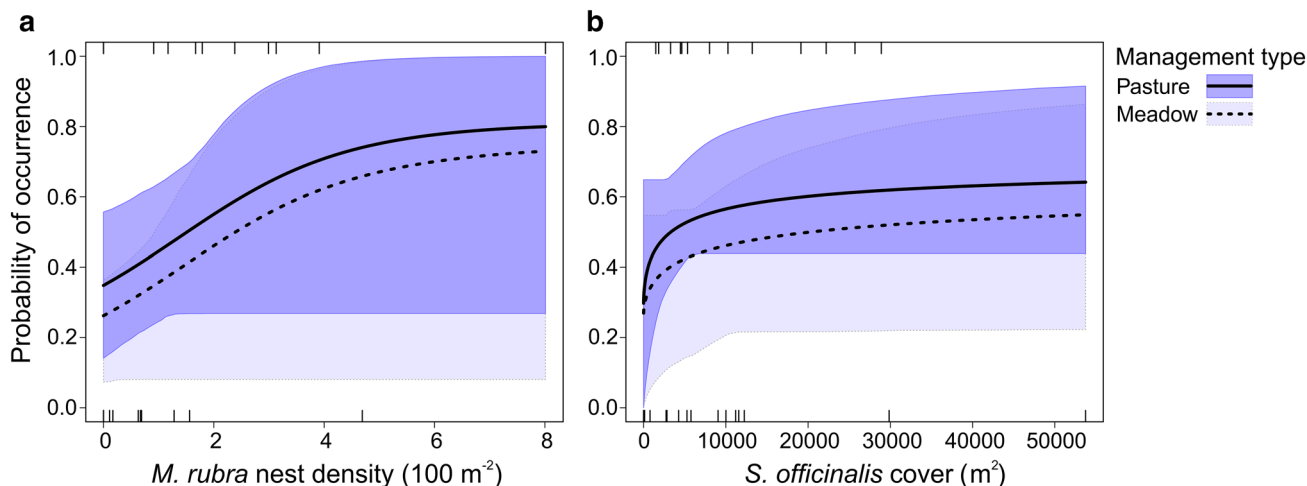
Fig. 4 Response plots of host ant and plant predictors in the ensemble. Probability of occurrence (line) and 95% confidence interval (shaded area) of *P. nausithous* in relation to **a** *M. rubra* nest density, **b** area covered ("dense" class) by *S. officinalis* in both management types: Pasture (solid line, dark shaded area) and Meadow (dashed line, light shaded area). Response plots are based on the ensemble predictions and can be accessed applying the functions response.curves.esm.prepare and response.curves.esm provided in Online Appendix 2
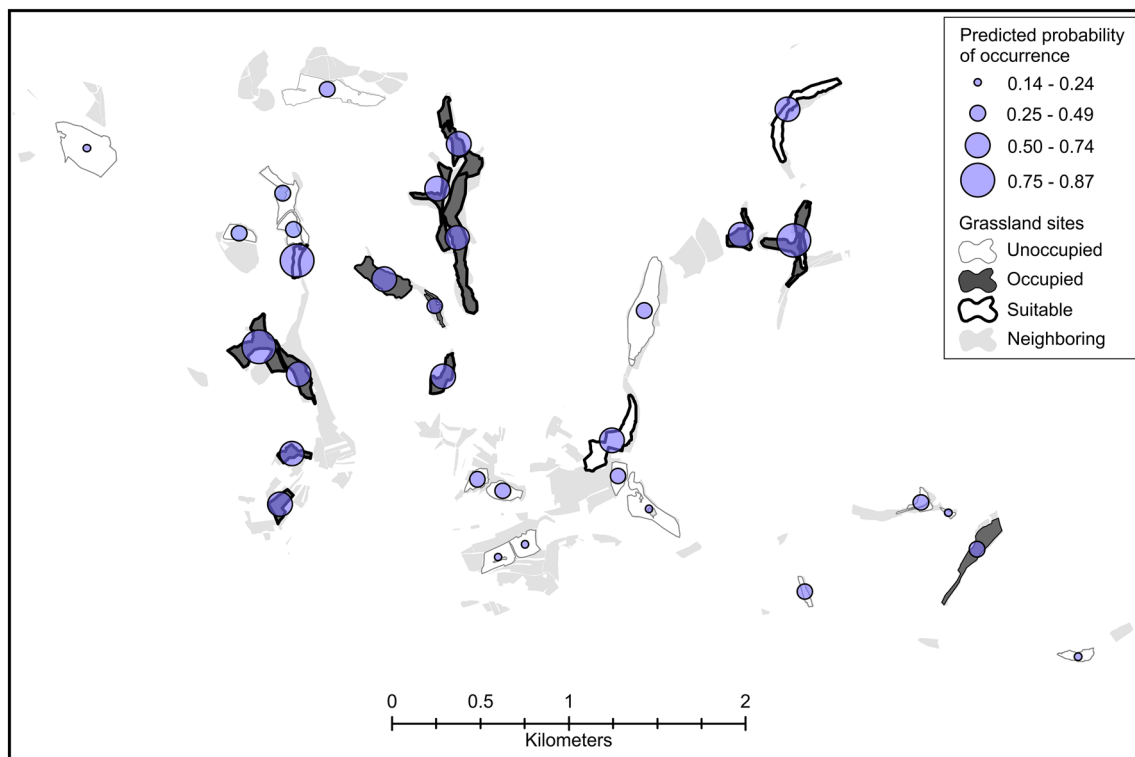
Fig. 5 Predicted and observed occurrence of *P. nausithous*. Scaled circles indicate the predicted probability of butterfly occurrence per grassland site based on the ensemble prediction. Polygons highlight grassland sites occupied (dark grey) or unoccupied (white) by the butterfly, and suitable according to $P_{crit} > 0.51$(black-lined). Neighboring grasslands (light grey) within 250 m geodesic buffer are presented to highlight the structural connectivity of each grassland site

plant abundance and density have been demonstrated to be less important for *P. nausithous* as long as suitable host plants and host ants are available (Anton et al. 2008; Batáry et al. 2009; Jansen et al. 2012). Host plant suitability is mostly related to host plant height and flower maturity (Thomas and Elmes 2001; Anton et al. 2008), which were highly correlated in our data set (Box 2 in Online Appendix 1). In our case, the occurrence probability of *P. nausithous* increases with the area covered by either "dense" or "sparse" classes, but grassland sites entirely covered by *S. officinalis* do not guarantee butterfly presence. This seems particularly true in some of our studied sites where *P. nausithous* occurred despite both "dense" and "sparse" cover-classes barely representing 50% of the total grassland area (*c.* 3500 m^2). This suggests that grassland sites covered by small areas of *S. officinalis* may shelter the butterfly, and even those areas covered sparsely by the host plant may constitute suitable habitats for *P. nausithous* (Thomas 1984; van Langevelde and Wynhoff 2009). Since the host ant nests and the host plant do not necessarily co-occur in very close vicinity (Kempe et al. 2016), the presence of buffer zones with scattered host plant and host ant may have contributed to *P. nausithous* occurrence at the local scale.

Local grassland features such as management type (pasture or meadow) and topography (slope and aspect) also influenced the occurrence pattern of *P. nausithous*. There is evidence that low intensity grazing creates a small-scale mosaic of disturbances in the soil and the vegetation structure thereby enabling niches for plant species establishment, including *S. officinalis* (Settele and Henle 2009). Slope and aspect are generally considered important factors determining microclimate and habitat choice of invertebrates in uplands (Weiss et al. 1988, 2013). The combined effect of grazing, slope, and aspect on butterflies has previously been reported in upland grasslands (Thomas et al. 1998; Settele and Henle 2009; Spitzer et al. 2009). For example, *Phengaris arion* (Linneus, 1758) is restricted to intensively grazed grasslands on south-facing slopes at cooler and higher elevations in the UK and northern Europe due to the thermal ecology of its host ant *Myrmica sabuleti* (Meinert, 1861); while at lower elevations this butterfly species is associated with less intensively grazed and flat sites (Thomas et al. 1998; Settele and Henle 2009). In our study, most of the butterfly observations were associated with extensively managed pastures on the steeper slopes facing east or southeast. Grassland sites on south and southwest-facing slopes receive more solar radiation in the northern

hemisphere and therefore have warmer/drier environments with variable microclimate (Bennie et al. 2008). In contrast, east-facing sites receive radiation earlier in the day when the air temperature is lower, which involves lower rates of evapotranspiration than the west-facing sites and therefore moister habitats (Ashcroft et al. 2008). The rotational system of low-intensity grazing in our study region may further provide a spatio-temporal heterogeneity in vegetation structure, thereby buffering the cool upland conditions towards warmer but moist conditions favorable not only for larval development of *P. nausithous* (e.g. Weiss et al. 1988) but also for the *M. rubra* nest establishment (Wynhoff et al. 2011; Pérez-Sánchez et al. 2018). The significant difference in densities of the host ant between the grassland management types ($\chi^2 = 5.88$, df = 1, p = 0.01) clearly indicates more suitable conditions for *M. rubra* in pastures than in meadows.

From a landscape perspective, the surrounding forest cover and structural connectivity were also important factors determining the occurrence pattern of *P. nausithous*. Grassland sites surrounded mostly by forest and having few neighboring grasslands showed a higher probability of occurrence of *P. nausithous* compared to sites entirely surrounded by grassland or built-up areas. The positive effect of neighboring forest on butterflies has been reported in temperate grasslands where a higher proportion of forest-grassland edges may provide significant gradients in solar radiation, temperature, wind speed and moisture (Krämer et al. 2012; Öckinger et al. 2012; Liivamägi et al. 2014). In our case, such gradients may offer favorable moisture levels for the establishment of *S. officinalis* and *M. rubra* in grassland sites, and thus promote the occurrence of *P. nausithous*. The fact that *P. nausithous* has a strong preference for occupying areas where the host plant is located next to tree-lined edges in forest-dominated landscapes may support this idea (Batáry et al. 2009; Kőrösi et al. 2012; but see Nowicki et al. 2013). However, surrounding forests also impose a physical barrier for the butterfly and increase grassland isolation (Krämer et al. 2012; Skórka et al. 2013; Nowicki et al. 2014). Importantly, our results revealed that low rather than high levels of connectivity between grassland sites increase the occurrence probability of *P. nausithous*. In contrast, Nowicki et al. (2007) found a positive relationship between connectivity and the occurrence of this species. However, both findings were based on different patch-scale units and should therefore not be compared. Nowicki et al. (2007) considered areas densely covered by *S. officinalis* as habitat patches and measured their isolation in a matrix dominated by meadows, while our approach was based on grassland sites as potential habitat for *Phengaris, Myrmica and Sanguisorba* species within a forest-dominated landscape. More comparable results have been found for *Phengaris alcon* in the Netherlands where site connectivity along with habitat quality contributed to explain heathlands occupancy by the butterfly (WallisDeVries 2004). Our results demonstrated that grassland sites containing suitable host resources and forming spatial clusters of few grassland sites have a higher probability of being occupied by *P. nausithous*. These findings likely reflect the importance of small-scale networks of suitable grasslands for species with low mobility such as *P. nausithous* (van Langevelde and Wynhoff 2009), and suggest that maintaining and improving such connected small networks may be an effective conservation strategy in forest-dominated upland landscapes.

Our application of an ensemble of small models (ESM) based on 13 predictors (host resources, local and landscape variables) proved useful to explain and predict the occurrence of *P. nausithous* in upland grasslands. Despite the small sample size, the internal evaluation of the ESM by means of LTOCV indicated a strong predictive performance (Breiner et al. 2015). Furthermore, the implementation of a very strict performance threshold during the ensemble construction resulted in a more parsimonious and robust model for prediction. Overall, these specifications translated into more reliable results concerning the detection of grassland sites that may constitute suitable habitats for this endangered species. An overall accuracy of 0.84 indicated a high performance on predicting suitable sites, and the number of false negatives (2 sites) and false positives (3 sites) has an ecological explanation and implications for conservation planning and management. False negatives corresponded to isolated grassland sites discussed before where the host ant was not detected and therefore the butterfly is not expected to occur; while false positives correspond to three different grassland sites that, despite being unoccupied by *P. nausithous*, offer suitable conditions in terms of host resources, local and landscape conditions. The latter situation commonly occurs in butterfly metapopulations where not all suitable habitats are necessarily occupied by local populations and there is a constant turnover through local extinction and re-colonization (Thomas and Hanski 1997). It may be also possible that *P. naustihuos* were present in such sites but as larvae inside the nests rather than flying adults. Larvae with biennial development have been detected in *Phengaris* species, and there is evidence suggesting polymorphic growth is present in *P. nausithous* (Witek et al. 2006). In any case, we are confident of having detected true absences in our studied grasslands due to we performed repeated butterfly counts in three different sessions throughout the flying period, fulfilling the effort required to avoid false absences with 95% of certainty (Pellet et al. 2007). Therefore, since colonization events are frequent within metapopulations of *P. nausithous* (Nowicki et al. 2007 but see van Langevelde and Wynhoff 2009), those suitable sites detected by the ESM approach are relevant for the conservation of *P. nausithous* and should be prioritized for butterfly natural colonization.

This study makes an important contribution to assessing known *Phengaris-Myrmica-Sanguisorba* patterns and provides a novel approach for evaluating and predicting unknown patterns of *P. nausithous* occurrence regarding local and landscape conditions. However, our results are limited to one-year sampling and one system of grasslands that, despite of being representative of central Germany uplands, may not be necessarily extrapolated to all upland landscapes of central and northern Europe. Multiyear sampling and site-specific historical records would be needed to draw better conclusions since occurrence and abundance in *P. nausithous* may vary considerably between years (Nowicki et al. 2005; Jansen et al. 2012). Nevertheless, an expansion of the sample size by adding data from neighboring grassland sites would improve this approach consistently and would allow transferring it to other upland regions.

Conclusions and implications for conservation

Our study confirmed the presence of the dusky blue *Phengaris nausithous* in upland grasslands of the region Thuringian Forest but with rather low numbers of individuals per grassland sites. Although alarming such low numbers are in accordance with the range of patterns reported across Europe where *P. nausithous* populations may vary locally from very small populations of few individuals to large populations of several hundreds of individuals (Thomas 1984; Mungira and Martín 1991; Nowicki et al. 2005). Although the assessment of *P. nausithous* density was not part of our research aim, our species occurrence approach may be considered as a proxy for the local metapopulation abundance. In this sense, the low abundance detected must be considered as premise in further conservation actions for the species in the region.

Disentangling the complex effects of host resources, local and landscape variables on the occurrence pattern of the specialist dusky large blue butterfly contributed to identifying key parameters for the assessment of habitat quality (sensu Wallis DeVries 2004; Mortelliti et al. 2010). Our results emphasize that not only the availability of host resources, but also local grassland management, topography, landscape composition and connectivity are crucial for preserving *P. nausithous*. Nest density of *M. rubra* as well as cover and height of *S. officinalis* are key host resources required by this highly specialist butterfly (Thomas 1984; Thomas et al. 2001; Anton et al. 2008). Grasslands with low-intensity grazing, steep slopes facing east (or south-east), high percentage cover of forests in the surrounding landscape matrix, and small connected networks of grassland sites positively affected the occurrence of *P. nausiothous*. Hence, conservation actions should

first aim at preserving existing populations in the study region by maintaining the traditional low-intensity grazing management on grassland sites where *P. nausithous* was detected. Ideally, the grazing pressure should be reduced from early-June to mid-September to guarantee female oviposition and larvae adaption of the host ant (van Swaay et al. 2012). Secondly, grassland sites unoccupied by *P. nausithous* but suitable in terms of host resources, local and landscape conditions should be targeted as potential habitats for natural colonization. Connectivity between source and predicted suitable grassland sites would be feasible if the current rotational grazing system were maintained and even expanded (Fig. 2 in Online Appendix 3). Livestock movement between grasslands across mountain valleys and next to small water streams may contribute to keep small open areas within the forest matrix. Such areas may act as dispersal corridors since they offer potential stepping-stone habitats for *P. nausithous*, where the river corridor plant *S. officinalis* and flood-resistant *M. rubra* are expected to occur (Winter et al. 2008; Arndt et al. 2011). Hence, conservation actions such as agri-environment schemes should include a landscape perspective to promote connectivity and enable *P. nausithous* dispersal between semi-natural grassland sites in upland forest-dominated regions. More elaborated models based on landscape resistances including topographical features might prove to be valuable for establishing dispersal corridors for the dusky large blue butterfly and its hosts in upland grasslands of the region.

Compliance with ethical standards

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