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ORIGINAL PAPER

Habitat diversity and peat moss cover drive the occurrence probability of the threatened ground beetle *Carabus menetriesi* (Coleoptera: Carabidae) in a Bavarian mire

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Abstract

Within the Natura 2000 network, there is a legal imperative to protect endangered species. A lack of knowledge about habitat requirements for these species undermines the ability to make informed decisions about appropriate conservation measures, especially for isolated populations that may have developed habitat preferences specific to their region. *Carabus menetriesi* is an endangered ground beetle found in Europe and warrants protection under EU law. We collected occupancy data of *C. menetriesi* using live pitfall traps over two seasons in 2016 and 2018 at a protected nature reserve in southern Bavaria, Germany. Here, we present the results of a patch-occupancy modeling approach to determine habitat preferences for *C. menetriesi* at this site. Our model shows that increasing *Sphagnum* cover and habitat diversity led to higher occupancy levels for *C. menetriesi* at this site, while tree cover was negatively correlated with occupancy, but increased the detectability of the species.

Implications for insect conservation Measures for protecting the *C. menetriesi* population at the study site were taken in accordance with our results. Areas with high tree cover were thinned at several sites, although the success of this measure has yet to be determined. Our findings about habitat diversity suggest that expansion of low intensity grazing in the area, a measure that was suggested as a result of our survey and is currently in process of implementation, might benefit the species. Whether our results can be transferred to *C. menetriesi* populations in different habitats remains to be investigated, however, our methodological approach with regard to both the data collection and analysis can be used to assess other populations and provide important information about relevant habitat parameters for that population. This will allow conservation managers to make well-informed decisions about conserving *C. menetriesi,* or indeed other similar carabid species with isolated populations.

Keywords *Carabus menetriesi* · Ground beetle · Habitat diversity · Patch-occupancy · Habitat management · Raised bog · Transition mire

Introduction

In light of recent research into the global decline in insect populations, there have been renewed calls for focusing on invertebrate conservation (Cardoso 2012; Hallmann et al. 2017; Klink et al. 2020). The European Habitats Directive aims to conserve rare and threatened species and their habitat and has a high impact for conservation in the European Union. Within the context of this directive, although arthropods are significantly underrepresented (only 122 of listed species in Annex II), there is a legal imperative to protect those species listed (Cardoso 2012). *Carabus menetriesi* Hummel 1827 (Fig. 1) is a ground beetle (Coleoptera, Carabidae) with a high priority of protection within both EU and German national conservation frameworks (EU 1992; Schmidt et al. 2016), and the only priority carabid species covered under the European Habitats Directive in Germany (Annex II of the Natura 2000 directive). Therefore, there is both a high need and political backing for appropriate protective measures for this species as it seems to be a taxon with a long-term decline (e.g. Assmann 2003).

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Fig. 1 Male Carabus menetriesi at our study site in Southern Bavaria, 20.6.2016. Photo I. Harry

However, the habitat requirements for *C. menetriesi* are still uncertain and the subject of ongoing discussion in the literature: researchers agree that the species is stenotopic and limited to nutrient-poor wetland habitats, but perceptions about preferences for certain habitat variables differ, e.g. regarding canopy cover or water regime (Turin et al. 2003; GAC 2009; Müller-Kroehling 2017). Habitat requirements might also differ between small and isolated populations, as different subspecies have been described (Löbl and Löbl 2017). From other *Carabus* species it is known that subspecies (and populations) can differ regarding their habitat selection/preferences (Turin et al. 2003). Due to this uncertainty in habitat requirements, it is still unclear what conservation measures are required to appropriately protect the habitat of this species. For many insect species, "simple" habitat protection is not sufficient for the long-term conservation of the species (e.g. via progressive succession of vegetation). In many cases, it is necessary to conserve the specific habitat requirements of the given species through specific ecosystem processes. Such aspects of habitat management may include rewilding or regeneration approaches. This lack of sufficient information regarding specific habitat requirements makes it difficult to manage habitats in a way that is consistent with the specific habitat requirements of *Carabus menetriesi* (EU 1992, p. 7; Homburg et al. 2014).

Here, we attempt to address the knowledge gap surrounding the habitat preferences of *C. menetriesi* using site-occupancy modelling of detection data from a nature reserve in Bavaria in southern Germany. We use live pitfall-trap data collected over two field seasons to elucidate the habitat preferences for the species. The habitat variables collected were based on previous knowledge of *C. menetriesi* habitat preferences (along with other bog dwelling carabids). One additional habitat characteristic that we looked into was small-scale habitat diversity. We are interested as to whether the close interlinking of different habitats influences the occurrence of *C. menetriesi*, the only *Carabus* species adapted to the harsh conditions in this environment. Due to contradictions in the literature on subpopulations in different geographic areas, we did not go into the study with expectations about how each single environmental variable might positively or negatively affect *C. menetriesi* occupancy. However, we expect to find a relationship between the presence of *C. menetriesi* and some of the habitat variables we collected, and will highlight those with the strongest effects in order to inform conservation management decisions. We thus present a natural history study in order to help guide conservation management and further research.

Methods

Study area

The study area is an upland wetland complex in the district of Swabia, Bavaria in southern Germany. Due to the sensitive nature of this rare species, the exact location is not given here to avoid illegal collecting. The region, located in the foothills of the Alps, is characterised by a high density and diversity of wetlands (detailed below).

The study area is a nature reserve with an area of approx. 5 km^2 at an elevation of about 800 m asl. The area is classified as a terrestrialisation mire (Succow and Joosten 2012) formed by the addition of silt and organic matter to the adjacent lake. Within the study area, habitat diversity is influenced by topography and hydrology, as well as the current and historical land-use. Topographically, there is an adjacent drumlin and sea-chalk deposits leading to calcareous fens at these sites. They alternate with raised peat bog sites without any groundwater influence. In between are large swaths of transition mires with different characteristic vegetation depending on the level of groundwater influence, which varies across these sites.

Land use in the nature reserve historically was, and currently still is, diverse. Parts of the reserve are subject to low-intensity grazing by cattle in a large commons area, and one of the former four commons pastures is now fallow land. Other parts have been used for hay production. These areas have fallen fallow for different periods of time over the past 70 years, creating a mosaic of habitats in different successional stages. Small-scale peat ditches (formed by past peat harvesting) as well as drainage ditches also exist in the area. As a result of the varied land-use and topography, the study area contains a variety of wetland habitats (active raised bogs, degraded raised bogs, transition mires, alkaline fens, *Molinia* meadows, sedge swamps, thin and dense stands of *Pinus mugo* ssp. *rotundata* bogs, *Picea abies* dominated woodland bogs and others). The size of these habitat patches varies, and different habitats are often located in close proximity to each other.

Data collection

Carabus menetriesi sampling

Sampling was conducted from May to July in 2016 and 2018, a time with high locomotory activity of this spring-breeding carabid species (Turin et al. 2003; Harry et al. 2005). Live pitfall traps were used in order to avoid impacting the population of this protected species. Traps had a diameter of 10 cm and depth of 11 cm and were filled with a bed of *Sphagnum* moss to prevent harm to any captured beetle. A transparent plastic roof placed 3–5 cm above the trap protected the traps from precipitation and predation. In each year, different transects of traps were set. Five traps spaced 10 m apart were exposed per transect. In 2016, 102 transects with 510 traps were established on May 30 and checked every 5 days for a total of six revisits. Collected beetles were recorded and then released at a distance of at least 3 m from the nearest trap. The short exposition time led to survival rates of *C. menetriesi* individuals of over 95%. In 2018, 57 transects with 285 traps were established on May 18. After learning from the sampling experience in 2016 we chose a prolonged exposition time of 7 days which we kept for the sampling period for all transects. The survival rate also exceeded 95% in 2018.

Habitat surveys

In a 1.5 m radius around each individual trap, we recorded a number of site-level environmental parameters. We estimated ground vegetation cover for various vegetation classes (grass excluding *Phragmites*, herbaceous plants, *Phragmites* reed, *Sphagnum* moss, other mosses, bare ground, litter and water). Heights and cover of *Sphagnum* mounds were also recorded. In the same radius around each trap, we recorded the median of three pH-value measurements determined with a soil pH meter (PCE-PH20S from PCE instruments). Woody plants, classified as either shrubs (< 1.5 m) or trees (> 1.5 m), were surveyed in a 5 m radius around each pitfall trap. We used a larger radius for woody plants, as we expected larger-scale effects due to shading. To take different canopy densities into account, tree cover was measured as the vertical shading effect of trees. We also determined a variable reflecting the habitat diversity in a 30 m radius around each trap, a distance that is regularly covered by *C. menetriesi* individuals (Harry et al. 2005) with QGIS (QGIS Development Team 2021). We then intersected circles with a 30 m radius around the trap with data from a detailed vegetation survey from the nature reserve (Wagner 2012). The survey mapped biotopes for the whole nature reserve according to regional standards (LfU 2010). We then calculated the Shannon diversity index for habitat types for each trap with the R package vegan (Oksanen et al. 2018). This index reflects both the diversity and the evenness of different habitat types, with sites having more diverse and more evenly distributed habitats receiving a higher index value.

Statistical analysis

We collected data on the abundance of trapped individuals, but as live traps were used, it is possible that once a single *C. menetriesi* individual was caught, further individuals were lured towards the trap by pheromones or other chemical attractants, especially if the initially trapped individual was a female (Weeks and McIntyre 1997; Baumgartner 2000). This would invalidate the independence of the data and provide potentially inaccurate results (Steel et al. 2013). Instead of a Poisson regression, we thus opted for a hierarchical site-occupancy model (also called a patch-occupancy model) to model binary detection/non-detection of *C. menetriesi* (MacKenzie et al. 2002; Tyre et al. 2003). This type of model is used when individuals are not marked and sites are revisited multiple times. It is useful to model occupancy in this way when detection is imperfect (Royle et al. 2005), especially when dealing with inconspicuous study organisms that occur in low densities at a landscape scale. The model consists of two parts: one equation to model the detection probability (p) and one to model the actual occupancy of the species (ψ). By incorporating the detection probability into the analysis, we can reduce the bias in the occupancy estimations. We then model:

$$\text{State process: } \mathrm{z_i} \sim \text{Bernoulli}(\psi)$$

$$\text{Observationprocess}: y_{ij}|z_i \sim Bernoulli\left(z_i \cdot p_{ij}\right)$$

where z_i is the true occurrence state of *C. menetriesi* at trap i and the Bernoulli parameter ψ is the expected value of z, i.e. the probability of a trap being occupied (presence). The observed variable $y_{\{ij\}}$ is the measurement of occurrence at trap i during survey j, which is conditional on z_i, and p is the detection probability of *C. menetriesi* at trap i during survey j.

As the outcome of the observation process is dependent on the state process, we assume that there are no false positives, or, in other words, that it is possible for a *C. menetriesi* individual to not be recorded where it occurs, but impossible for one to be recorded where it is absent (Kéry and Royle 2015).

Environmental covariates

For each site, a number of environmental variables that may affect the habitat quality and therefore occupancy of *C. menetriesi* were recorded as mentioned above (see Table 1). Site-level covariates were selected *a-priori* based on previous

Table 1 Environmental predictors used in the global model. Also included were the categorical variable 'year' as well as latitudinal and longitudinal coordinates along with their polynomial terms. Only tree cover, *Sphagnum* cover, Shannon diversity and longitude (not shown here) were selected as occupancy covariates in the unmarked model, while tree cover was additionally selected as a detection covariate

Covariate	Year	Mean	Min	Max
Tree cover*	2016	10.96	0	90
	2018	23	0	95
Shrub cover	2016	9.3	0	60
	2018	14.24	0	70
Herb cover	2016	9.71	0	80
	2018	5.15	0	75
Sphagnum cover*	2016	38.46	0	90
	2018	55.57	0	100
Grass cover	2016	32.18	0	85
	2018	35.16	0	100
Bare soil	2016	2.73	0	20
	2018	3.41	0	95
pH	2016	4.9	2.4	7.5
	2018	4.54	2.7	7.7
Shannon diversity*	2016	0.56	0	1.59
	2018	0.79	0	1.55

*Covariates selected for inclusion in final model

knowledge of the ecology and habitat use of *C. menetriesi* (Harry et al. 2005). We also included interaction terms for tree cover with shrub cover, herb cover, and grass cover (*tree:shrub, tree:herb, tree:grass, tree:sphagnum).* In the case of collinearity between predictors, we excluded one of them from the analysis, choosing the ecologically more relevant variable. Additionally, we included the geographic coordinates of each trap (along with multinomial terms) to represent unmeasured environmental predictors and account for spatial autocorrelation between samples. Below we describe the shrinkage that prevents this trend-surface from introducing bias to the regression results. We also included 'year' as a predictor to account for any differences in environmental conditions between 2016 and 2018. A dummy predictor with two levels (0 = 2016, 1 = 2018) was used in place of this categorical variable. All predictors were centered and scaled to a mean of 0 and standard deviation of 1 prior to analysis.

Model fitting and selection

All data handling and analyses were conducted using the statistical software R (R Core Team 2020). We first fit a model within a Bayesian framework in JAGS using the R2jags package (Su and Yajima 2020) in order to perform model selection. We fit a global model including all predictors in both the state and observation process. By using a Bayesian lasso with a Laplace double exponential prior, we were able to provide shrinkage to model parameter estimates and effectively remove unimportant predictors from the model. See Appendix for details regarding model selection.

We then used the retained model parameters from the JAGS model to fit essentially the same model using the 'occu' function with the R package unmarked (Chandler et al. 2020), which fits a hierarchical occupancy model based on zero-inflated binomial models. This was done to be able to present the analysis and results within the traditional frequentist framework and at minimal statistical jargon; both approaches are equivalent in their estimates and ecological interpretation. Tree cover was borderline insignificant for occupancy in the JAGS model, so we ran models both with and without this covariate in unmarked and chose the model with a lower AICc (with tree cover was lower, see Appendix). Tree cover was the only parameter to be included in the observation model, while tree cover, *Sphagnum* cover, Shannon diversity index and latitude parameters were included in the occupancy model, as well as a random intercept for the transect number, resulting in the following model structure:

$$\text{State process (occupancy)}: logit(\psi_i) = \beta_0 + \beta_1 \cdot \text{Tree cover}_i + \beta_2 \cdot \text{Sphagnum cover}_i + \beta_3 \cdot \text{Shannon}_i + \beta_4 \cdot \text{latitude}_i$$

where β_0 is the logit-linear intercept for the probability of occurrence of *C. menetriesi,* and β_1, β_2, β_3, and β_4 respectively represent the slopes of the effects of the environmental covariates tree cover, *Sphagnum* cover, Shannon diversity and latitude at each site i.

$$\text{Observation process (detection)}: logit(p_{ij}) = \alpha_0 + \alpha_1 \cdot \text{Tree cover}_i$$

where p_{ij} is the probability of detection of *C. menetriesi* at site i during survey j,α_0 is the logit-linear intercept and α_1 is the linear effect of tree cover at site i across all surveys. No survey level effects were included.

A Mackenzie-Bailey goodness-of-fit test fit with the 'mb.gof.test' function from the R package AICcmodavg (Mazerolle 2020) suggests mild overdispersion in the model, with a c-hat value of 3.4, greater than the ideal value of 1, but still less than the value of 4 regarded as problematic (Kéry and Royle 2015; Mazerolle 2020). Moreover, after plotting the model residuals (aggregated by site) against modeled covariates, we could not detect any systematic patterns, indicating that there was no systematic fitting error in our model.

Table 2 Model estimates for the hierarchical patch occupancy model. Shown are the model estimates for each parameter along with standard errors (SE) and p-value. Statistical significance of a predictor is denoted with an asterisk

Model parameter	Estimate	SE	P
Tree cover (detection)	– 0.232	0.115	0.044*
Tree cover (occupancy)	– 0.375	0.251	0.135
Sphagnum cover	0.645	0.245	< 0.01*
Shannon diversity	0.606	0.257	0.018*
Latitude	– 1.532	0.321	< 0.01*

Results

In total, 297 *C. menetriesi* specimens were captured at 129 of 795 traps (16.2%) across both sampling years, with 15.3% of traps occupied in 2016 and 17.9% of traps occupied in 2018. A large variety of microhabitats was covered by the sampling, according to the range of the environmental covariates recorded in both 2016 and 2018 (see Table 1). The range of habitat diversity as calculated by the Shannon index also shows that the surrounding of some traps were homogeneous with respect to habitat, while others contained a variety of habitat types within a 30 m radius around the trap.

The model selection in JAGS revealed that tree cover was the only covariate affecting detection, while tree cover, *Sphagnum* cover, Shannon diversity and longitude had an effect on occupancy. For details on the results of the JAGS model see the Appendix.

In the selected model (Table 2), we found a positive effect of tree cover on detection probability, with detection probability nearly twice as high at sites with 95% tree cover than those with no tree cover (Fig. 2a). The model also revealed significant positive effects for occupancy driven by *Sphagnum* cover and Shannon habitat diversity (Fig. 2c–d), while tree cover showed a negative effect (Fig. 2b). There was also a pattern detectable related to the latitudinal coordinates.

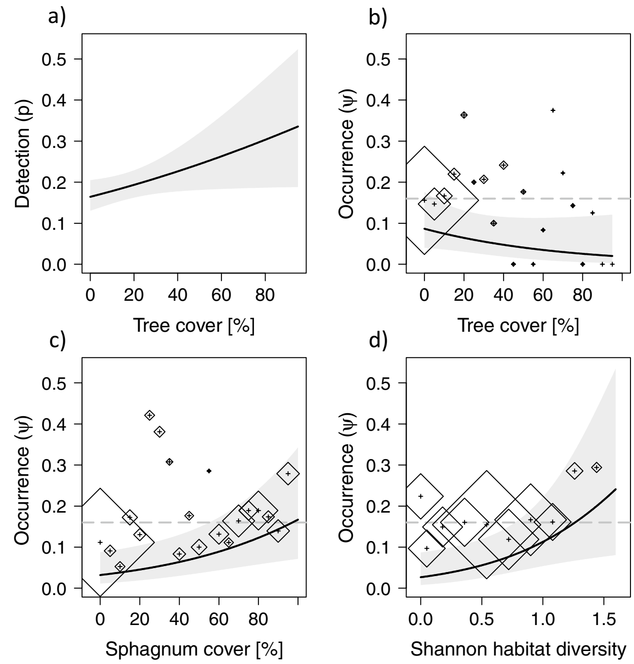

Fig. 2 Effect plots from our selected model for detection (**a**) and occupancy (**b–d**) of C. menetriesi. Shown are the response scale effects of the individual habitat covariates in the ‘unmarked’ model, along with the 95% confidence interval (grey area). The mean occupancy rate (**b–d**) are shown as horizontal dashed lines. The real data are superimposed on plots b-d and show the mean occupancy for each class of covariates. The size of each diamond represents the proportion of samples taken in each class relative to all samples. For each plot, all other covariates were held constant at their mean value

Discussion

With this study, we illustrate an approach to identify and estimate the effect of conservation-relevant habitat characteristics for a stenotopic ground beetle species, while taking potential observational errors into account by modeling both occupancy and detection probability. We highlight the importance of analysing both of these aspects, which gives us more accurate prediction estimates for this type of study design, especially when the target species is rare and there are many traps without any recorded individuals. Importantly, this study has given us insight into the habitat requirements for *C. menetriesi,* a threatened ground beetle species, which can help guide conservation measures for this species. We found that higher *Sphagnum* cover and higher Shannon diversity of habitat types surrounding the traps increased occupancy, while tree cover showed a negative, but insignificant effect. Increasing tree cover did, however, increase the detectability of the species.

Habitat characterisation

Tree cover was the only predictor with an effect on detection probability in our selected model. The effect was positive, i.e. the higher the tree cover, the easier it was to detect the species. This may be due to the fact that under the unfavourable conditions at these sites, the locomotory activity and therefore detectability of these ground beetles increases. Baars (1979) showed that individuals of *Poecilus versicolor* and *Calathus melanocephalus* in Dutch heathlands move longer distances per unit time when they are in unfavourable habitats (directed movement). When beetles show higher activity levels, the probability of

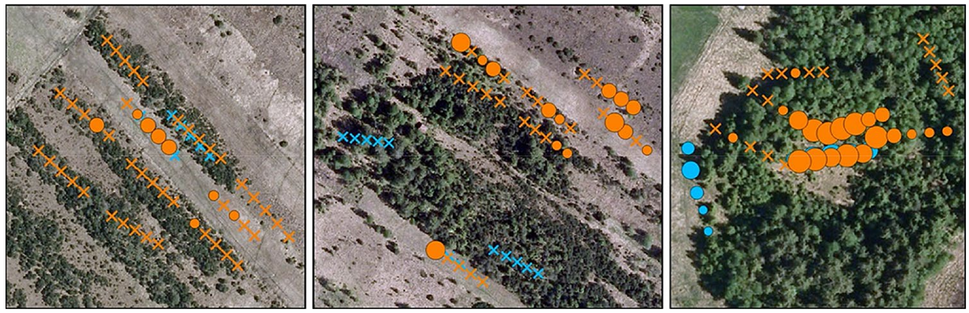

Fig. 3 Occupancy of exemplary sites in the years 2016 (blue) and 2018 (orange). Position of sites with no catches are indicated by crosses; points indicate position of sites with recorded specimen; the bigger the points are the more individuals were caught. Each transect consisting of five traps is 40 m long

detection in pitfall traps increases (Thiele 1977; Spence and Niemela 1994). In contrast, tree cover had a negative effect on occupancy. While this trend was not significant in our model, we observed several cases where we exposed parallel transects in open and forest habitats where we determined much higher densities in open habitats (Fig. 3). We conclude that individuals are less likely to occupy areas with high tree cover, but if they are present, it is easier to detect them. Analysing the data without considering the detection rate may thus have missed this dual effect of tree cover and hence an important contributor to habitat preferences.

With increasing Shannon habitat diversity, occurrence of *C. menetriesi* increased. The preference for areas with high structural heterogeneity is not unique to *C. menetriesi*. Habitat suitability models for other carabid species have also shown that they do not primarily occupy forests or open areas, but rather prefer structurally rich edges and transition habitats. For *Carabus nitens*, Volf et al. (2018) observed a preference for transition habitats or a diverse mosaic of microhabitats, and Pokluda et al. (2012) shows the importance of moist and tall vegetated patches in steppe habitats for *Carabus hungaricus*, indicating the importance of small scale habitat diversity for this species as well. Furthermore, even typical forest species such as *Carabus variolosus* tend to avoid areas with high tree density (Matern et al. 2007). One explanation for the preference of areas with higher habitat diversity might be the extreme conditions in the habitats where *C. menetriesi* occurs. In almost all sites we sampled, *C. menetriesi* was the only species of the genus *Carabus* we observed, and other large carabid species were rarely found. Even if *C. menetriesi* is a clearly stenotopic species adapted to moorland conditions, high habitat diversity might support a shift to more suitable habitats depending on weather conditions, life cycle stage or time of year. Seasonal migration between habitats is documented for *Anchomenus dorsalis*, but also other other species including *Carabus granulatus* (Thiele 1977: 153f), the sibling species of *Carabus menetriesi*. The *Carabus* species mentioned here are similar in that they populate rather extreme habitats where other *Carabus* species rarely occur, and the aforementioned studies as well as our work suggest that heterogeneity might play an important role within these extreme habitats.

Sphagnum is clearly important for the persistence of this species in many populations. A study on habitat traits affecting carabid diversity from Belarus, where *C. menetriesi* is listed as vulnerable on the national red-list, found that *C. menetriesi* was mostly associated with hummocks and open bog areas, which have a high level of *Sphagnum* cover (Sushko 2019). Other ground beetles are also known to prefer or even exclusively inhabit *Sphagnum* moss cover (e.g. *Agonum* species *A. ericeti* and *A. munsteri*, Lindroth and Bangsholt 1985). For a semi-aquatic *Carabus* species it was shown that it apparently avoids such *Sphagnum* areas (Koth 1974). The conservation of *Sphagnum* plays an important role in preserving the microclimatic conditions of these habitats, as *Sphagnum* species are known for their ability to retain moisture both in living and dead plant cells. This could play an increasingly important role in Central Europe, where summers are predicted to become hotter and drier in the future (Suarez-Gutierrez et al. 2020). *C. menetriesi* individuals have also been observed using *Sphagnum* hummocks for overwintering, as they help to buffer the cold temperatures (Keddy 2010). The preference for *Sphagnum* cover observed for *C. menetriesi* in the study area indicates that the species apparently prefers living, growing bogs. Habitat management must address this. However, there are habitats where *C. menetriesi* occurs where *Sphagnum* is completely absent and significantly higher pH values are present in the peat. Another stenotopic *Carabus* species, *C. clathratus*, is hygrophilous and occurs from peat pits with lush, *Sphagnum*-dominated vegetation to habitats with very different characteristics; namely salt marshes with small tideways and complete absence of any *Sphagnum* (Turin et al. 2003).

Interestingly, we did not find any relationship between occupancy of *C. menetriesi* and soil pH. Especially in montane habitats, *C. menetriesi* is sometimes described as a species of ombrotrophic peat bogs (Müller-Kroehling 2017), which are characterised by low pH. For the evaluation of habitats for the European Habitats Directive, the presence of plant species indicating influence of ground water is even listed as an adverse effect (PAN and ILÖK 2010). Others have stated the species prefers transition mires over raised peat bogs and suggest that the latter are of subordinate importance (Turin et al. 2003; Rietze and Harry 2004). In our study we identified sites with high occupancy of *C. menetriesi* which are mapped as calcareous fens (also free from *Sphagnum* mosses) and show a pH-value around 7. We conclude that a much broader spectrum of moorlands is inhabited by the species than expected in montane habitats as well, at least if there is connection to peat bogs and transition mires.

Habitat management

Based on the results of our study, potential habitat management measures could include the manual thinning out of tree stands or the re-introduction of a managed grazing regime. While parts of the area are still managed by low-intensity grazing other parts became fallow within the last decades (Lederbogen et al. 2004), *C. menetriesi* was able to prosper under low intensity grazing (Rietze and Harry 2004). Extensive grazing would have the additional benefit of increasing the structural heterogeneity of the vegetation, leading to habitat mosaics and higher Shannon diversity index values. In addition, care should be taken not to alter the water levels at the site, especially by the use of drainage ditches.

While we were able to show that certain parameters have a significant effect on presence or absence of *C. menetriesi* at our study area, our results should only be transferred to other populations of *C. menetriesi* with caution. We expect that the isolated and often small populations of the species have developed some adaptations to local conditions. At larger scales, these differences are obvious; for example, we observed a preference for sites with high cover of *Sphagnum* mosses in our study area (as well as in other populations of the species in Bavaria, Harry et al. 2005; Müller-Kroehling et al. 2013) while in the northeastern lowland populations of *C. menetriesi*, *Sphagnum* is not present (Müller-Motzfeld 2005). Our results with respect to tree cover correspond with the results of Paill and Mairhuber (2006) for Upper Austria. However, Müller-Kroehling et al. (2013) describes a preference of *C. menetriesi* for woodland bogs and *Pinus mugo* ssp. *rotundata* stands in low altitude sites and a preference for open habitats in high altitudes in the Bavarian Forest. In some northern populations of *C. menetriesi,* trees are totally absent in the vicinity of populated habitats (Görn et al. 2014; Aleksandrowicz et al. 2016). But even at smaller scales, local adaptations might be strong, due to the isolated nature of these populations. Through personal observations of other populations in southern Bavaria, our findings seem to match habitat preferences of many populations, but even within this region some populations seem to prefer different conditions. We would therefore caution against a general transferability of our results to *C. menetriesi* populations more widely.

Conclusion

With this study, we provide further evidence on important habitat characteristics for *C. menetriesi*, a red-listed bog-dwelling ground beetle. Our study shows that with a sufficient sampling programme a clear picture of distribution and habitat preferences of *C. menetriesi* within a populated habitat can be gained. As a consequence of our research the management regime of our research area was adjusted.

Instead of simply transferring our results to other habitats, we suggest to use similar sampling programmes when studying further populations of *C. menetriesi*. Rather than using a point-approach (i.e. single sampling site), which is the current standard in carabid research projects, a flat approach (i.e. a close network of sampling sites), which is the normal approach in investigations in Natura 2000 context for other taxa groups, should be the standard for assessing and monitoring *C. menetriesi* populations. Multiple re-visits per season also make it possible to fit a patch-occupancy model. In this way, we can learn much more about habitat choice and spatial distribution of the species and create tailored management strategies for local populations.

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Author contributions IH: designed the study, conducted the field work and co-wrote the manuscript. CJS: led the statistical analysis and co-wrote the manuscript. TA: provided pivotal input regarding the interpretation of the results and provided comments on the manuscript. CFD: helped with the statistical analysis and provided comments on the manuscript.

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Declarations

Conflict of interest No funding was received to assist with the publication of this manuscript. The Authors have no competing interests to declare that are relevant to the content of this article. All animal collection was done in accordance with local regulations.

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