Life traits of ground beetle assemblages of spruce forests in north-eastern Poland

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Abstract

Assemblages of epigeic ground beetles living in spruce forests in three age ranges: 20-30 years (A); 40-50 years (B); 70-80 years (C) were submitted for research. The investigations were carried out in spruce forests in north-eastern Poland. In each age forest category, 4 plots with 5 Barber traps were set up. Ground beetle assemblages were compared in terms of their abundance, species richness, and the Shannon H' Index value. Quantitative ecological description of carabids captured in the analysed age-classes of spruce forests was performed, and the values of the MIB (mean individual biomass) were calculated. To determine the dependencies between the values of the MIB and abundance of Carabidae trophic groups, the Spearman rank correlation coefficient was calculated. The assemblages of ground beetles living in the spruce forests in north-eastern Poland were characterised by quite large species richness. Significant differences were determined in the number of species richness between the Carabidae assemblages inhabiting the analysed age ranges of spruce forests. The oldest spruce stands had a smaller number of species and specimens of ground beetles as well as the highest MIB values in comparison with the younger spruce forests (30 to 50 years old). It was found that high MIB values were positively correlated with the presence of large ground beetle species with higher moisture requirements. Lower values of the MIB index were due to the presence of smaller, macropterous species, with the spring type of breeding and associated with open areas.

Introduction

In the late 18$^{\mathrm{th}}$ century, forests in Poland covered around 40% of the country's area, and declined to 20.8% in 1945, soon after World War Two (Zajączkowski *et al.* 2016). The undesirable environmental changes caused by this process, as well as the great demand for timber were the reasons why the forest cover in Poland was enlarged to 27.0% between 1945 and 1970. This increase was achieved mainly by growing monoculture forest stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) (Krawczyk 2014). The latter species in its natural range is one of the main forest-forming species. It grows in the mountains of central and southern Europe and also covers extensive areas in the north and east of this continent. Nowadays, spruce in Poland occurs in two ranges: north-eastern (on lowlands) and south-western (in the mountains), and makes up around 6% of all forests. The dying of spruce stands observed in recent years may be caused by several factors. The following are mentioned: decreasing soil moisture content, changes in soil chemistry connected with acidification, and shortage of nutrients, e.g. magnesium [Zwoliński 2003; Małek 2014]. Another reason why spruce forests are dying is the way they are grown, as a monoculture, where this species forms dense single-storey stands; spruce a foreign species in Poland. Monoculture spruce forests are a specific habitat, with poor litter, not very rich understorey and groundcover, and extensive shading of the soil surface [Holeksa and Szwagrzyk 2004].

Descriptions of the state and condition of a variety of habitats often include bioindicator methods. One of the groups of organisms used for bioindication is the Carabidae family. Carabidae make very good bioindicators, and are often used to evaluate changes occurring in agricultural, woodland, and urban habitats [Niemelä et al. 1993, 2007; Pizzolotto et al. 2018]. They are also one of the simple indicators employed in descriptions of the development of succession in forests [Szyszko 1983; 1991; Butterfield 1997; Skłodowski 2009]. Assemblages of ground beetles dwelling in pine forests are quite well recognised [Schwerk and Szyszko 2007; Skłodowski et al. 2018]. Numerous studies provide the characteristics of ground beetle assemblages in pine forests of different ages, growing on different types of soil and using different forest management practices or having the understorey composed of different deciduous species [Szyszko 1990; Jukes et al. 2001; Finch 2005; Taboada et al. 2008; Barsoum et al. 2014; Lange et al. 2014; Kosewska et al. 2019]. Having explored the complex relationships between ground beetle assemblages and the pine forests they inhabit, it became possible to develop a synthetic indicator that describes these dependences [Szyszko 1990]. The Mean Individual Biomass (MIB) of carabid fauna has been proposed as an indicator of the stage of succession in forests and is now employed in research and forest management [Szyszko et al. 2000; Schwerk and Szyszko 2007; Instrukcja ochrony lasu (Forest Protection Legislation) 2012; Skłodowski et al. 2018]. Regarding spruce forests growing in North America, the Fennoscandian Peninsula, and most of Europe, the research results concerning this group of beetles have been well documented [Reeves et al. 1983; Abildsnes and Tommeräs 2000; Elek and Magura 2001; Jukes et al. 2001; Koivula and Niemelä 2002; Lange et al. 2014]. In contrast, we lack such reports on ground beetles in Polish spruce forests. Should the species and quantitative composition of Carabidae assemblages in spruce forests be known, such information might be useful for the determination of the advancement of forest succession, and the evaluation of the condition of a given forest habitat, especially in view of the progressing death of spruce stands and risk of increase presence of pests.

The study reported in this paper aimed to determine the quantitative and species composition of epigeic assemblages of Carabidae dwelling in spruce forests in north-eastern Poland. The hypothesis was that these assemblages differ from one another depending on the age of the forest, type of woodland habitat, and its humidity. It was assumed that older forests would have:

- a greater share of large forest zoophagous species accompanied by a decreasing percentage of open-space hemizoophagous species, - a higher value of the MIB, - diminishing ground beetles species richness.

Materials and methods

Study area

The research covered the area of 4 Forest Subdistricts in north-eastern Poland: subdistrict Sosnowo (Forest District Skrwilno) in 2016 (plots: A1, A2 – area: 1.0 ha); subdistrict Zielony Dwór (Forest District Giżycko) in 2015 (plots: B1, B2 – area: 1.39 ha; A3, A4 – area: 1.83 ha); subdistrict Maruny (Forest District Wipsowo) in 2018 (plots: B3, B4: – area: 3.00 ha) and subdistrict Przejmy (Forest District Przasnysz) in 2015 (plots: C1, C2, C3, C4 – area: 5.4 ha) (Figure 1). Areas with a dominant share of spruce (70 – 100 %), representing 3 age categories, were selected:

- A – 20 - 30 years old (plots: A1, A2, A3, A4),
- B – 40 - 50 years old (plots: B1, B2, B3, B4),
- C – *ca* 80 years old (plots: C1, C2, C3, C4).

More information about the research sites is given in table 1. In each age category, 4 plots treated as replications were established. In each research plot, 5 Barber traps were set up, which were plastic containers measuring 9 cm in diameter and 13 cm in height. The traps were filled with a a preservative liquid and submerged into the soil to be level with the ground surface (Kotze et al. 2011). Traps in each plot were spaced along a transect, at a distance of 10 m from each another. The transects were placed in the central part of the spruce stands; the distances between the transects and the arrangement of traps are shown in Figure 1.

Twenty traps were set up in each age variant of spruce forest, that is, 60 traps in the entire experiment (3 variants x 4 replications x 5 traps). A trap served as an elementary sampling unit. Traps were placed in the ground in spring (May), emptied every two weeks while replenishing the preservative liquid, and the species of captured beetles were identified (Hůrka 1996). The traps were removed in autumn (October), and the duration of their exposure (days) for each of the research areas was as follows: Przejmy (135), Zielony

Dwór (160), Sosnowo (153) and Maruny (141). Moran's I index was calculated (SAM v.4.0; Rangel et al. 2010) to measure spatial autocorrelation of carabid abundance in the sampling plots of the studied areas. The distribution of the abundance of carabid beetles along the spatial arrangement of sampling plots was not autocorrelated (Moran's I = 0.264, p = 0.117).

Life traits of carabids

Assemblages of ground beetles in the analysed age categories of spruce forests were compared, taking into account the number of beetles, species richness, and values of the Shannon H' species diversity index. The species-identified beetles were classified in terms of body size and food preferences, breeding strategy, preferred habitat, habitat moisture content, and ability to fly (Meijer 1974, Lindroth 1985, 1986, Hůrka 1996, Aleksandrowicz 2004) (Table 2). Regarding the ecological traits, the captured Carabidae representatives were divided into large zoophages (Lz) – predatory species with a body length of more than 15 mm, small zoophages (Sz) – also predators but with a body length no more than 15 mm, and hemizoophages (Hz) – ingesting mixed food. Concerning the breeding strategy, the ground beetles were classified as spring (Sb) and autumnal (Ab) types of breeding. Depending on habitat preferences, the following groups of ground beetles were distinguished: forest (F), open area (Oa), eurytopic (Eu), and wetland (Wet) species. According to the moisture preferences, the distinguished groups of ground beetles were: hygrophilous (H), mesophilous (M), and xerophilous (Xe). The ability to fly was also considered, giving rise to the following division: able to fly, with developed wings, i.e. macropterous species (Ma), species with reduced wings, not flying, i.e. brachypterous (B), and dipterous (D), i.e. those which can be found to present either of the forms of wing development.

Analysis of ground beetle assemblages in terms of their ecological characteristics can be useful in assessing the advancement of the forest succession process. Assemblages of carabid beetles associated with early phases of the forest succession progress are distinguished by a relatively large share of small species with large dispersion power, often connected with open space areas. In advanced stages of succession, large, forest-type species with lesser dispersion power begin to appear (Magura et al. 2002; Niemelä et al. 2007).

Data analysis

The mean individual biomass (MIB) of Carabidae was calculated using the formula (Szyszko et al. 2000) which describes dependencies between the body length and biomass of beetles. Evaluation of the distribution of the abundance of a catch rate species and specimens of Carabidae as well as the abundance of the distinguished trophic groups in the analysed variants was supported by the Shapiro-Wilk W test. Data characterised by unimodal distribution were assessed by applying the GLM (Generalised Linear Model), which included Poisson's data distribution. Groups of means not statistically different were assigned the same lettered index: a, b (Bonferroni test). Data having normal distribution were examined by ANOVA test. Spearman's correlation rank coefficient (r_s) was derived to determine the correlation between values of the MIB index and the abundance of specific trophic groups of Carabidae.

To visualize the differences of ground beetle assemblages living in the analysed age variants of spruce forests, non-metric multidimensional scaling (NMDS) was performed, using the Bray-Curtis similarity index. This method enabled us to evaluate the ground beetle assemblages based on the similarity between individual beetles and by analysing data concerning the number of captured species and specimens. Samples with a high degree of similarity are plotted close to one another in the NMDS diagram. An assessment of the significance of differences between the analysed assemblages using the NMDS method was performed using the ANOSIM non-parametric statistical test (Clarke 1993). The ordination methods were used to assess relationships between the presence of Carabidae species and their specific ecological groups versus the distinguished environmental variables (forest age, canopy, humidity, fertility, MIB, and the number of treatments, such as stand cleaning and thinning) (ter Braak and Smilauer 1998). The RDA method (Redundancy Analysis) was used because the distribution of the analysed data was linear (SD = 2.09). This type of analysis arranges samples in order along a gradient represented by axes of the ordination diagram, in our case based on data concerning the species composition of ground beetle assemblages. The Jackknife 2 estimator was used for abundance data (using EstimateS v. 9.1.0 statistical software) and the species accumulation curves were calculated to assess the adequacy of the sampling efficiency (Zahl 1977; Colwell 2005).

All statistical calculations and their graphical presentation were supported by the following programmes: Statistica 13.3 (Shapiro-Wilk W test, GLM, Spearman's correlation rank coefficient), Canoco 4.51 (RDA), and Past 2.01 (NMDS and ANOSIM).

Results

During the study, 3,105 specimens belonging to 44 carabid species were captured (Table 2). Species accumulation curves for individual transects in the 3 years of the study confirmed that the sampling effort was adequate (Figure 2). The dominant species in the analysed forest stands was *Carabus hortensis* , which composed 34.72 % of the total species captured. Other numerous species were: *Pterostichus niger*(14.98 %), *Pterostichus oblongopunctatus* (11.56 %),*Pterostichus melanarius* (9.15 %), and *Calathus micropterus* (7.50 %). The remaining species of ground beetles did not exceed a 5 % share in the examined assemblages. Most species (40) were caught in the youngest spruce forest classified as A (up to 30 years old), while in the 50-year-old spruce forest (B) there were 28 species, and the 80-year-old spruce stands (C) were home to the smallest number of ground beetle species, namely 22. The GLM analysis confirmed significant differences in the average number of ground beetle species caught between the three age categories of spruce stands. The*post-hoc* Bonferroni test arranged these average values into three uniform groups (Figure 3a). The smallest average catch rate of carabids was found in 80-year-old spruce stands (3.9 individuals on average). Significantly more individuals were captured in younger spruce forests (A, B), where their number was on a comparable level (Table 2, Figure 3b). The highest MIB value was found in the assemblages inhabiting the oldest stands (C) Figure 3c, Table 2).

In the three age categories of spruce stands, the dominant share of ground beetles was composed of forest species, and the highest average number of individuals representing this class of ground beetles was noted in the youngest spruce forest (A) - 49.25 individuals on average (Table 3). An increase in the age of the forest did not generate a higher mean abundance of forest species of ground beetles (B - 39.85 and C - 33.85). The second most numerous group consisted of eurytopic species, most abundant in the 50-year-old forest (14.90) and 80-year-old forest (7.10). The least numerous group of eurytopic species was observed in the youngest forest (A). Open-area and wetland beetles composed the least numerous groups, presenting a similar distribution in all three age categories of forests. Our analysis of ground beetle moisture preferences revealed that mesophilous beetles were the dominant group, and they appeared in the highest number in the oldest stands (C). The youngest spruce stands (A) comprised the highest percentage of individuals classified as xerophilous ones as well as the ones associated with higher moisture content in the soil. Concerning the trophic preferences, the examined age categories of spruce stands were populated by the prevalent share of predatory ground beetles. Large zoophagous beetles were most frequently encountered in the 50-year-old spruce forest (44.00). In the other two age categories (youngest and oldest), the number of large zoophages was lower and similar in both cases. The dominant type of breeding among the ground beetles was the autumnal strategy, with the most numerous representatives found in the 50-year-old forest (B). As for the spring type of breeding, such species were observed to gradually increase in number as the age of the examined forest was lower. The most brachypterous individuals (36.70) appeared in the 30-year-old spruce forest. The smallest number of beetles with no ability to fly was found in the 50-year-old spruce forest (B). In this forest, the dominant beetles were winged ones (macropterous and dipterous) (Table 3).

To determine the correlations between MIB values in the analysed age ranges of spruce forests and the abundance of the identified ecological groups of ground beetles, values of Spearman's rank correlation coefficient (r_s) were calculated. Higher MIB values were significantly positively correlated with the ascending age of spruce forests (r_s =0.26), and with the occurrence of large zoophagous beetles (r_s =0.34) and the group of ground beetles having a high demand for moisture, i.e. hygrophilous (r_s =0.38) and wetland species (r_s =0.29) (Table 3). Low values of the MIB index were caused by the presence of numerous small zoophagous beetles (r_s =-0.87). A significant correlation, in this case, was also found with the numerous occurrence of open area (r_s =-0.61), macropterous (r_s =-0.58) and xerophilous (r_s =-0.58) beetles, and spring breeders (r_s

=-0.55). Higher values of the Shannon H' index were also correlated with a decrease in the MIB index values (r_s =-0.80) (Table 3).

The ANOSIM analysis indicated significant differences (R=0.31, p<0.01) between the carabid assemblages inhabiting the three age ranges of spruce stands; this significant differences are shown on the NMDS diagram (Figure 4). More information about the ground beetle assemblages is shown on the RDA diagram (Figure 5). The RDA analysis presents the distribution of ground beetle species and indicates their ecological groups along environmental gradients, represented by two main canonical axes, describing 67.8 % of the variance. The redundancy analysis RDA showed that the B objects (40-50 years old), situated in two different forest habitats (also different in terms of humidity) are grouped in one part of the ordination diagram. Similar regularity is observed for most objects located in stand A (20-30 years old), which are grouped in the upper, left-hand quarter of the diagram and correlate with the 2nd ordination axis, in addition to which they are also localised in different types of forest habitat. Our analysis of this part of the diagram also indicates that the high shading of soil (canopy) was correlated with the presence of open area species (Oa), small zoophagous species (Sz) with the spring type of breeding (Sb), and xerophilous (Xe) species.

Further analysis of the RDA diagram shows that the first ordination axis correlated with the presence of large zoophagous species (Lz), which is also linked to high values of the MIB. This axis is also strongly correlated with habitat humidity and to the presence of hygrophilous species (H) and species associated with wet areas (Wet), e.g. *Carabus granulatus* , *Oxypselaphus obscurus* . The fertility of the habitat was not correlated with the first two ordination axes describing most of the ground beetle assemblages.

Discussion

The species richness obtained in this study on ground beetles in spruce forests was relatively high, although it needs to be added that this is the total of ground beetles caught in 4 localities situated in 2 macroregions of Poland (the Masurian Lakeland, and the Chełmińsko-Dobrzyńskie lake District) (Kondracki 2011). Considering the above, the number of species caught was similar to the reported number of species in Finland (Koivula and Niemelä 2002, Koivula et al. 2019), Canada (Niemelä et al. 1993), Slovakia (Macko 2016), and Germany (Lange et al. 2014). There were differences in the average number of ground beetle species in the examined spruce forests, with a tendency towards smaller species richness in older stands (Figure 3a). The same tendency is seen in the number of caught beetles.

The NMDS analysis showed significant differences between ground beetle assemblages from the three age classes of spruce stands (Figure 4). Qualitative and quantitative changes in the assemblages of ground beetles identified in the older stands (B and C) were mainly due to a more numerous presence of large forest (*C. hortensis* , *C. violaceus*) and eurytopic species (*P. melanarius* , *C. nemoralis*). The frequent occurrence of *C. hortensis* is not an unusual finding. This species, in Scandinavia, is characteristic of deciduous and mixed forests, and in central Europe it appears in large numbers in coniferous forests (Lindroth 1985). At the same time, *C. hortensis* is considered to be typical of mature tree stands (Niemelä et al. 2007). The more numerous appearance of *C. violaceus* in spruce stands over 80 years old is worth noting in the context of the observed decline in its presence in Polish forests. An interesting finding is the frequent presence of *P. melanarius* and *C. nemoralis* in the spruce forests covered by our study. These are eurytopic species, which also appear in forests. However, they belong to the group of deciduous forest specialists, characteristic of native forests (Magura et al. 2000). *P. melanarius* is not a species that lives in abundance in spruce forests (Lynikiene 2006, Schwerk and Szyszko 2007), but it is more abundant in younger forests (Tarwacki 2012).

In the youngest age range (up to 30 years), the dominant ground beetles were typical forest zoophagous species with poor dispersal power (brachypterous): *C. micropterus* and *C. arvensis* . *P. oblongopunctatus* also appeared in large numbers (Table 2). The two former species were described by Magura et al. (2000), in a study on ground beetle assemblages in managed and unmanaged spruce plantations, as species associated with the presence of deciduous trees. These authors also suggested that tree thinning in managed spruce plantations induces the growth of a leafy understory, which leads to the accumulation of leafy litter. In such habitats, the frequent presence of *P. oblongopunctatus* has been noted. The spruce forests which were in the youngest age class in our research were also distinguished by the presence of Carabidae species classified as an open area species with the spring type of breeding, xerophilous, small zoophagous, and hemizoophagous. These groups are shown in the ordination diagram (RDA) and are associated with the objects in this age class of spruce forests (A).

The above ecological description of species composing assemblages of ground beetles is typical of forests at an early stage of forest succession (Buddle et al. 2006, Skłodowski 2017, Kosewska et al. 2018). It was only in the youngest spruce stands (besides the typical forest species that appeared in all tree stands, i.e. *Amara brunnea*) that open area species of the genus *Amara* were detected (*Amara bifrons* , *Amara communis,* and A*mara similata*). These species are connected with open areas (meadows, agrocenoses, etc.), and have uniquely strong dispersal power owing to their ability to fly (Hurka 1996). A similar relationship was determined concerning two species of the genus *Harpalus* : *Harpalus rufipes* and *Harpalus tardus* . This group of hemizoophagous species associated with open areas is capable of inhabiting coniferous forests at the early stages of succession, which may be explained by their ability to find plant food in these habitats (Kosewska et al. 2019). The conditions which are suitable for the development of these species disappear as a forest grows older (disappearance of plant food). The number of early-succession species decreases when the tree canopy closes, that is when the forest is 20 to 30 years old (Niemelä et al. 2007).

One of the most popular indicators used to identify stages in the succession of forests is the mean individual biomass (MIB) index (Szyszko 1983, Szyszko et al. 2000, Cárdenas and Hidalgo 2007, Jelaska et al. 2011). The results obtained in our study indicate a growth in the MIB values determined for ground beetles in older spruce forests (Figure 3c). The calculated values of Spearman's rank correlation coefficient (Table 3) indicate that high MIB values are related to the presence of species classified as large zoophages, having high moisture requirements (hygrophilous and wetland species). Low MIB values were significantly correlated with the higher species richness (Shannon H') of Carabidae, the frequent presence of small zoophagous, xerophilous species, and open area species with high dispersal capability (macropterous). The presence of species having specific ecological features in younger and older age classes of spruce forests is closely similar to the situation described by many other authors (Szyszko 1983, Magura et al. 2002, Niemelä et al. 2007, Skłodowski 2009). A certain divergence consists in the decreasing abundance within the species typical of forest habitats with the growing age of the spruce forests, which we observed in this study. The most probable reason was the frequent occurrence in the youngest forests (class A) of *C. micropterus* and *C. arvensis* (Table 2). This might be attributed to the fact that all the research sites are habitats typically inhabited by the forest species of ground beetles, and the more frequent presence of certain species in one of the age classes of forests might be due to some specific habitat-related characteristics (e.g. the type of microhabitats) (Pearce and Venier 2006).

Conclusions

Assemblages of ground beetles dwelling in spruce forests in the north-eastern part of Poland are characterised by quite high species richness. In all age classes of spruce forests, the most numerous carabids were those classified as large, forest zoophages. However, significant differences were determined between the assemblages of ground beetles living in the three age classes of spruce forests. The oldest forests (around 80 years old) were the sites where the smallest number of carabid species and specimens were captured, but these were species characteristic for forests at an advanced stage of succession, which translated into the highest MIB values. The 30- to 50-year-old spruce forests (objects A and B) were characterised by higher species richness and a greater number of ground beetles, accompanied by lower MIB values. The calculated values of Spearman's rank correlation coefficient reveal that high MIB values are positively correlated with the presence of large Carabidae species that require more moisture. Lower MIB values are associated with the presence of smaller, macropterous species with the spring strategy of breeding, associated with open areas.

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Table 1. Description and characteristics of spruce forests

Age variant	District	Plot	Age [years]	Height above sea level [m]	Soil	Type of forest
A	Sosnowo	A1	28	135	haplic brunic arenosol	mixed fresh conifer
		A2	28	135	haplic brunic arenosol	mixed fresh conifer

Age variant	District	Plot	Age [years]	Height above sea level [m]	Soil	Type of forest
	Zielony Dwór	A3	28	151	haplic luvisol	fresh forest
		A4	28	151	haplic luvisol	fresh forest
B	Zielony Dwór	B1	43	150	haplic luvisol	fresh forest
		B2	43	150	haplic luvisol	fresh forest
	Maruny	B3	48	139	albic brunic arenosol	mixed fresh forest
		B4	48	139	albic brunic arenosol	mixed fresh forest
C	Przejmy	C1	78	120	mucky soils	moist forest
		C2	78	120	mucky soils	moist forest
		C3	78	119	mucky soils	moist forest
		C4	78	119	mucky soils	moist forest

* Treatments: cleaning; thinning

Table 2. Abundance, ecological classification and species name abbreviations used in the RDA analysis of ground beetles in age variants of spruce forests

	Abbre-viations	Ecological characteristic	Individuals / Percentage	Individ
Species			A*	A*
			A1, A2	A1, A2
			n	%
Amara bifrons (Gyllenhal,1810)	A_bifr	Oa/Xe/Hz/Ab/Ma	2	0.3
A. brunnea (Gyllenhal, 1810)	A_bru	F/M/Hz/Ab/Ma	4	0.6
A. communis (Panzer, 1797)	A_com	Oa/M/Hz/Sb/Ma	1	0.1
A. similata (Gyllenhal,1810)	A_simi	Oa/M/Hz/Sb/Ma	1	0.1
Badister lacertosus Sturm, 1815	Ba_lace	F/M/Sz/Sb/Ma		
Calathus ambiguus (Paykull,1790)	Ca_amb	Oa/Xe/Sz/Ab/Ma	1	0.1
C. erratus (Sahlberg, 1827)	Ca_err	F/Xe/Sz/Ab/D	2	0.3
C. fuscipes Goeze, 1777	Ca_fusc	Oa/M/Sz/Ab/B	26	3.9
C. melanocephalus (Linnaeus, 1758)	Ca_mela	Oa/M/Sz/Ab/B	3	0.4
C. micropterus (Duftschmid, 1812)	Ca_micr	F/M/Sz/Ab/B	181	26.3
Carabus arvensis Herbst,1784	C_arv	F/Xe/Lz/Sb/B	89	12.9
C. cancellatus Illiger,1798	C_canc	Eu/M/Lz/Sb/B	3	0.4
C. convexus Fabricius, 1775	C_conv	F/Xe/Lz/Sb/B	12	1.8
C. coriaceus Linnaeus, 1758	C_coria	F/M/Lz/Ab/B		
C. glabratus Paykull, 1790	C_glab	F/M/Lz/Ab/B	3	0.4
C. granulatus Linnaeus, 1758	C_gran	Wet/H/Lz/Sb/B	1	0.1
C. hortensis Linnaeus, 1758	C_hort	F/M/Lz/Ab/B	118	17.2
C. marginalis Fabricius, 1794	C_marg	F/M/Lz/Sb/B	2	0.3
C. nemoralis O.F.Muller, 1764	C_nemo	Eu/M/Lz/Sb/B	1	0.1
C. violaceus Linnaeus, 1758	C_viol	F/M/Lz/Ab/B	10	1.5
Clivina fossor (Linnaeus,1758)	Cl_fos	Oa/M/Sz/Sb/D		
Cychrus caraboides (Linnaeus, 1758)	Cy_cara	F/M/Lz/Ab/B		
Harpalus laevipes Zetterstedt, 1828	H_leav	F/M/Hz/Sb/Ma	1	0.1
H. rufipes (De Geer, 1774)	H_rufipe	Oa/M/Hz/Ab/Ma	4	0.6
H. tardus (Panzer, 1797)	H_tar	Oa/Xe/Hz/Sb/Ma	3	0.4
Leistus rufomarginatus(Duftschmid, 1812)	L_rufo	F/M/Sz/Ab/B	2	0.3
L. terminatus (Hellwig, 1770)	L_term	Wet/H/Sz/Ab/B		
Limodromus assimilis (Paykull, 1790)	Li_ass	F/H/Sz/Sb/Ma		
Loricera pilicornis (Fabricius,1775)	Lo_pili	Wet/H/Sz/Sb/Ma	Wet/H/Sz/Sb/Ma	

	Abbre-viations	Ecological characteristic	Individuals / Percentage	Individ
Nebria brevicollis (Fabricius, 1792)	N_brev	Eu/M/Sz/Ab/Ma		
Notiophilus biguttatus (Fabricius, 1779)	No_big	F/M/Sz/Sb/D	18	2.7
N. palustris (Duftschmid, 1812)	No_pal	Oa/M/Sz/Sb/B	1	0.1
Ophonus rufibarbis (Fabricius,1792)	Op_rufi	Eu/M/Sz/Ab/Ma		
Oxypselaphus obscurus (Herbst, 1784)	Ox_ob	F/H/Sz/Sb/Ma		
Patrobus atrorufus (Strom,1768)	Pa_atr	Wet/H/Sz/Ab/B		
Poecilus lepidus (Leske,1785)	Po_lep	Oa/Ks/Sz/Sb/D	3	0.4
P. versicolor (Sturm, 1824)	Po_ver	Oa/M/Sz/Sb/Ma	1	0.1
Pterostichus anthracinus (Illiger,1798)	P_anth	Wet/H/Sz/Sb/D	1	0.1
P. melanarius (Illiger, 1798)	P_mela	Eu/M/Lz/Ab/D		
P. niger (Schaller, 1783)	P_nige	F/M/Lz/Ab/Ma	86	12.5
P. oblongopunctatus (Fabricius, 1787)	P_obl	F/M/Sz/Sb/Ma	109	15.8
P. strenuus (Panzer, 1797)	P_str	F/H/Sz/Sb/D		
P. vernalis (Panzer,1796)	P_ver	Oa/H/Sz/Sb/Ma		
Syntomus truncatellus (Linnaeus,1761)	Sy_tru	Oa/Xe/Sz/Sb/B	1	0.1
Individuals - Total			690	100

* A: 20-30 years; B: 40-50 years; C: 70 - 80 years

Hz- hemizoophages, Sz- small zoophages, Lz- large zoophages, Ab- autumn breeders, Sb- spring breeders, F- forest, Oa- open area, Eu- eurytopic, Wet - wetland, M- mesophilous, Xe- xerophilous, H- hygrophilous, Ma- macropteric, B- brachipteric, D- dipteric

Table 3. Results of statistical tests (GLM, ANOVA) and values of Spearman's rank correlation coefficient for species richness, abundance, diversity and MIB values of Carabidae ecological groups within age classes of spruce forests

Specifications	Means for the analysed age classes of spruce forests A	Means for the analysed age classes of spruce forests B	Means for the analysed age classes of spruce forests C	Wald's statistic
Individuals	5.12	5.10	3.90	45.65
Species	2.78	2.43	1.50	84.75
Shannon H'	0.78	0.75	0.71	0.07
MIB (mg)	273.82	286.67	341.84	173.1
Eu	3.65	14.90	7.10	138.18
F	49.25	39.85	33.85	58.29
Oa	2.40	1.00	1.55	11.51
Wet	1.00	0.35	0.35	9.08
H	1.65	1.00	1.30	3.17
Xe	5.65	0.10	0.15	69.01
M	49.00	55.00	41.40	-
Hz	1.05	0.65	1.20	3.26
Lz	34.85	44.00	32.10	41.70
Sz	20.40	11.45	9.55	93.60
Ab	38.60	43.90	32.85	31.61
Sb	17.70	12.20	10.00	46.33
B	36.70	23.65	28.60	57.85
D	2.70	9.05	4.15	76.28
Ma	16.90	23.40	10.10	100.78
Age of forest	< 80	< 50	< 30	-

Specifications	Means for the analysed age	Means for the analysed age	Means for the analysed age	Wald's statistic
(years)				

* n. s. non sagnificant; ** - explanations of the abbreviations is given in Table 2

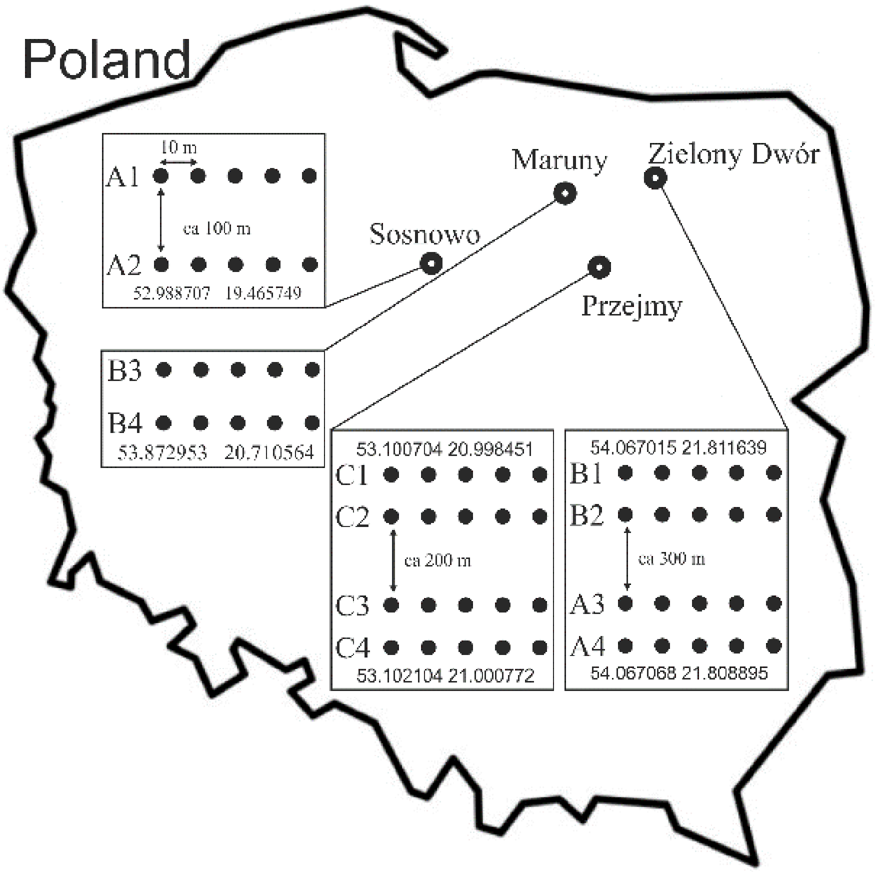

Figure 1. Location of the study area, with distribution of sampling sites and transect of traps

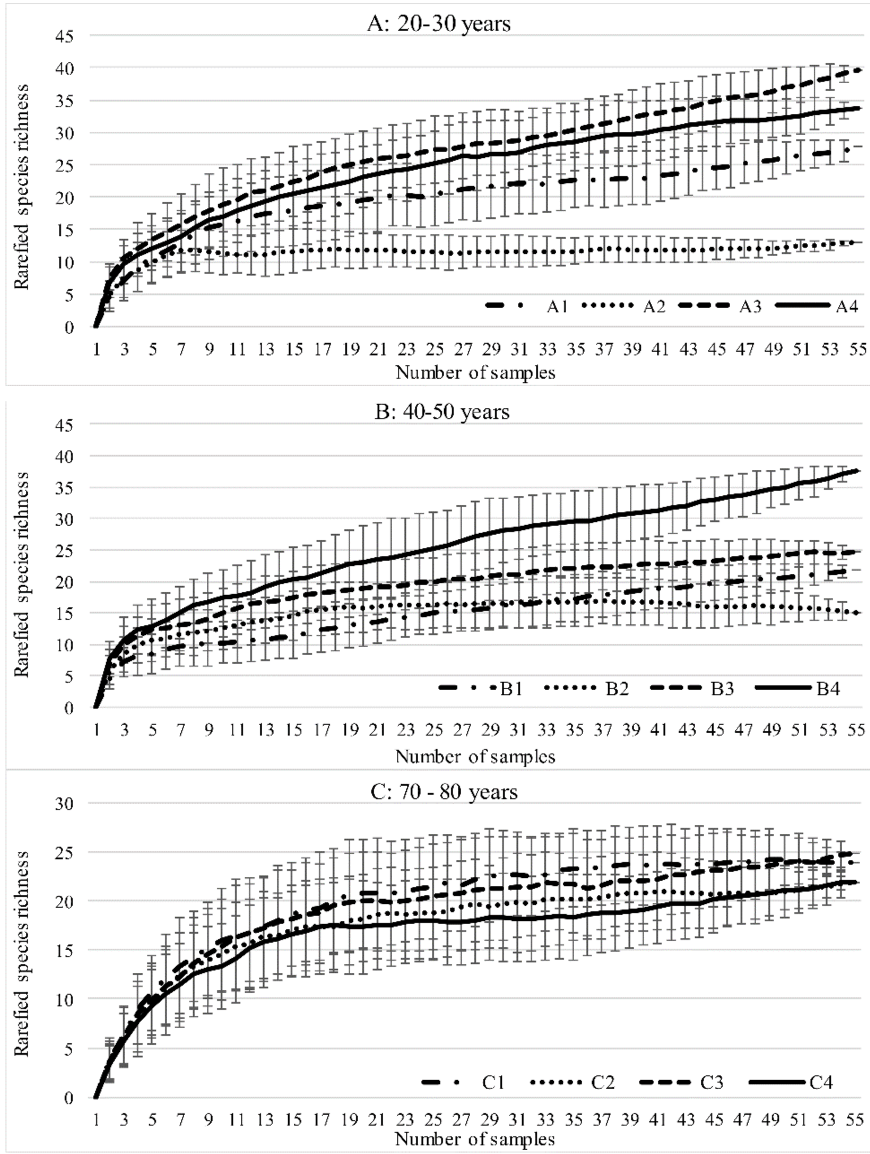

Figure 2. Expected number of carabid species caught in spruce forests using the Jackknife estimator (±SD) of species richness

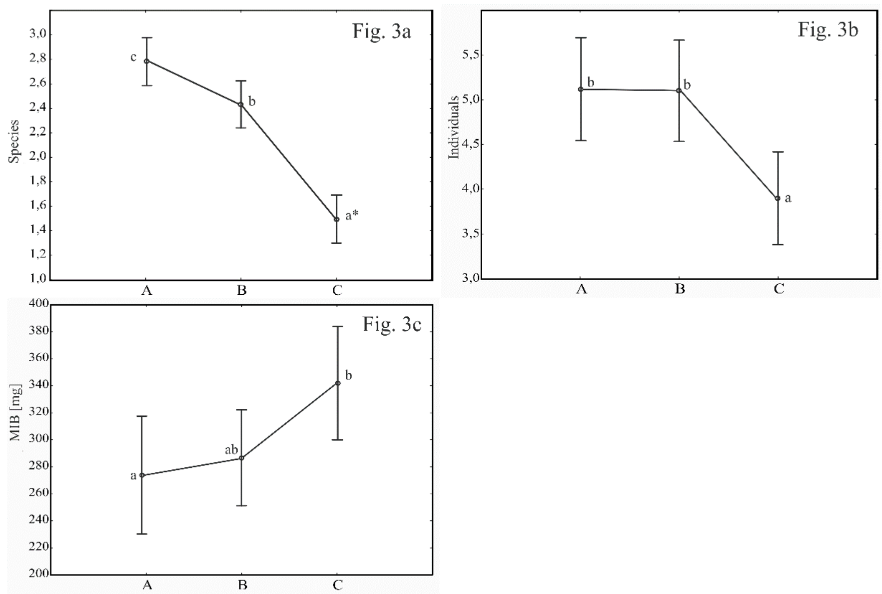

Figure 3. Mean values of species richness (1a), abundance (1b) and MIB (1c) of ground beetles in the three age classes of spruce forests (* Vertical lines denote SE; a, b… - means indicated by the same letter do not differ according to the Bonferroni test)

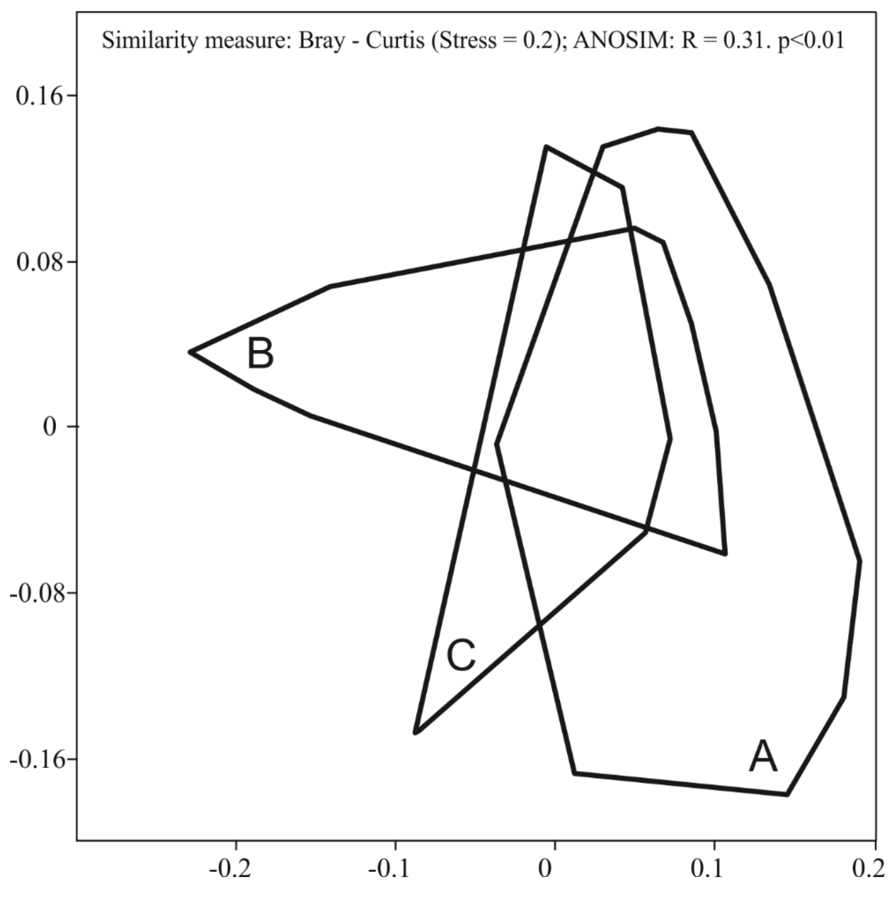

Figure 4. Diagram of non-metric multidimensional scaling (NMDS) for carabid assemblages in relation to age classes of spruce forests (A: 20-30 years; B: 40-50 years; C: 70-80 years)

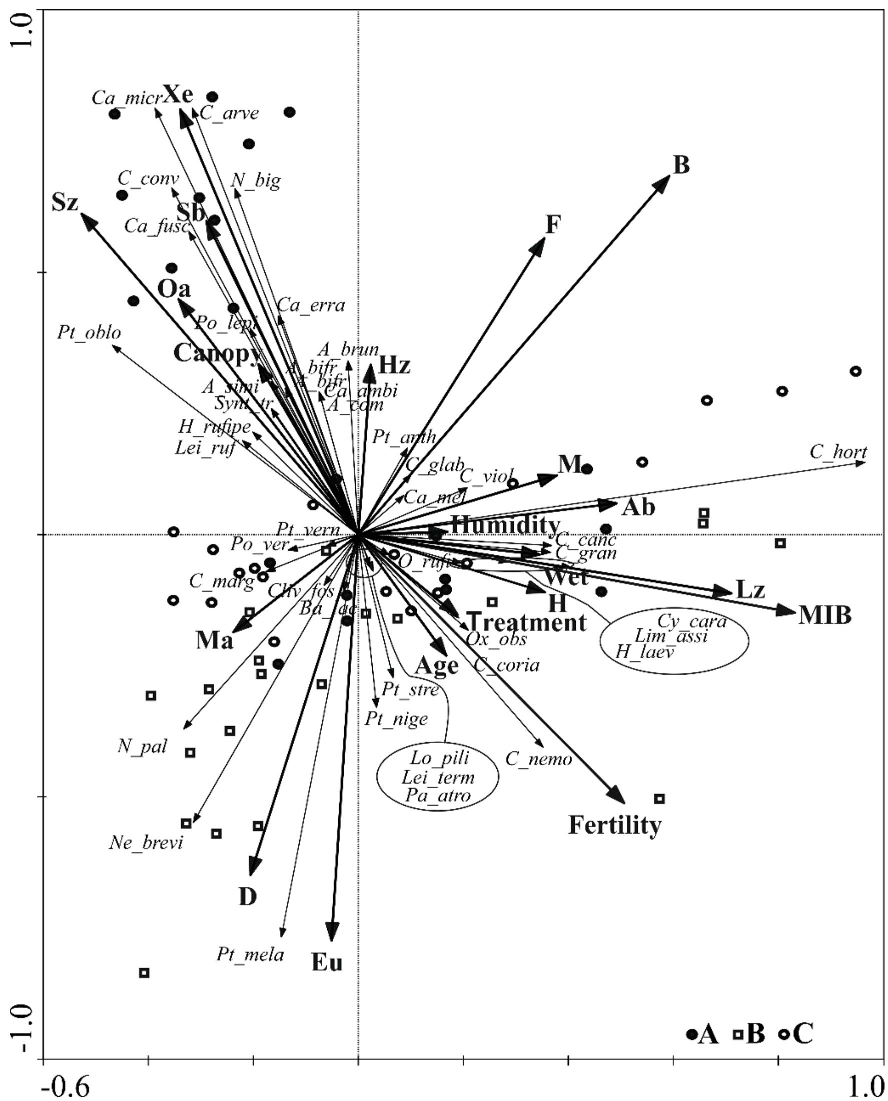

Figure 5. Diagram of redundance analysis (RDA) illustrating dependences between captured species of Carabidae, their ecological groups, and environmental variables (MIB, humidity, no of treatments, fertility, canopy and forest age) (Abbreviations are given in Table 2)