Journal of Insect Conservation (2020) 24:399–407
https://doi.org/10.1007/s10841-020-00239-x

ORIGINAL PAPER

Ecology and calculation of population density of the protected saproxylic beetle species *Boros schneideri* (Panzer, 1796) (Coleoptera, Boridae) in capercaillie lek areas

Jānis Ozols[1] · Margarita Ozola[1] · Maksims Balalaikins[2] · Uldis Valainis[2]

Received: 27 June 2018 / Accepted: 10 April 2020 / Published online: 18 April 2020

Abstract

Boros schneideri is an endangered saproxylic beetle species in Europe, included in the list of species for which micro-reserves are established in Latvia. Micro-reserves for capercaillie lek areas are created in similar habitats in Latvia; therefore, these sites might be suitable for *B. schneideri* and play an important role in the protection of the species. This study aimed to identify ecological factors affecting the occurrence of *B. schneideri* and to estimate the species' population density in Central Latvia. In total, six micro-reserves (primarily established to protect capercaillie lek areas) and six, randomly picked, control territories were examined, including 304 forest stands and 312 pine snags. In total, 109 *B. schneideri* specimens were found. The most important ecological factors for *B. schneideri* were the age of the forest stand, the presence of deadwood in different stages of decomposition, and the number of snags per forest stand. All mentioned factors are important structural elements of natural forests; hence, *B. schneideri* can be considered as an indicator species of natural forest habitats. The most important ecological factors for *B. schneideri* on a micro-habitat scale are the area and thickness of the remaining bark, presence of Ascomycota fungi mycelium on a trunk, and trunk's circumference. We suggest that *B. schneideri* is a pioneer species since larger areas of bark, as well as Ascomycota fungi mycelium are more often found on recently dead trees.

Keywords *Boros schneideri* · Ecology · Conservation · Population density · Capercaillie lek areas · Central latvia · Pine forests · Saproxylic species · Endangered species

Introduction

About 20–25% of species in boreal forests are saproxylic. We define a species as saproxylic if it depends, during some part of its life cycle, on wounded or decaying woody material of living, weakened, or dead trees. In Northern Europe, most saproxylic insects are beetles (Coleoptera) (1447), flies (Diptera) (1550), and hymenopterans (Hymenoptera) (803 species) (Ozols 1985; Siitonen 2001; Alexander 2008; Stokland et al. 2013).

In Northern Europe due to intensive forestry in the last decades, the area of old natural forests has decreased to less than 3% of forests. As a result, the percentage of deadwood in forests has decreased by 90–98% and saproxylic insect species diversity has decreased by one third. Martikainen et al. (2000) showed that species richness in natural old-growth boreal forests was significantly higher than in managed forests. Moreover, about 78% of saproxylic species had a higher and more stable population size in natural old-growth forests than in managed forests. Intensive forestry strongly affects endangered saproxylic beetles that need large diameter deadwood. Successful protection of these species requires more than simply protecting the forest stands where the saproxylic species are observed. It is highly important to protect also potential forest stands so that populations can grow and disperse. Many of these species live only on

✉ Jānis Ozols
janis.ozols1408@gmail.com; jo13020@lanet.lv

Margarita Ozola
margarita.bildina@gmail.com

Maksims Balalaikins
maksims.balalaikins@biology.lv

Uldis Valainis
uldis.valainis@biology.lv

[1] Entomological Society of Latvia, Juglas 49-16, Riga 1064, Latvia

[2] Institute of Life Sciences and Technology, Daugavpils University, Vienibas 13, Daugavpils 5400, Latvia

one tree species or on a group of tree species, allowing us to use them as indicator species of a natural forest and to protect larger areas of forest—based on species' presence therein (Martikainen et al. 2000; Schiegg 2000; Siitonen 2001; Prieditis 2002; Alexander 2008; Stokland et al. 2013).

More than half of the forests in Latvia are boreal, but most of the entomological research until now has been focused on rare and protected habitats. Hence, more attention should be devoted to protecting and investigating species living in boreal forests. Several protected species such as *Boros schneideri, Chalcophora mariana, Ergates faber, Nothorhina punctata,* and *Tragosoma depsarium*, for instance, have been observed in Scots pine forests (Ozols 1985; Prieditis 2002; Lārmanis 2013).

Boros schneideri (Panzer, 1796) is included in Annex II of the European Union Habitats Directive (EU Directive 1992). In Europe, it is most commonly found in the Baltic states (Blažytė-Čereškienė and Karalius 2011; Horák et al. 2011; Gutowski et al. 2014; Valainis et al. 2014). For the first time in Latvia, *B. schneideri* was found in 2003 near the Pededze river in the nature reserve "Lubana Wetland complex" under the bark of an oak tree (Vilks and Telnov 2003). Since then, scientists from Lithuania and Poland have undertaken investigations into the life history of this species.

B. schneideri is mainly found in dry Scots pine (*Pinus sylvestris*) forests exceeding 20,000 hectares. Its second most suitable habitat is wet coniferous forests (Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011), and J. M. Gutowski et al. (2014) have also observed this species in dry and wet mixed forests and broad-leaved forests. Usually, *B. schneideri* is not present in intensively managed forests, near forest edges, or forests near cities. However, some specimens have been found in clear-cuts under the bark of snags (Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011; Gutowski et al. 2014).

Boros schneideri larvae are found mainly under the bark of standing deadwood of Scots pine trees. However, exceptionally, specimens have also been observed under the bark of silver fir (*Abies alba*), pedunculate oak (*Quercus robur*), European white birch (*Betula pendula*), Japanese white birch (*Betula platyphylla*), Siberian larch (*Larix sibirica*), Norway spruce (*Picea abies*), black alder (*Alnus glutinosa*), and European ash (*Fraxinus excelsior*) (Telnov et al. 2006; Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011; Müller et al. 2013; Gutowski et al. 2014; Plewa et al. 2014; Polevoy & Humala 2014).

Some studies stipulate that *B. schneideri* mainly occurs under the bark of semi-shaded trees (60–80%) and less often under the bark of trees in the high shade (> 80%) (Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011; Gutowski et al. 2014). Blažytė-Čereškienė and Karalius (2011) found that *B. schneideri* was not present in forested areas of Lithuania where shading is more than 80% and where Norway spruce constitutes 25% or more of all the trees in a forest. However, J. M. Gutowski et al. (2014) reported that *B. schneideri* may also be present in forested areas of Poland with more than 80% shading and that Norway spruce does not affect the presence of the species.

B. schneideri larvae are usually found under the bark of trees whose phloem has started to separate from the other tissues, and whose wood is still moist. Larvae are more abundant on snags, which have a lower amount of bark left. However, it was found that the minimal area of bark on snags should be at least 0.08 m^2. Specimens are usually found under the bark of average thickness (10–20 mm); however, they have also been observed under the bark which is as thin as 4.7 mm or, to the other extreme, as thick as 35.7 mm (Blažytė-Čereškienė and Karalius 2011; Gutowski et al. 2014).

It is still unclear what exactly *B. schneideri* larvae food resource is. The common opinion is that larvae feed on the mycelium of fungi of the Ascomycota division – *Ophiostoma minus* or genus *Aureobasidium*. Some scientists postulate that *B. schneideri* may also be necrophagous or exhibit predatory behavior (Andersen and Nilssen 1978; Heliövaara 2001; Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011; Horák et al. 2011; Gutowski et al. 2014).

Usually, *B. schneideri* larvae are found at the bottom of the trunk, however, it depends on the trunk diameter. On large trees, larvae can be found even on the highest branches (Blažytė-Čereškienė and Karalius 2011; Gutowski et al. 2014).

Generally, *B. schneideri* is a natural forest species that has become endangered due to intensive forestry. As a result, its population densities are decreasing throughout Europe (Blažytė-Čereškienė and Karalius 2011; Gutowski et al. 2014; Valainis et al. 2014).

The research in Latvia has mainly been done in microreserves in capercaillie (*Tetrao urogallus*) lek areas—forest territories where several natural forest structures such as old, large trees, sparse canopy cover, and deadwood are present. Those are important factors contributing to the survival of many protected saproxylic species exhibiting decreasing populations (Ek et al. 2002; Lārmanis 2013; Stokland et al. 2013).

The aim of this work was to develop a formula for calculating *B. schneideri* population density, taking into account ecological factors such as light intensity, standing dead tree circumference, number of dead trees in forest stands, number of standing dead trees with Ascomycota fungi mycelium, forest stand age, deadwood continuity, possible removal of deadwood and bark area of standing dead trees. We hypothesize that *B. schneideri* is a species of old or natural boreal forests, that the population densities of *B. schneideri* in micro-reserves located in capercaillie lek areas are higher than in maintained pine forests, and that *B. schneideri* depends on trees with Ascomycota fungi mycelium as its micro-habitat.

Materials and methods

We investigated two different forest areas located in Central Latvia, selected on the basis of the division of forest areas in Latvia described by Ozols (1985) from the 1st of October, 2015 to 21th of April, 2016.

Three capercaillie lek micro-reserves (Latvian Ministry of Agriculture 2016) and three control forest territories were randomly selected in each of the three forest areas. The control territories were located at least one kilometer away from the closest capercaillie lek micro-reserve. The dominant tree species in all forest areas were Scots pine. As the average area of micro-reserves was 102 hectares, the control territories were also chosen of the same size. Circular areas with a radius of 570 m around random points (so that they were approximately 102 ha large) were selected as the control territories.

The primary task in all territories was to inventory the occurrence of *B. schneideri*, and other protected saproxylic species such as *Tragosoma depsarium, Nothorhina punctata, Chalcophora mariana*, and *Ceruchus chrysomelinus*. In each territory, data were collected separately for every forest stand, according to the State Register of Forests. The current study was performed in twelve different forest territories, six forest territories were situated in micro-reserves, and six in production forests outside protected areas as a control. Altogether 304 forest stands were examined, i.e., approximately 25 forest stands in each forest territory. The average forest stand size was approximately 4 hectares. In each stand, a 10 m wide transect was set in the direction of the maximal length of the examined forest stand. To precisely calculate the length of a transect, the start and the endpoints of each transect were marked with a handheld GPS unit (Garmin Etrex 20). Moving along the transects, each forest stand was characterized by ecological factors as follows:

1. Light intensity—canopy coverage (0: < 25% shading, 1: 25–50% shading, 2: 50–80% shading, 3: > 80% shading);
2. Deadwood continuity (0—no deadwood, 1—deadwood occurs in one stage of decomposition, 2—occurs in two or more stages of decomposition, 3—occurs in four stages of decomposition)—recently fallen tree with bark, fallen tree with solid trunk without bark, fallen tree with soft trunk that can be split by knife and fallen tree with completely soft trunk that can be split with hands;
3. All standing dead Scots pine trees and those with Ascomycota fungi mycelium were counted;
4. Information about forest stand age, forest type, and tree species composition in each stand was obtained from the State Register of Forests;
5. The removal of deadwood was evaluated.

Each of the standing dead Scots pine trees on transects was characterized on following ecological factors:

1. Light intensity—canopy coverage (0: < 25% shading, 1: 25–50% shading, 2: 50–80% shading, 3: > 80% shading);
2. Circumference of the trunk at the height of 130 cm;
3. Bark area (0—no bark, 1—bark < 1m^2, 2—bark < 50%, 3—bark > 50%, 4—dead tree has not lost any bark);
4. If the bark was present at all heights of the tree, it was removed at different altitude up to 2 m from ground level, and examined sections were divided in to following height categories from 1 to 5 (1: 0–40 cm from ground level, 2: 40–80 cm, 3: 80–120 cm, 4: 120–160 cm, and 5: 160–200 cm respectively);
5. Presence of Ascomycota fungi mycelium (0—no, 1—yes);
6. Presence of ants under the bark (0—no, 1—yes);
7. Presence of *Pytho depressus* (count of larvae);
8. Bark thickness, as measured with a sliding caliper (mm).

From each standing dead Scots pine tree, a 40 cm long and 20 cm wide bark patch was removed using a knife. Each trunk was inspected and *B. schneideri* larvae counted. All bark was removed from ten randomly chosen standing dead Scots pine trees with more than 50% of the initial bark area left to evaluate the number of *B. schneideri* larvae on the whole trunk. GPS coordinates were taken for every tree with *B. schneideri* larvae. After completing the work, the removed bark was carefully nailed to the trunk to protect the habitat of *B. schneideri.*

Statistical analysis

Data processing and visualisation was performed using Microsoft Office Excel 2007 and R i386 3.2.3 software. In R, the Shapiro–Wilk test was used for normality testing. Spearman's rank correlation was used to estimate the relationship between different characteristics of forest stands and the occurrence of *B. schneideri* larvae and between different characteristics of micro-habitat and the number of larvae. Correlation was very strong if rho > 0.8, strong if 0.5 < rho < 0.8, or weak if rho < 0.5. Poisson regression models were used to identify the ecological factors affecting the occurrence of *B. schneideri* in forest stands and on standing dead trees, depending on their properties. Wilcoxon Rank-Sum test was used to evaluate differences in ecological factors and numbers of *B. schneideri* larvae between managed forests (control territories) and micro-reserves.

In Microsoft Office Excel 2007, the average numbers of *B. schneideri* and *P. depressus* larvae, trees with Ascomycota fungi mycelium, and dead standing trees per hectare were counted for each forest area. To calculate the average number of *B. schneideri* in forest stands and population density of *B. schneideri*, the following formulas were used: $BN = \frac{Bt*S*k}{s}$ and $BM = \frac{Sum(BN)}{Sum(S)}$, where BN is the mean number of *B. schneideri* larvae in a forest stand, Bt is the number of dead trees with *B. schneideri* within a transect, S is the size of a forest stand, k is the mean number of *B. schneideri* larvae per standing dead tree, s is the transect area, BM = population density of *B. schneideri*—number of specimens per hectare (1 ha = 0.01 km^2).

Results

Boros schneideri was observed in all micro-reserves and in five out of six control territories. In total, 312 Scots pine snags in 304 forest stands were investigated, and 109 larvae of *B. schneideri* were found. No other rare saproxylic species were observed during this study.

Differences between micro-reserves and control territories

Differences between micro-reserves and control territories are shown in Table 1. The differences between micro-reserves and control areas are not similar among the regions. In the territories of "Sandru smiltāji", micro-reserves had a higher light intensity and older forest stands. In the territories of "Sēlija", micro-reserves had a higher diversity of deadwood, but in control areas, *P. depressus* displayed greater population density (4.80 ± 1.60 > 2.70 ± 0.90) (Fig. 1).

Together in all micro-reserves, there was a higher average number (31.60 ± 3.30) of standing dead trees per hectare compared to the average number of 22.40 ± 2.00 in all control areas. Population density of *P. depressus* was 2.72 ± 0.90 specimens per hectare in micro reserves and 4.87 ± 1.58 specimens in control areas (Fig. 1). The average forest stand age in micro-reserves was 120–140 years, but in control areas, forest stand age varied between 80 and 100 years (Fig. 2).

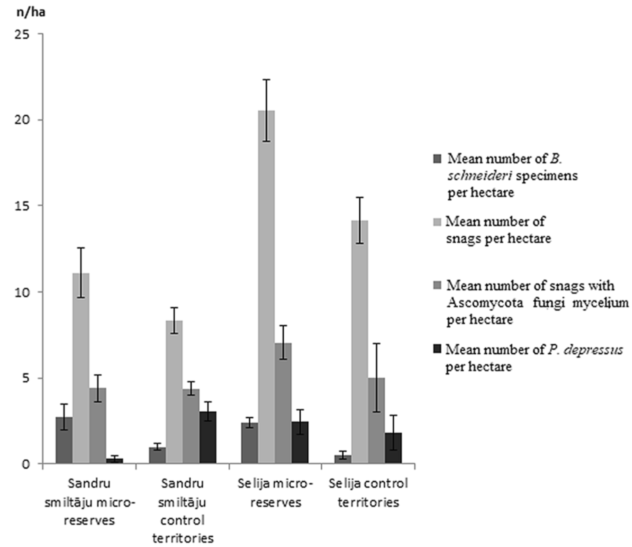

Fig. 1 Difference between micro-reserves and control territories. Mean number of *B. schneideri*, *P. depressus*, snags and snags Ascomycota fungi mycelium per hectare. Sample size = 304 forest stands

Ecological factors that impact occurrence of *B. schneideri* in forests

Statistically significant ecological factors affecting occurrence and number of specimens of *B. schneideri* in forest stands are shown in Table 2 and in Fig. 2.

As can be seen in Table 2, it is important for *B. schneideri* that there are plenty of suitable micro-habitats with Ascomycota fungi mycelium and that they (and also the forest stand itself) have been there for a long period.

Table 1 Differences between micro-reserves and control area territories ($p < 0.05$*)

	B. schneideri population density in micro-reserves (nr/ha)	*B. schneideri* population density in control areas (nr/ha)	p value	Ecological factors with a statistically significant difference between control areas and micro-reserves
"Sandru smiltāji" territory	2.72 ± 0.70	0.97 ± 0.20	0.408	Light intensity (p = 0.017); forest stand age (p = 0.01)
"Sēlija" territory	2.40 ± 0.30	0.50 ± 0.20	0.015*	Continuity of deadwood (p < 0.001); number of *P. depressus* specimens per hectare (p = 0.014)
All	5.12 ± 1.00	1.48 ± 0.40	0.038*	Number of standing dead trees (p = 0.01); number of *P. depressus* specimens (p = 0.02); forest stand age (p < 0.001)

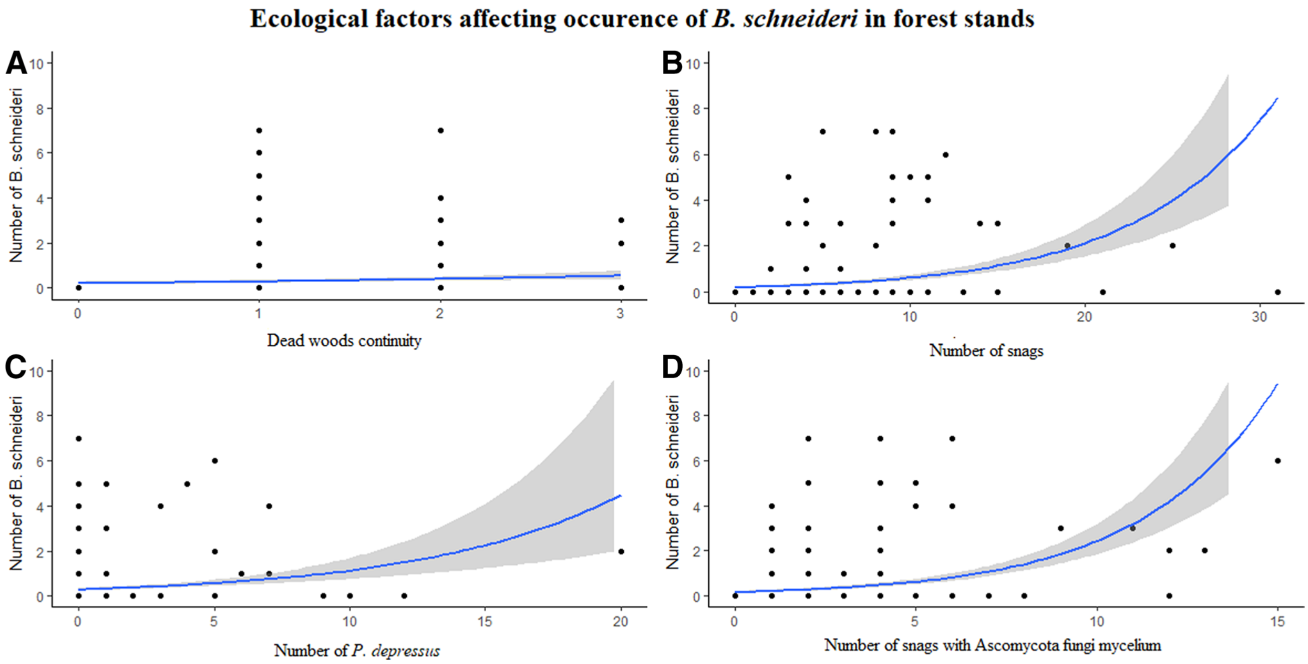

Fig. 2 **a** Deed woods continuity affecting occurrence of *B. schneideri* in forest stand ($p < 0.001$), **b** number of snags affecting occurrence of *B. schneideri* in forest stands ($p < 0.001$), **c** number of *P. depressus* affecting occurence of *B. schneideri* in forest stands ($p < 0.001$), **d** number of snags with Ascomycoto fungi mycelium affecting of *B. schneideri* in forest stands ($p < 0.001$). Sample size = 304 forest stands

Table 2 Ecological factors affecting the occurrence of *B. schneideri* in forest stands using Spearman's rank correlation

	p value	Rho
Continuity of deadwood	0.026	0.18
Number of dead trees	< 0.001	0.4
Occurrence of *P. depressus*	< 0.001	0.4
Dead trees showing Ascomycota fungi mycelium	< 0.001	0.49
Forest stand age	< 0.001	0.35

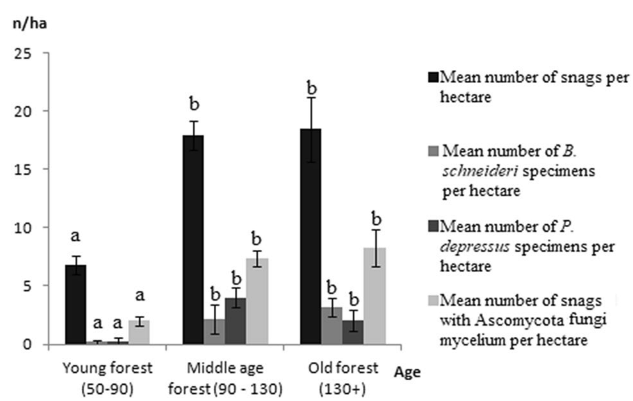

Fig. 3 Forest stand age affecting mean number of *B. schneideri* ($p < 0.001$) and snags with Ascosmycota fungi mycelium ($p < 0.001$) per hectare. Sample size = 304 forest stands

Moreover, forest stand age correlates with light intensity ($p < 0.01$), continuity of deadwood ($p < 0.01$), present deadwood ($p < 0.01$), number of dead standing trees ($p < 0.01$), population density of *P. depressus* ($p < 0.01$), and the number of dead trees with present Ascomycota fungi mycelium ($p < 0.01$) (Fig. 3).

We used a Poisson regression model to check for ecological factors affecting the abundance of *B. schneideri* in forest stands. As we show in Table 3, amongst all the factors evaluated by the first model, there were several factors (light intensity, presence of deadwood in different decomposition stages, removal of deadwood) with no significant effect on the abundance of *B. schneideri,* even though their coefficient might be high. So a new model containing only the significant factors was made and compared to the previous one using the AIC criterion. Both models were statistically significant ($p < 0.01$). Models show that the ecological factors that have a statistically significant impact on the abundance of *B. schneideri* in forest stands include the quantity of deadwood per hectare, deadwood with present *Ascomycota* fungi mycelium per hectare, number of *P. depressus* individuals per hectare and forest stand age (Table 3).

Table 3 Ecological factors that affect *B. schneideri* in forest stands using a Poisson regression model

Abundance of *B. schneideri*	Coefficient	p value	AIC	R^2 (McFadden)
Light intensity	− 0.103	0.286		
+ Deadwood continuity	0.042	0.633		
+ Removal of deadwood	− 0.215	0.244		
+ Deadwood per ha	0.016	0.029		
+ Deadwood showing	0.09	< 0.001	816.76	0.517
Ascomycota fungi per ha				
+ *P. depressus* per ha	0.926	< 0.001		
+ Forest stand age	0.015	< 0.001		
Deadwood per ha	0.019	0.002		
+ Deadwood showing	0.089	< 0.001		
Ascomycota fungi per ha			813.3	0.516
+ *P. depressus* per ha	0.974	< 0.001		
+ Forest stand age	0.015	< 0.001		

Table 4 Ecological factors affecting *B. schneideri* in micro-habitats using Spearman's rank correlation

	p value	Rho
Circumference of the trunk of a dead tree	< 0.001	0.26
Remaining size of bark on trunk	< 0.001	0.23
Ascomycota fungi mycelium upon trunk	< 0.001	0.19
Thickness of bark	0.029	0.12
Height from the ground	< 0.001	0.10

Ecological factors that affect the occurrence of *B. schneideri* in micro-habitats

Ecological factors affecting the occurrence and number of specimens of *B. schneideri* in a micro-habitat are shown in Table 4.

The smallest circumference of a dead tree trunk with *B. schneideri* was 36 cm, and the largest was 194 cm. *B. schneideri* were more often observed on standing dead trees with larger circumference, and also, the number of specimens was higher on the larger trees. Although we counted more *B. schneideri* individuals per certain area size on dead trees with less bark on the trunk, we found the species more often on dead trees with larger areas of the bark left or fully covered with bark. Most specimens were found in the middle (40–120 cm), and the highest levels examined (160–200 cm) (Fig. 4).

All specimens of *B. schneideri* were found under the bark of thickness from 6 to 36 mm. Most often, specimens were found under a 10–20 mm thick bark (Fig. 4).

We used a Poisson regression model to check for ecological factors affecting the abundance of *B. schneideri* on micro-habitats. As we show in Table 5, in the first model containing all factors, there were several (height at which bark was removed (hbr), ants, bark thickness, and abundance of *P. depressus*) with no significant effect on the abundance of *B. schneideri,* even though their coefficient was high. A new model was made using factors that had a statistically significant effect on *B. schneideri* and compared to the previous one using AIC function. By using this model, we determined that the most important factors were light intensity, tree circumference, bark area, and presence of *Ascomycota* fungi mycelium. The presence of fungi has the highest coefficient, suggesting a close ecological relationship with *B. schneideri* (Table 5). Only one *B. schneideri* larva was discovered on a dead tree with no Ascomycota fungi mycelium.

Discussion

B. schneideri as an indicator species of old boreal forests

The most important ecological factors that impact the occurrence of *B. schneideri* in forest stands are forest stand age, presence and continuity of deadwood, number of standing dead trees, the occurrence of *P. depressus*, and number of dead trees with Ascomycota fungi mycelium. The presence of different types of deadwood (snags, fallen trees) and continuity of deadwood are structural bioindicators of old boreal forests. The amount of deadwood is higher there compared to managed forests. Also, as the number of standing dead trees increases, the number of standing dead trees with Ascomycota fungi mycelium increases too.

Forest stand age shows a significant positive correlation with a population density of *B. schneideri* (Rho = 0.35, $p < 0.001$). Age of the forest is clearly linked to important ecological factors that affect the occurrence of *B.schneideri*: circumference of standing dead trees, light intensity; bark thickness. Results of our study allow to safely conclude that

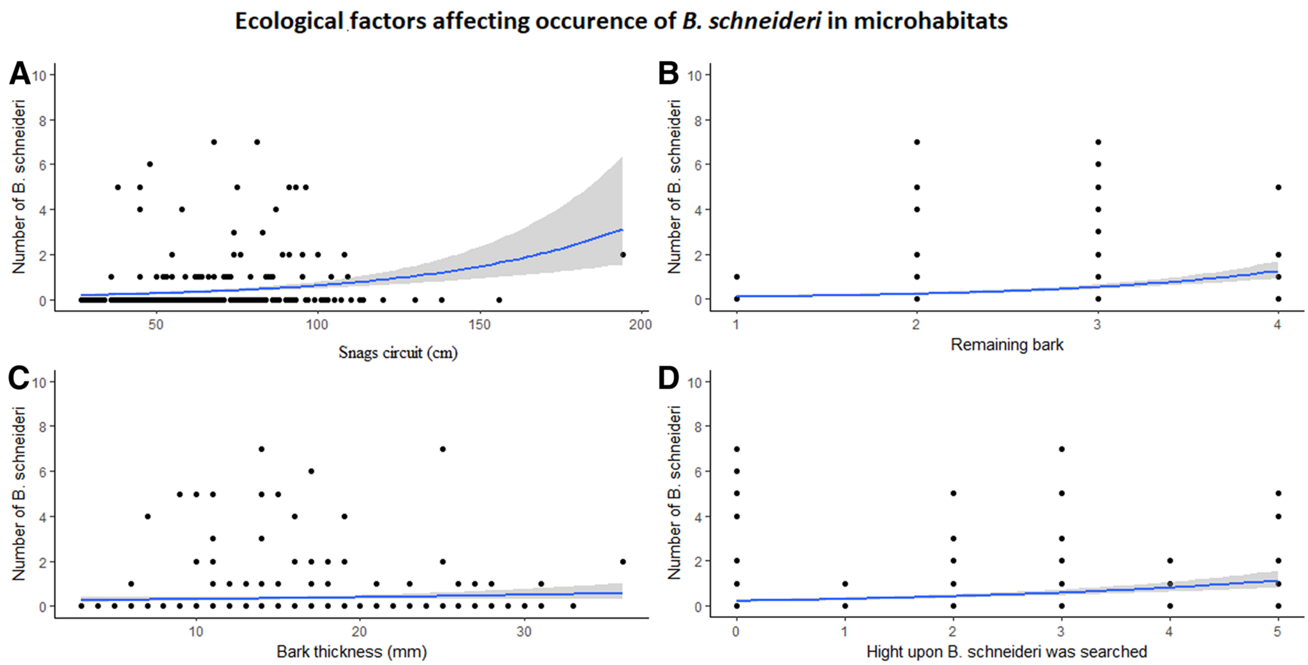

Fig. 4 **a** Snags circuit affecting occurence of *B. schneideri* ($p < 0.001$), **b** remaining bark area (1: 0–25%, 2: 25–50%, 3: 50–75%, 4: 75–100%) on snags affecting occurence of *B. schneideri* ($p < 0.001$), **c** bark thickness affecting occurence of *B. schneideri* ($p < 0.001$), **d** height classes (1: 0–40 cm, 2: 40–80 cm, 3: 80–120 cm, 4: 120–160 cm, 5: 160–200 cm) affecting occurence of *B. schneideri* ($p < 0.001$). Sample size = 312 snags

Table 5 Ecological factors were affecting *B. schneideri* in microhabitats using a GLM Poisson regression model

Abundance of *B. schneideri*	Coefficient	p value	AIC	R^2 (McFadden)
Light intensity	– 0.647	< 0.001	479.57	0.702
+ Tree circumference	0.013	< 0.001		
+ Bark area	0.526	< 0.001		
+ hbr	0.054	0.482		
+ Ascomycota fungi	2.575	< 0.001		
+ Ants	– 0.19	0.408		
+ Bark thickness	0.001	0.947		
+ *P. depressus* abundance	– 0.017	0.754		
Light intensity	– 0.639	< 0.001	472.86	0.701
+ Tree circumference	0.012	< 0.001		
+ Bark area	0.623	< 0.001		
+ Ascomycota fungi	2.582	< 0.001		

B. schneideri may be regarded as an indicator species for old or natural boreal forests.

However, *B. schneideri* can also be found in 50-year-old managed forests given certain ecological factors such as high light intensity, presence of snags with Ascomycota fungi mycelium.

Even though light intensity did not correlate significantly with the occurrence of *B. schneideri* in forest stands ($Rho = 0.10$, $p > 0.001$), we speculate that it could still be an important factor nevertheless. Our study sites differed very little in terms of available light, hence, precluding us from properly testing the significance of this factor. A large number of *B. schneideri* individuals found on edges of examined stands, where the light intensity is higher, suggests that even one snag in opened conditions could be a valuable micro-habitat for current species preservation. Furthermore, we state that the light intensity needed for *B. schneideri* varies in different parts of species distribution range because of different climate conditions, as can be seen from differences of Poland, Lithuania, and our study.

Capercaillie as an umbrella-species

In all capercaillie lek areas (all having status of a micro-reserve) the population density of *B. schneideri* was higher than in the control territories. Capercaillie lek areas differed from control sites with higher light intensity, older forest stand, greater diversity of deadwood in various stages of decay, more snags, and smaller population density of *P. depressus*.

Even though the protection of capercaillie lek areas protects necessary ecological factors and structural components for *B. schneideri* as well, we state that it is not a good umbrella species, as we did not find any other protected saproxylic beetles. Populations of *B. schneideri* can also be found outside capercaillie lek areas if the necessary ecological factors are present.

B. schneideri as a pioneer species

The medium duration of development (2 years), and suitable ecological conditions for *B. schneideri,* such as remaining bark area on a trunk, height at which it is found, and presence of Ascomycota fungi mycelium suggests that *B. schneideri* might be a pioneer species on standing dead trees. This idea is supported by the work of Müller et al. (2013), who also reported that *B. schneideri* often occurs on standing recently dead trees.

We observed *B. schneideri* more often on standing dead trees with 50% or more of the remaining bark area. Depending on where the remaining bark is located, the species can be found at different heights from the ground. On trees with at least 50% of the bark remaining, we found *B. schneideri* at the middle of examined levels (80–120 cm). Considering that bark starts to fall off exactly from the middle and finally remains only on the lower part of the trunk, it may not be surprising that most *B. schneideri* larvae were found at the lowest levels.

In accordance with previous publications, we suggest *B. schneideri* larvae to be associated with Ascomycota. Many authors (Heliövaara 2001; Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2011; Horák et al. 2011; Gutowski et al. 2014) report that *B. schneideri* larvae are mycetophagous and feed on the mycelium of *Aureobasidium* spp. or *Ophiostoma minus*. These fungi have been reported to colonize live wood and to facilitate its decomposition (Cooke 1959; Gorton and Webber 2000; Romón et al. 2007; Bueno et al. 2010). Consequently, if indeed there is a relation between larvae and fungi, this would support the notion of *B. schneideri* being a pioneer species on dead trees.

Competition of *B. schneideri* with *P. depressus* might also confirm its status as a pioneer species. We observed the presence of both species in some micro-habitats; however, *B. schneideri* was not present if the population size of *P. depressus* was large.

B. schneideri population density

There are several limitations concerning the estimated population density of *B. schneideri* in this study. The primary limitation is that we did not remove all the bark from tree trunks, so the exact number of individuals per standing dead tree, as well as the number of trees populated, is not known. Hence, the calculated population size likely will be smaller than the real abundance. We assumed that every dead tree in a forest stand is populated if we observed *B. schneideri* on every dead tree on the transect.

Conversely, when we did not find any *B. schneideri* specimens on the transect, we concluded that it is not present in a forest stand. Both extrapolations from observations from the transect to the whole forest stand to increase the uncertainty in the calculations, and nevertheless, we state that our population density measurements are at least internally comparable. More accurate estimates of population density shall be made through developing and utilising ecological niche models to evaluate population densities.

Conclusions

The most important ecological factors affecting *B. schneideri* are forest stand age and the number of standing dead trees, as well as lasting micro-habitats. *B. schneideri* is a species of old boreal forests, but it can also live in managed forests if necessary ecological factors are present. Capercaillie lek areas provide certain protection for *B. schneideri,* but we emphasize the importance of protecting territories with suitable micro-habitats.

Compliance with ethical standards

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

Research involving animals The authors declare that during this study, no beetles were killed.

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