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ORIGINAL PAPER

Microhabitat mosaics are key to the survival of an endangered ground beetle (*Carabus nitens*) in its post-industrial refugia

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Abstract

Biota dependant on early seral stages or frequently disturbed habitats belong to the most rapidly declining components of European biodiversity. This is also the case for *Carabus nitens*, which is threatened across Western and Central Europe. We studied one of the last remaining populations of this ground beetle in the Czech Republic, which inhabits post-extraction peat bogs. In line with findings from previous studies, we show that *C. nitens* prefers patches characterized by higher light intensity and lower vegetation cover. Abundance of females was positively correlated with the cover of plant species requiring higher temperature. In addition, we demonstrate its preference for periodically moist, but not wet or inundated plots, suggesting that the transition between dry heathland and wet peat bog might be the optimal habitat for this species. This hypothesis is further supported by results showing a positive correlation between the abundance of *C. nitens* and vegetation cover comprising of a mix of species typical for heathland, peat bog, and boreal habitats. Our results show that *C. nitens* mobility is comparable to other large wingless carabids. The maximum covered distance was ~ 500 m in a month. To ensure the survival of this population, sites of recent peat extraction should be spared from reclamation and afforestation. In contrast, active measures should be taken to facilitate nutrient removal, disturbance of vegetation cover, and the creation of depressions with a humid microclimate. These actions will create a mosaic of heath, bog, and bare ground, which seems to be the preferred habitat of *C. nitens* at our study site.

Keywords Heathland · Habitat preferences · Peat bog · Insect conservation

Introduction

Biota depending upon early seral stages or frequently disturbed habitats is among the most rapidly declining components of European biodiversity (Bakker and Berendse 1999; Spitzer and Danks 2006). Nature conservation often focuses on habitats with well developed, rich or distinct

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plant communities, while attempts to maintain early seral stages with low plant cover are scarcer. Many highly endangered plant and invertebrate species that rely on bare soils and sands with sparse and short-turf vegetation survive in brownfields, mining or post-mining sites rather than in protected areas (Tropek et al. 2010, 2013).

This is also the case of the ground beetle *Carabus nitens* (Linne 1758). This beetle has a Western-Palearctic distribution and exploits a wide variety of habitats including heathlands, peat bogs, sand dunes, and open boreal forests (Assmann and Janssen 1999; Eyre et al. 2003; Filippov 2007). In southern areas of its distribution range, adults are active mainly in spring (April–June) and larval development lasts 35–40 days and takes place in mid-summer (Arndt 1989; Filippov 2007; Turin 2000). Adults overwinter and are active for several years (Assmann and Janssen 1999; Filippov 2007).

This attractive, heliophilous species is declining due to habitat loss in most of Europe and has thus been extensively studied (e.g. Assmann and Janssen 1999; Mathyl 1990). In Western and Central Europe, the beetle inhabits mainly heathlands and peat bogs, preferring disturbed habitats in the building phase (Assmann and Janssen 1999; Gardner 1991). It has also been reported in disturbed semi-open wooded habitats, which may serve as migration corridors or stepping stones (Eggers et al. 2010; Koivula 2002). Many studies suggest that, additionally, humidity might be an important factor affecting the presence of this beetle (Eyre et al. 2003; Luff 1998). As such, understanding how humidity impacts beetle occurrence may be potentially critical for the conservation of the species. However, the information available on humidity requirements of the species is somewhat inconsistent, with its presence being reported in both dry and wet habitats (Assmann and Janssen 1999; Eyre et al. 2003; Gardner 1991; Luff 1998).

In the past, the beetle inhabited a wider variety of habitats with low vegetation cover, including sandy river banks and pastures, and even arable land (Clavier 1977; Gersdorf and Kuntze 1957; Jeannel 1941; Niedl 1959). The land use changes of the past century in Western and Central Europe have thus likely pushed the species towards restricted areas of heathlands and peat bogs, as it similarly occurred for several Lepidoptera species, such as *Lasiocampa quercus, Rhagades prunii*, or *Phyllodesma ilicifolia* (Spitzer and Danks 2006). These traditionally heavily disturbed, nutrient poor habitats are characterized by relatively slow succession and are more likely to retain the vegetation structure required by *C. nitens*. Even there, however, the abandonment of traditional land uses, together with eutrophication resulting from increased nutrient deposits, has led to changes in vegetation structure characterized mainly by increased turf height and density (Bakker and Berendse 1999; Halada et al. 2011; Telfer and Eversham 1996). This pushes the beetle towards extirpation on the remaining inhabited sites, leading to its threatened status in large parts of its distributional range.

Conservation management of heathlands has recently received substantial attention. It has been shown that conventional approaches such as grazing are unlikely to completely halt succession (Bokdam and Gleichman 2000; Eyre et al. 2003; Niemeyer et al. 2005). Thus, in order to support beetle populations, it is necessary to supplement these approaches with active management strategies such as prescribed burning or sod-cutting and top-soil removal (Kotze et al. 2011; Mathyl 1990).

The situation of *C. nitens* in the Czech Republic mirrors its situation in most of Europe. In the past, the species was distributed in several regions of the country (Fig. 1; Niedl 1959). During the second half of the past century, it disappeared from most inhabited sites (Hůrka 1996; Veselý et al. 2009). It, however, became common in parts of northern Bohemia following die-off of mountain forests in the 1980s. There, it inhabited areas where the topsoil, acidified by acid rains, was removed in order to allow growth of subsequently replanted trees. The beetle disappeared following successful

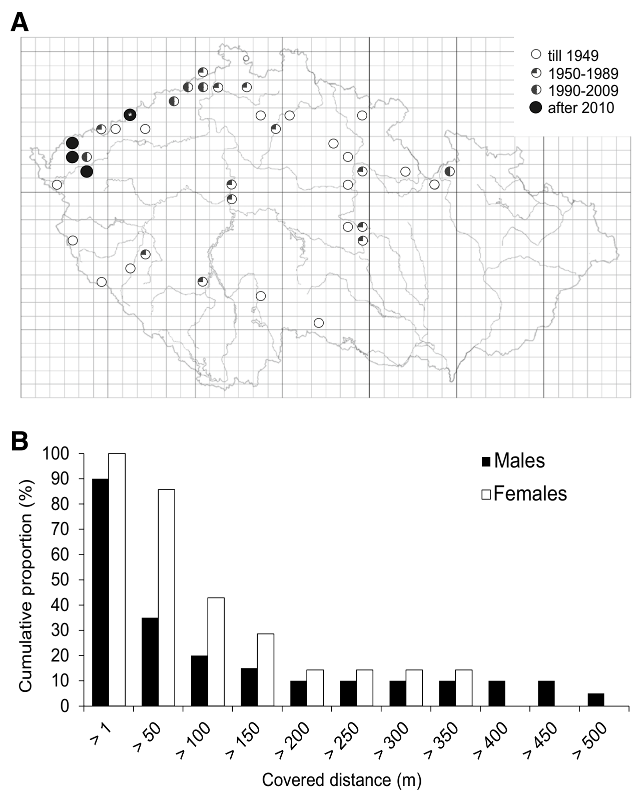

Fig. 1 Distribution of *Carabus nitens* in the Czech Republic (**a**) and distance covered by recaptured *C. nitens* males (N = 20, black) and females (N = 7, white) (**b**). The columns show cumulative proportion of individuals (in %). The data on distribution of *C. nitens* in the Czech Republic were taken from Digital Register of the Nature Conservation Agency of the Czech Republic. The studied population is marked with an asterisk

afforestation and has not been found at several sites of its previous occurrence after 2006, despite efforts to locate it (Pokorný 2006; Trýzna M., *pers. comm.*). Currently, only a few populations are known to survive in the north of the country. Interestingly, two of them inhabit post-industrial habitats. One is located on heaps of former surface coal mines (Prach et al. 2015), the other one inhabits a raised bog that has been subjected to peat extraction since the nineteenth century. Very little is known of the first population, whereas the latter has been continuously frequented by beetle collectors since at least the 1970s.

While most information available on the biology and habitat needs of the species comes from more "natural" habitats such as heathlands, bogs, tundra and the boreal forest zone (Assmann and Janssen 1999; Eyre et al. 2003; Filippov 2007; Koivula 2002), this study focusses on a unique population inhabiting a post-industrial site in the Czech Republic. It is important to study the requirements of this species in post-industrial habitats as their importance for its survival is likely to increase in the future. In order to obtain information on population size, mobility and habitat preferences, which is critical for conservation of the species, we performed a capture-mark-recapture study of the *C. nitens* population and examined the relationship between beetle abundance and microhabitat characteristics.

Methods

Study site and sampling

The study site was a peat bog found 1.75 km NW of Hora Svatého Šebestiána (Sebastiansberg) in NE Czech Republic on the plateau of Krušné hory (Erzgebirge, 50°31′N, 13°13–14′E, 850 m a.s.l.). It is protected under the Nature Reserve Prameniště Chomutovky and as a Site of Community Importance (CZ0420144—Novodomské a Polské rašeliniště, total area: 2614.3 ha). Its topography is flat, its vegetation includes meadows, raised peat bogs, bog woodlands, and heathlands. The study was performed mainly on a regenerating bog following peat extraction and in the surroundings of the extraction site (Online Resource 1). The area has been used for peat extraction since the late nineteenth century and most of the sampling site itself was harvested in the first half of the twentieth century.

Beetles were sampled using the capture-mark-recapture approach with unbaited pitfall traps. All traps consisted of two identical plastic 0.5 L cups and a plastic rain shelter. One cup was permanently placed in the ground, while the other was inserted into it. To cover the peak of *C. nitens* spring activity, traps were activated on 9th April 2016 and removed on 16th June 2016, when beetle activity ceased. Traps were inspected 2–4 times a week. Beetles were individually marked using codes engraved to the sides of elytrae and pronotum. The sex of the captured beetles was recorded. Marked beetles were released 2 m from the respective trap.

A total of 171 traps were positioned across the peat bog and in its vicinity, distributed at various distances but kept at a minimum of 5 m apart. Sampling covered a range of habitats and vegetation types so that all locally abundant habitats were represented with an emphasis on the habitats preferred by *C. nitens* according to Assmann and Janssen (1999), Eyre et al. (2003), Gardner (1991), and Luff (1998). The selection of sampled habitats included closed birch forest, *Pinus mugo* plantation with small trees situated in drained peats, *Pinus mugo* wet peats dominated by *Carex* and *Eriophorum*, heather and sphagnum peats with solitary birch, periodically inundated dump heather and sphagnum peats, peats dominated with bare soil, drained peats dominated with heather, blueberry and grasses, dry heath, and forest edge dominated by grasses and solitary trees.

For each trap, we recorded environmental variables describing abiotic factors, vegetation structure, and composition. The environmental variables were measured on 15th June and on 4th August 2016. We measured the environmental variables on two spatial scales—within circles of 1 and 3 m diameters surrounding the traps. First, we visually estimated the relative cover of (i) the inundated area, (ii) bare ground, and four plant strata: (iii) mosses (E0 plant stratum), (iv) herbs (E1), (v) shrubs (E2), and (vi) trees (E3). Second, we estimated cover of individual plant species using the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1964). In total, we recorded 61 plant species in the patches around the traps. Third, we estimated habitat characteristics for the patches surrounding the traps as community weighted means of Ellenberg's indicator values based on the cover of individual plant species following Ellenberg et al. (1992). The habitat characteristics based on Ellenberg's indicator values have been shown to correlate well with real values (Schaffers and Sýkora 2000). Therefore, we used the computed community weighted means of Ellenberg's indicator values as proxy variables for (vii) light, (viii) temperature, (ix) humidity, (x) soil reaction, and (xi) soil nitrogen and used them in our statistical analyses (at both 1 and 3 m spatial scales; see below). Moreover, we divided plant species preferring or tolerating periodic inundation into three categories corresponding to their Ellenberg values for moisture (Ellenberg et al. 1992) and then created three other variables representing the cover of these three groups, as (xii) moist—species preferring periodically moist, but not wet, soils (Ellenberg values of 7~), (xiii) wet—species preferring periodically wet soils (8~), and (xiv) soaked—species preferring periodically wet and soaked (low-air) soils (9=).

We observed an amateur collector at our experimental site. This incident made us aware of the possibility that some of our traps may have been emptied by amateur collectors, biasing our results. We thus installed several camera traps to monitor our transect and increased the number of visits to the site. The camera traps did not record any other attempts to empty our traps. In addition, we did not observe any change in ratio between common carabid species and *C. nitens* in traps placed in the areas previously frequently visited by amateur collectors (based on the remains of old pit fall traps) and traps in more remote parts of our transect. This gives us some confidence that our traps were not emptied by amateur collectors, although we cannot rule out this issue completely.

Statistical analysis

The population size of *C. nitens* at the site was estimated based on Craig's model (Method 1 formulation) (Craig 1953) using Craig Estimator (Šebek and Šebek 2011). Craig's model is a simple method for population size estimation. Although originally designed for closed populations, it is often used as an alternative to the more data demanding Jolly–Seber model (its POPAN parametrization) (Schwarz and Arnason 1996) because it gives similar results.

In order to explore habitat preferences of the beetle, we tested the effect of environmental variables on abundance of *C. nitens* in traps using *generalized linear regression models* (GLM) with Poisson or quasi-Poisson distribution (log link function). For each trap, representing an observation unit, we pooled the number of unique individuals that were caught through the whole sampling period (recaptures were excluded). We ran analyses for abundance of both sexes together, but also separately for males and females, to investigate whether there were some sex dependent trends in habitat preference.

Following different research questions, the analyses were performed with three separate sets of explanatory variables and always separately for both 1 and 3 m scales. In the first analysis, we tested the effect of abiotic factors and covers of plant strata on abundance of *C. nitens*. We used the following explanatory variables in the model: inundated area, bare ground, mosses, herbs, shrubs, trees, light, temperature, humidity, soil reaction, and soil nitrogen. In the second analysis, we had strong prior expectations that humidity and periodic inundation might be important drivers of the beetle's occurrence. We thus tested the effect of periodic inundation on abundance of *C. nitens*. We used the following explanatory variables in this model: moist, wet, and soaked. In the third analysis, we tested the effect of plant community composition on abundance of *C. nitens* using the cover of individual plant species as explanatory variables. Only plant species occurring in more than two patches were used in the analyses, making it 33 and 56 explanatory variables in the analysis of 1 and 3 m scales, respectively. In this analysis, we did not test the response of males and females separately due to their rather low abundances and high variability in the plant data.

To find the model of greatest explanatory power in a particular analysis, we first fitted a null model with Poisson distribution and then added significant explanatory variables using forward addition procedure. If the resulting model exhibited signs of overdispersion, we re-fitted the model with quasi-Poisson distribution and then eliminated potential nonsignificant variables by backward elimination procedure until the final model contained only significant variables with their effects corrected for overdispersion.

Finally, we visualized the correlation between abundance of *C. nitens* and environmental variables using multivariate methods. Only the variables identified as significant by our GLM analyses were considered in the multivariate visualization. We visualized the correlation between *C. nitens* abundance and abiotic factors, cover of plant strata (our first GLM analysis), and cover of plant species preferring periodic inundation (our second GLM analysis) by *Redundancy Analysis* (RDA). Then we visualized the correlation between abundance of *C. nitens* and cover of individual plant species (our third GLM analysis) using *Canonical Correspondence Analysis* (CCA), assuming unimodal response to compositional plant data. The abundances of males and females were also considered in the CCA, although not tested by the above described GLM. The response data were log-transformed prior to the analysis.

The analyses were carried out using R 3.3.3 (R Development Core Team 2017) for GLM and Canoco 5 (ter Braak and Smilauer 2012) for ordination analysis.

Results

In total, we sampled 177 individuals of *Carabus nitens*, including 108 males and 58 females (information on sex of 11 individuals was not recorded). 11 individuals were found dead in the traps or escaped before marking and were not marked. Out of the 166 marked individuals, 27 individuals were recaptured. This resulted in 35 recaptures as several individuals were recaptured more than once. The estimated population size was 508 ($\pm$ 151) individuals. There was high variability in the distance covered among recaptures, on average females moved further than males (132 ± 123 m in the case of females vs. 88 ± 149 m in the case of males). The largest distance covered was 538 m in 26 days (Fig. 1).

The regression analysis (GLM) testing the effects of abiotic factors and cover of plant strata at the 1 m scale showed a higher abundance of *C. nitens* in patches characterized by vegetation preferring higher light intensity ($F_{(1,169)} = 30.3$, $p < 0.0001$) and with a lower cover of shrubs (E2 plant stratum) ($F_{(1,168)} = 6.60$, $p = 0.011$). When analysing the sexes separately, the abundance of males was positively related to the cover of vegetation preferring higher light intensity ($F_{(1,169)} = 20.3$, $p < 0.0001$), other variables being nonsignificant. The abundance of females, besides being positively related to the cover of vegetation preferring higher light intensity and negatively to the shrubs cover, was also positively related to the cover of bare ground ($\chi^2_{(1)} = 4.9$, $p = 0.027$) (for more details, see Online Resource 2—Table S1). The major positive effect of the cover of vegetation preferring higher light intensity was retained at the 3 m scale, for total abundance but also for males and females separately. Besides this, we found a negative effect of humidity on total abundance of beetles ($F_{(1,168)} = 4.4$, $p = 0.038$) and on abundance of females ($\chi^2_{(1)} = 11.5$, $p = 0.001$), and a negative effect of cover of inundated area on abundance of males ($F_{(1,168)} = 4$, $p = 0.047$). Moreover, the abundance of females was negatively related to the cover of mosses (E0 plant stratum) ($\chi^2_{(1)} = 6.01$, $p = 0.014$) and positively related to higher temperature ($\chi^2_{(1)} = 4.4$, $p = 0.036$) (Fig. 2, Online Resource 2—Table S1).

The regression analysis testing the effect of periodic inundation at the 1 m scale showed a higher abundance of the beetles in patches with a high cover of plants typical for periodically moist, but not wet, soils (Ellenberg values of 7~). This positive effect was similar when considering all the beetles but also males and females separately (all: $F_{(1,169)} = 10.8$, $p = 0.001$; males: $F_{(1,169)} = 10.1$, $p = 0.002$; females: $\chi^2_{(1)} = 37.3$, $p < 0.0001$). Other variables did not have any effect. At the 3 m scale, the positive effect of a high cover of plants typical for periodically moist, but not wet, soils was retained for all *C. nitens* individuals and both sexes. In all groups, the analysis also revealed a negative effect of the cover of plants preferring periodically wet soils (8~) (all: $F_{(1,168)} = 5.2$, $p = 0.024$; males: $F_{(1,168)} = 4.38$, $p = 0.038$; females: $\chi^2_{(1)} = 16$, $p < 0.0001$) (Online Resource 2—Table S2).

The abundance of *C. nitens* was related to the cover of individual plant species on both the 1 and 3 m scales (Fig. 3). On the 1 m scale, the abundance of *C. nitens* was positively correlated with the cover of *Juncus squarrosus* ($F_{(1,169)} = 16.9$, $p < 0.0001$), whereas it was negatively correlated with the cover of *Avenella flexuosa* ($F_{(1,168)} = 4.06$, $p = 0.045$). On the 3 m scale, the abundance of *C. nitens* was positively correlated with the cover of *Salix repens* ($F_{(1,169)} = 89.68$, $p < 0.0001$), *Juncus squarrosus* ($F_{(1,168)} = 79.85$, $p < 0.0001$), *Calluna vulgaris* ($F_{(1,167)} = 39.22$, $p < 0.0001$), *Betula pendula* seedlings ($F_{(1,164)} = 9.57$, $p = 0.002$), *Hieracium* sp. ($F_{(1,163)} = 9.33$, $p = 0.003$), and *Veronica chamaedrys* ($F_{(1,159)} = 5.34$, $p = 0.022$). It was negatively correlated with the cover of *Nardus stricta* ($F_{(1,166)} = 19.41$, $p < 0.0001$), *Carex nigra* ($F_{(1,165)} = 12.16$, $p = 0.001$), *Veronica officinalis* ($F_{(1,162)} = 8.05$, $p = 0.005$), *Carex ovalis* ($F_{(1,161)} = 6.25$,

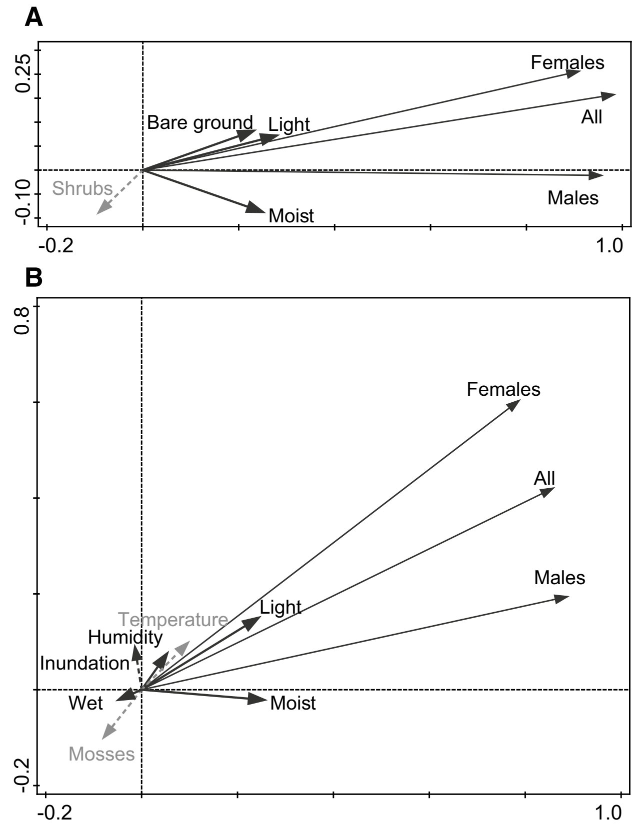

Fig. 2 Habitat preference of the ground beetle *Carabus nitens* as visualized by RDA. The diagrams include the response of all *C. nitens* individuals, males, and females to the environmental variables on 1 m (**a**) and 3 m (**b**) spatial scales around a trap. Only the variables with some significant correlation, analysed by GLM, are shown. The variables include cover of mosses, cover of shrubs, cover of bare ground, cover of inundated area, cover of plant species preferring periodically moist soils (moist), cover of plant species preferring periodically wet soils (wet), and community weighted means of Ellenberg's indicator values for light, temperature, and humidity. Variables with a significant effect on the total abundance of *C. nitens* are marked with full black lines. Variables with a significant effect only on males are marked with black dashed lines. Variables with a significant effect only on females are marked with grey dashed lines

$p = 0.013$), *Cystopteris fragilis* ($F_{(1,160)} = 5.91$, $p = 0.016$), *Calamagrostis villosa* ($F_{(1,158)} = 6.38$, $p = 0.013$), and *Sphagnum riparium* ($F_{(1,157)} = 4.62$, $p = 0.033$) (Fig. 3, Online Resource 2—Table S3).

Discussion

Here we studied a *C. nitens* population in Central Europe, where the beetle has been in severe decline and is now highly endangered. We focused on one of the last known viable populations in the Czech Republic, inhabiting a raised bog regenerating following peat extraction. We show that the transition between dry heathland and a wet peat bog

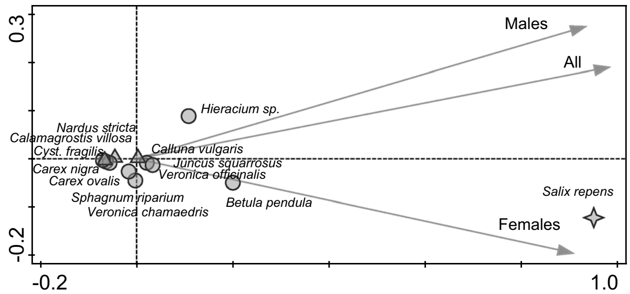

Fig. 3 Correlation between abundance of the ground beetle *Carabus nitens* and the relative cover of individual plant species as visualized by CCA on a 3 m scale. The diagram shows plant species with a significant effect on all *C. nitens* individuals as analysed by GLM. For the purposes of visualization the responses of males and females were also added into the figure although the significance of their responses to the cover of these plants was not tested. Plant species characteristic for secondary sub montane and montane heaths (based on Filippov et al. 2008) in the Czech Republic are marked with triangles. Rare plant species (based on Red List of Czech flora; Procházka 2001) are marked with stars. Other plant species are marked with circles

might be an optimal habitat for the species, and we discuss the management measures needed to support the studied population.

Habitat preference

Although *C. nitens* has historically utilized a broader range of habitats (Clavier 1977; Gersdorf and Kuntze 1957; Jeannel 1941; Niedl 1959), in Europe it is currently mostly confined to heathlands or peat bogs that remain among the last habitats characterized by low vegetation cover and nutrient load (Assmann and Janssen 1999). Our results underline previous findings as the beetle was most common in patches of vegetation typical for open habitats. Overgrowing of heathlands and peat bogs by denser and taller vegetation currently poses a major threat to these habitats (Bakker and Berendse 1999; Telfer and Eversham 1996).

European heathlands are highly dependent on traditional land uses such as pasture combined with burning, which remove nutrients and prevent eutrophication (Halada et al. 2011; Webb 1998). Without such disturbances the sparse, mostly short-turf vegetation becomes denser, and increasingly dominated by taller vegetation preferring higher soil nutrients. Such vegetation becomes unsuitable for *C. nitens*. This overgrowth and dominance by taller vegetation may then have negative effects on *C. nitens*, primarily females. The female abundance was positively correlated with the cover of bare ground and vegetation preferring higher temperature, while it was negatively correlated with the cover of shrubs and mosses (represented mainly by *Sphagnum riparium* and *Polytrichum formosum*). This is in line with the findings of other studies on carabids showing that females have more specialized habitat preferences than males, probably resulting from the need to find an optimal habitat for oviposition, such as warmer patches with optimal humidity (Pokluda et al. 2012).

Several previous studies have suggested that *C. nitens* might prefer patches with higher humidity (Eyre et al. 2003; Luff 1998). However, some studies report that *C. nitens* predominantly colonizes dry upland heathlands (Assmann and Janssen 1999; Gardner 1991) whereas others reported the species in wet heaths or peat bogs (Eyre et al. 2003; Luff 1998). Our results show that *C. nitens* did not prefer inundated patches characterized by high humidity and vegetation typical for wet soils. However, abundance of *C. nitens* was positively correlated with the cover of vegetation typical for soils which are periodically moist. The positive correlation was apparent on both 1 and 3 m scales. This indicates that *C. nitens* may prefer transient, periodically moist microhabitats of dry upland heathlands or peat bogs, but not the damp bog itself. This is further supported by the results which showed a positive correlation between the abundance of *C. nitens* and the cover of a mix of heathland (e.g. *Calluna vulgaris*), peat bog (e.g. *Juncus squarrosus*), and boreal (e.g. *Salix repens*) plants. *C. nitens* thus appears to belong among a growing group of rare or declining insect species known to require a fine, diverse mosaic of microhabitats that includes early seral stages (e.g. *Carabus hungaricus*, various *Meloe* spp., *Erebia aethiops* etc.; Pokluda et al. 2012; Slamova et al. 2013).

Mobility and population size

The maximal covered distance, 500 m in a month, shows that the dispersal ability in *C. nitens* is comparable to other large wingless carabids, such as *C. coriaceus, C. hungaricus, C. olympiae* or *C. ullrichii* (Elek et al. 2014; Negro et al. 2008; Riecken and Raths 1996; Růžičková and Veselý 2016). However, it is limited when compared to small winged carabid species. Indeed, smaller winged carabids can migrate up to 25–30 km and are able to colonize suitable habitats more efficiently than large wingless species (e.g. Den Boer 1970; Vanbergen et al. 2017). *C. nitens* needs open or disturbed woodlands, and forest roads as migration corridors or stepping stones for successful dispersal (Eggers et al. 2010; Koivula 2002). A successful colonization of suitable habitats by *C. nitens* thus require a presence of such stepping stones and a presence of a source population.

Implications for conservation management

Although we know little about the current status of the studied population, there are several causes of concern. First, the estimated local population size is small (508 individuals). The estimate is a tentative approximation due to the rather low number of recaptures. Despite that, the population is probably subject to erosion of its genetic diversity and its long-term viability is questionable (Traill et al. 2007). Further, the beetle has virtually disappeared from the wider surroundings of the studied site, where it was occasionally common up until the early 2000s (P. Krásenský, *pers. obs*.). The most likely reason is the successful afforestation of areas affected by forest dieback in the 1980s, resulting in the loss of suitable habitat for *C. nitens* (Pyšek 1992). Hence, the studied population is almost certainly becoming isolated, which further deteriorates its current situation.

Under such circumstances, intensive collecting may also contribute to the further decline of the population. Rather than persecuting collectors, however, active management measures should be urgently implemented. This is illustrated by the fate of populations in protected areas, where a lack of suitable management and afforestation are the most likely reasons for the species decline. The beetle has disappeared from the strictly protected Velké Dářko National Nature Reserve (Nenadál 1987), from Labské pískovce (Elbsandsteingebirge) Protected Landscape Area, and even from České Švýcarsko National Park in northern Bohemia (Pokorný 2006).

At our study site, the population survived owing to, perhaps, peat extraction and despite the intensive collecting. Hence, active management measures following the peat extraction are vital to the survival of the studied population, and should be applied also to the surrounding areas, where the beetle is currently not present. The sites of recent peat extraction have to be spared of any reclamation and afforestation (Online Resource 1). Further, active measures should facilitate nutrient removal and disturbance of the vegetation cover in order to create a mosaic that would also include bare substrate and sparse vegetation patches. These measures may include prescribed burning, sod cutting, topsoil removal, intensive grazing (preferably by large animals such as cows or horses) and depression by vehicles. Several of these approaches should be combined, as individual measures are unlikely to completely block succession or restore the habitat (Bokdam and Gleichman 2000). Attention must also be paid to the water regime in the area. After peat extraction, drainage canals should be blocked (Nature Conservation Agency of the Czech Republic 2012). Driving heavy vehicles or digging depressions is desirable as it creates humid patches, which prevents desiccation of the remaining peat and allows reestablishment of bog flora. Such a mosaic would provide habitat transient between heath and bog, preferred by *C. nitens* at the studied site. Woodlands should be kept open and subject to similar management measures as open land, in order to create habitats that allow the beetle to persist or disperse.

As the beetle needs stepping stone habitats to successfully colonize existing suitable habitats, the abovementioned measures should be carried out also in wider environs of the inhabited site. Further, they should be applied to areas where the beetle has disappeared relatively recently, such as Labské pískovce (Elbsandsteingebirge) Protected Landscape Area and České Švýcarsko National Park. This might save local populations if they still exist, or prepare habitats for future reintroductions of the species. Such measures would benefit numerous threatened species associated with early seral stages such as *Salix repens* or the black grouse (*Tetrao tetrix*), whose populations also benefited from the forest dieback in the 1980s, but are currently experiencing a decline similar to that of *C. nitens* (Svobodová et al. 2011).

The proposed management maintaining a mosaic of dry and wet early seral habitats could be also applied to other similar post-industrial sites. Such sites are likely to become increasingly important for the survival of *C. nitens* in many parts of Europe, as illustrated by the case of the Czech Republic where several of the last remaining populations inhabit heaps of former coal mines or the raised bog studied here. But the effects of such measures have to be closely monitored to identify their future potential. Further studies examining the habitat needs of *C. nitens* larvae are needed to improve our understanding of the biology of this beetle.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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