



# Carabids benefit more from pine stands with added understory or second story of broad-leaved trees favored by climate change than from one-storied pine stands

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## Abstract

The released excess anthropogenic nitrogen and carbon produces habitat enrichment, as exemplified by the modification of one-storied pine stands by introducing deciduous species into the understory or second story. In this study, we discuss the validity of pine stand modification by pitfall-trapping epigeic carabid beetles. Two hypotheses were formulated: (1) proportion of late-successional species is higher in assemblages inhabiting pine stands with understory or a second story than in one-storied pine stands; (2) plant litter composition affects carabid beetle assemblages more than other environmental variables. Additionally, characteristic carabid species of the respective pine stand types were identified. GLMM analysis revealed a higher proportion of late-successional species in pine stands with understory or a second story than in one-storied ones. NMDS separated those pine stand types. RDA analysis indicated that pine litter and humus had the strongest effect on carabid beetle assemblage structure in one-storied stands, being drier and thicker in this stand type than in the others. Indicator value analysis identified two characteristic non-forest species in one-storied stands. The study revealed that the introduction of understory and particularly a second story into pine stands increased carabid beetle diversity and the proportion of late-successional species, confirming the validity of pine stand modification.

**Keywords** Stand reconstruction · Second floor · Canopy closure · Litter layer · Ecological traits

## Introduction

A large number of factors affect the condition of forest stands and may induce their decline. The most commonly listed factor is climate change. Climate changes affect species composition of tree stands, among other factors, due to different sensitivities to temperature-driven drought stress of various tree species (Van Mantgem and Stephenson 2007). Particularly in the case of coniferous tree species (e.g.,

those that belong to the genera *Picea*, *Abies*, and *Pinus*), an increase in the mortality rate and decrease in the recruitment rate have been observed. Furthermore, other factors affect forests as well: for instance, the accumulation of anthropogenic nitrogen may lead to excessive enrichment of forest habitats and thus contribute to a gradual replacement of coniferous species with broad-leaved ones, since the growth of the latter increases significantly under the conditions offered by fertile habitats (Pretzsch et al. 2014). Nowadays, a slow recession of coniferous trees, especially the spruce, is observed (Rehfuess 1985; Andreassen et al. 2006; Hlásny and Sitková 2010). In lowland forests of Central Europe, including Poland, the Scots pine (*Pinus sylvestris*) has become the dominant species.

At the beginning of the 1990s, climatic and environmental changes, including forest habitat enrichment, provided a stimulus to commence the modification of species composition of Polish pine stands. Such modification consists in increasing the number and proportion of deciduous tree species while renewing clear-cut areas as well as in implementing methods that offer an alternative to clear-cut systems,

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such as shelterwood, selection or edge systems. Another alternative that may be implemented in pre-mature pine forest is to plant a second story of deciduous species and, if this is not possible, to introduce understory in order to improve the functioning of the pine stand ecosystem and increase biodiversity. It seems that the increased structural heterogeneity and productivity and the conversion of Scots pine monocultures into mixed forest might result in forestry contributing progressively to a higher carbon storage and sequestration (Pretzsch et al. 2016).

The question arises whether modifying the species composition and structure of tree stands can influence ecosystems and increase the diversity of the organisms that inhabit them. In order to answer this question, it is necessary to study the consequences of implementing various ways of monoculture conversion by monitoring changes in the structure and composition of invertebrate assemblages. For this purpose, it is best to monitor invertebrates living in plant litter, and predatory ones in particular, as the observation of fauna representing the high, third trophic level in an ecosystem does not produce random results. Carabid beetles, which are mostly predatory, are often used for the purpose of environmental studies, because they frequently occur in forests and in other ecosystems, they are easy to capture and have a well-understood ecology (for a review see: Lövei and Sunderland 1996; Niemelä et al. 2007; Koivula 2011). The structure and composition of carabid assemblages are strongly affected by such factors as primeval forest transformation in managed forest (e.g., Skłodowski 2014), clear-cutting (Szyszko 1983; Beaudry 1995; Beaudry et al. 1997; Koivula and Niemelä 2003), the presence of the forest edge (Magura 2017), and others.

However, the diversity and structure of carabid assemblages are also affected by local factors connected with various ages of tree stands (du Bus de Warnaffe and Lebrun 2004), diameter distribution of trees, understory thickness, and the percentage share of deciduous species (Barkley et al. 2016) as well as by the thickness and humidity of the litter layer and humus. According to Humphrey et al. (1999) and Jukes et al. (2001), extensive spruce canopy cover and high organic matter content in soil will lower carabid diversity and species richness. Furthermore, carabid species composition depends on plant litter and its thickness (Koivula et al. 1999; Magura et al. 2001).

In two-storied tree stands, access to light and wind activity are limited, so plant litter in such stands is more shaded and moister than litter in one-storied tree stands (Brooks and Kyker-Snowman 2008; von Arx et al. 2013). Introducing understory to pine stands should have a similar effect, though probably to a lesser degree. Bearing this in mind, our study of carabid beetle assemblages was conducted in one-storied pine stands and one-storied pine stands with understory and separately in two-storied stands with

deciduous species in the second story. As carabid beetles respond to canopy closure with an increase in the proportion of late-successional species and with lower species diversity (Magura et al. 2015), a higher proportion of individuals representing late-successional species may be expected in carabid assemblages in stands with understory or a second story. Carabid beetles respond to changes in forest brought about by ecological succession. It has been demonstrated that the proportion of late-successional species in the carabid fauna is higher in stands with a more complex vertical structure growing on fertile soils compared to one-storied stands on poor soils (e.g., Skłodowski 2014). However, there have been no studies of carabid beetles in stands growing on poorer substrates where understory and a second story were introduced.

As the introduction of deciduous trees in the second story or understory contributes to the diversification of litter composition, carabid assemblages in pine stands where deciduous trees have been introduced should have a distinctive structure and composition. An increase in the thickness of the litter layer composed of pine needles or leaves, especially in poor forest ecosystems, results in an increased occurrence of species associated with the shaded forest floor and with forest species (Guillemain et al. 1997; Koivula et al. 1999; Koivula 2001; Magura et al. 2001). Therefore, the following two hypotheses have been formulated: (1) the proportion of late-successional species is higher in assemblages inhabiting pine stands with understory or a second story than in one-storied pine stands; (2) carabid beetle assemblages that do not inhabit the first or second story are affected by plant litter composition to a greater degree than by the thickness or moisture of the humus.

As the species composition of ground beetle assemblages depends on the type of ecosystem, fertility level and, most importantly, on soil type and humidity level, we decided to identify characteristic carabid species for the respective tree stand types as an additional aim of our study. Another supplementary aim was to explain potential differences between carabid assemblages on the basis of environmental indicators describing habitat conditions.

## Materials and methods

### Study area

The study was conducted in Chojnów Forest Inspectorate, Chojnów Forest District (near Warsaw, Poland), in nine forest divisions: 129b, 122f, 101d, 102c, 102d, 79a, 74g, 73c, and 92g. All pine stands where the research plots were selected grew on the same soil type (rusty-podzolic), had similar litter layer types (moder or moder turning into mull) and 80% closure of the canopy. The height of the pine stand

canopy was up to 25 m and the average breast height diameter did not exceed 30 cm. Three tree stand types were distinguished as treatments: one-storied pine stands, one-storied pine stands with understory, and pine stands with a second story composed of deciduous species. Three replicates of each of the three treatments were selected for a total number of nine research plots (3 treatments  $\times$  3 replicates).

The first treatment was the one-storied pine stand without understory. The second treatment was the one-storied pine stand with an understory composed of beech, oak, rowan, hackberry, and buckthorns, which covered 50% of the research plot area. In the third treatment, the first story was composed of pine and there was a second story of oak with the breast height diameter of 20 cm. The ground cover of the tree stands featured mosses and individual grasses (e.g., *Poa annua*, *Deschampsia flexuosa*). The plots were set up at a distance of more than 150 m from ecotone zones.

### Sampling design

Carabids were captured in 2016 and 2017, with three pitfall traps buried with their rims flush with the soil surface in the research plots established in each pine stand type. The pitfall traps were set up on 1 June (both in 2016 and in 2017). The traps were subsequently replaced on 1 July, 1 August, 1 September, and 30 October. In both years, the study period lasted 184 days. The total of 27 (3 treatments  $\times$  3 replications  $\times$  3 traps) pitfall traps were replaced during each of the three surveys every year. That involved replacing the jar and its contents with a new, empty one. The traps (0.5 l glass jars with a plastic funnel, 12 cm in diameter a lower diameter of 2.0 cm, containing 100 ml of 70% ethylene glycol) were set 10 m apart, so that the transects were 20 m long. Data

obtained from the three traps set in each plot were subsequently pooled.

### Environmental variables

In each plot, data were collected around each pitfall trap on the percentage cover of the first story, the second story and the understories, as well as the litter composition and humidity of the humus layer and its temperature. Soil and litter data were collected in four places (crosswise) around each trap, at a distance of 1 m from the trap. In the litter, percentage shares of pine needles and—if present—oak and birch leaves were measured. In the same places, litter and humus thickness, as well as humus temperature and humidity were measured, using a Pro-Check, Decagon Devices, Inc. meter with a GS3 probe for measuring humidity. The mean values of the environmental variables investigated in the three treatments are shown in Table 1.

### Carabid classification for the analysis

Individual carabid species were assigned to groups according to four criteria defining their ecological traits: diet (trophic groups), preferred habitat (environmental groups), humidity preferences (humidity groups) and the possibility of aerial dispersal (dispersal groups). The classification was based on the knowledge of the biology and ecology of the species (Burakowski et al. 1973, 1974; Szyszko 1983; Hürka 1996; Turin 2000). Carabid nomenclature is given according to Homburg et al. (2014).

Trophic grouping comprised hemizoophages (mainly early-successional semi-herbivorous ones), small zoophages (carnivorous species with body length under 15 mm) and

**Table 1** Environmental variables with standard error determined for individual treatments: pine stands with one story (S), understory (SU) and two stories (D) with coordinates of replicated treatments

Environmental variables	S	SU	D	F
Moisture of the humus layer	10.25 $\pm$ 0.51	11.66 $\pm$ 0.22	10.73 $\pm$ 0.18	4.493*
Temperature of the humus layer	13.06 $\pm$ 0.79	12.95 $\pm$ 0.54	12.76 $\pm$ 0.43	0.061
Percentage share of pine needles	75.56 $\pm$ 7.78	61.11 $\pm$ 2.94	41.11 $\pm$ 10.60	4.946*
Percentage share of oak leaves	21.39 $\pm$ 9.67	20.56 $\pm$ 3.38	42.22 $\pm$ 2.22	4.112
Percentage share of birch leaves	3.89 $\pm$ 3.89	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	1.000
The percentage cover of the first story	48.89 $\pm$ 2.22	62.22 $\pm$ 4.01	60.00 $\pm$ 5.09	3.263
The percentage cover of the second story	0.00 $\pm$ 0.00	0.00 $\pm$ .00	68.89 $\pm$ 11.28	37.320**
The percentage cover of understory	13.33 $\pm$ 3.33	57.78 $\pm$ 2.94	18.89 $\pm$ 4.84	40.714**
Humus thickness	2.50 $\pm$ 0.60	2.11 $\pm$ 0.28	2.11 $\pm$ 0.89	0.125
Litter thickness	1.17 $\pm$ 0.35	1.33 $\pm$ 0.33	1.00 $\pm$ 0.35	0.237
Coordinates (WGS'84) of				
First replications	21.1173, 52.0656	21.0392, 52.0484	21.1271, 52.0692	
Second replications	21.0413, 52.0294	21.0426, 52.0514	21.1218, 52.0678	
Third replications	21.0437, 52.0336	21.0448, 52.0529	21.0731, 52.0476	

\*  $p = 0.05$ ; \*\*  $p < 0.001$

large zoophages (carnivorous species with body size above 15 mm—often late-successional species). The percentages of large zoophages and hemizoo-phages in the carabid assemblages were taken into account.

Environmental grouping distinguished open-habitat species, generalist species and species inhabiting closed-canopy forests, further referred to as forest species. In order to verify the hypotheses, the percentages of open-habitat and forest species were analyzed.

Humidity grouping distinguished xerophilous, mesophilic, and hygrophilous species. A high proportion of xerophilous species in carabid assemblages indicates high sun exposure, as in the case of clear-cut areas or open forests. Xerophiles are usually absent from mature and closed stands, while hygrophilous and mesophilous species are the most abundant. The analysis took into account the percentage shares of hygrophilous and xerophilous species.

Dispersal grouping relied on the presence or absence of wing muscles and on wing length (wingless, wing-polymorphic and winged species). Wingless species had limited mobility, which made long-distance dispersal difficult and would also be an obstacle in quick colonization of the stands. The analysis took into account the respective percentage shares of winged and wingless species.

Late-successional fauna comprises large zoophages, forest species, hygrophilous species, and wingless species. Early-successional species comprise hemizoo-phages, open area species and long-winged species (Szyszko 1983; Niemelä et al. 2007; Skłodowski 2014; Magura et al. 2015).

## Data analysis

The first hypothesis was verified by comparing the Chao estimator, the abundance of carabids and their ecological traits, i.e., the percentages of large zoophages, hemizoo-phages, open-habitat species, forest species, hygrophilous species, xerophilous species, winged species and wingless species (calculated according to abundance data), describing the carabid assemblages in the three types of pine stands (with and without broad-leaved tree or shrub species). The carabid catches from three traps set in each research plot were combined for the analysis. Species richness was estimated using the abundance-based data, bias-corrected by the Chao estimator (Colwell 2013).

Data were analyzed with GLMM, including time (years) as random effect and pine stand types as fixed effects. The GLMM was performed using the Chao estimator, abundance and ecological traits. The response variables were defined following the Poisson distribution with log link function. Predicted and observed residuals were compared during the analysis in order to rule out any autocorrelation. The computations were performed using Statistica 13.0 software (Dell Inc 2016). The number of carabid species and Shannon's

index in individual treatments were also analyzed, but this information was not included in the paper as the differences were not statistically significant. However, relevant diagrams can be found in Appendix.

In order to verify the second hypothesis about litter composition having the strongest effect on carabid beetle assemblages, a redundancy analysis (RDA) was performed using CANOCO 4.5 (Ter Braak and Šmilauer 2003). In order to reduce the number of variables to one main environmental gradient and eliminate the risk of autocorrelations and synergistic or antagonistic relations between variables, principal component analysis of the environmental variables was analyzed. The first PCA axis explained 69% of the variation in environmental factors, in the first and second year. PCA analysis showed the loadings of all environmental variables on the first axis. The highest value ( $R=0.99$ ) was noted for the second-story cover. Lower values for loadings on the first PCA axis were noted for the percentages of pine needles ( $R=-0.86$ ) and oak leaves ( $R=0.81$ ) in the litter layer, litter layer thickness ( $-0.42$ ), understory cover ( $-0.36$ ), humus thickness ( $R=-0.35$ ), percentage of birch leaves in the litter layer ( $R=-0.29$ ), humus temperature ( $R=-0.12$ ), first-story cover ( $R=0.10$ ), and humus humidity ( $R=-0.05$ ).

In order to link the observed differences between carabid assemblages inhabiting particular study areas to the environmental variables analyzed, a redundancy analysis (RDA) was performed on pooled data for the 2 years (without data transformation, sample weights, or centering by species) using CANOCO 4.5 software (Ter Braak and Šmilauer 2003). The RDA was conducted after prior testing of the length of the gradient in detrended canonical correspondence analysis (DCCA). The RDA was conducted following preselection of the environmental variables using the ANOVA function with a permutation test. The analysis included variables with significant P values. It comprised four environmental variables, namely the proportion of pine needles in the litter layer, understory cover, the second-story cover and humus humidity.

In order to achieve the additional aim of the study, i.e., to detect the characteristic species for different treatments, the IndVal (indicator value) procedure (Dufrene and Legendre 1997) was used on pooled data for the 2 years. It is a commonly used method for evaluating how strongly individual species are associated with predefined groups of sites in the collected data. The indicator attains the maximum value (1.00) when all individuals of a species are found in a single treatment (high specificity) and when the species occurs in all replicates of a treatment (high fidelity). The statistical significance of the species indicator values was evaluated by Monte Carlo procedure. The computations of IndVal (“indispecies package”) were performed using R Statistics (ver. 3.1.2.) (R Core Team 2014).

## Results

### Carabids in the three pine stand types

In total, 1217 specimens representing 29 ground beetle species were captured in the course of the 2 years. The most numerous species were the large hygrophilous zoophage *Pterostichus niger* (321 individuals), the large xerophilous zoophage *Carabus arvensis* (179 individuals), the mesophilous hemizoophage *Amara communis* (137), the large

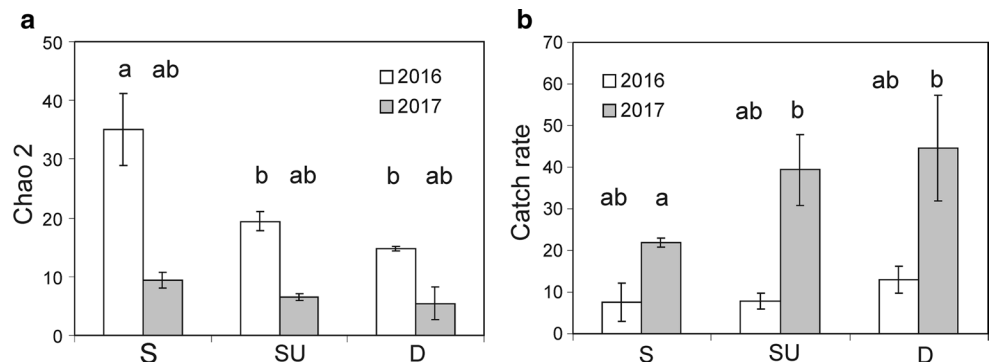
mesophilous zoophage *Carabus nemoralis* (122), and the small zoophage *Pterostichus oblongopunctatus* (95).

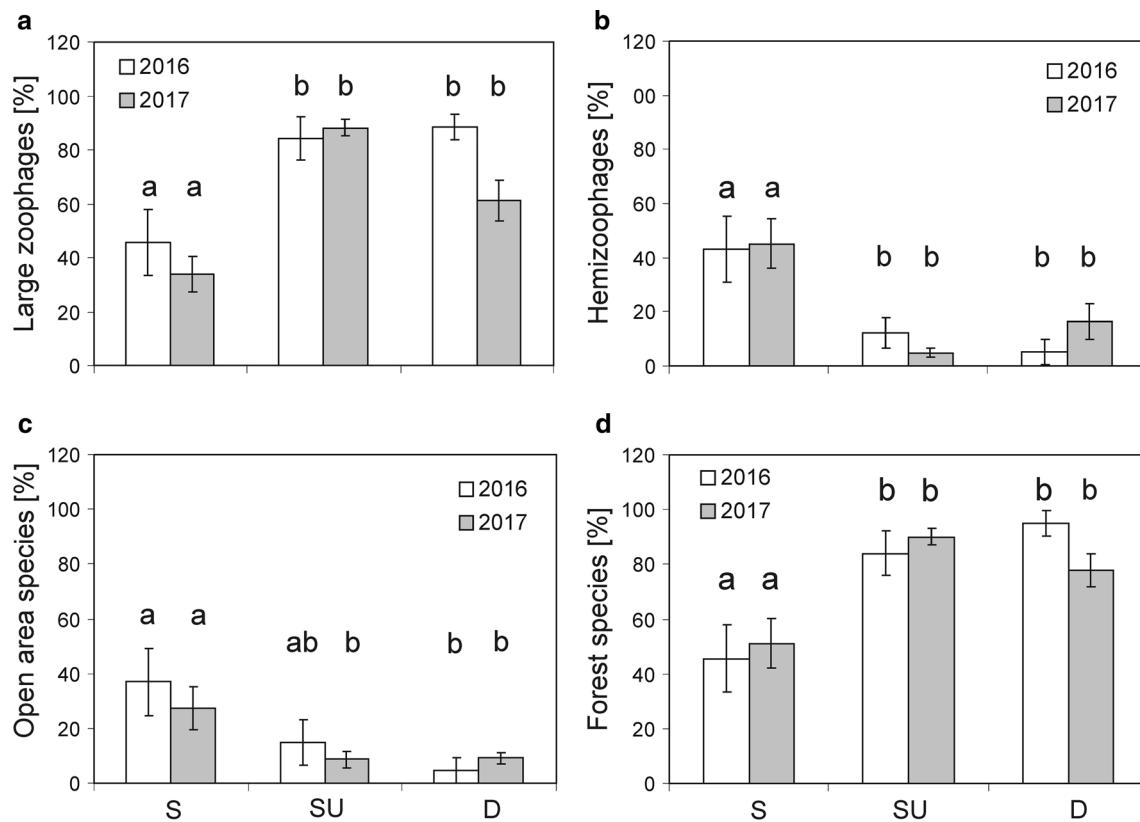
The Chao value decreased and the abundance of carabids increased with increasing vertical complexity of the pine stand (Table 2, Fig. 1a, b). Large zoophages, forest species, hygrophilous and wingless species responded strongly to stand type, with their percentages in the assemblages being higher in the two-storied stands and in the stands with understory than in the one-storied stands (Table 2, Figs. 2a, d, 3a, d). The opposite reaction to stand type was observed in hemizoophages, open-habitat species and long-winged

**Table 2** Results of the GLMM test of significance (Wald statistics) of the effect of different stand structure on abundance, Chao2 index and different life traits of ground beetle assemblages; Year—year of study. Stand—different stand structure

Traits	df	Wald Stat	p	Traits	df	Wald Stat	p
<b>Chao2</b>				<b>Abundance</b>			
Intercept	1	14.775	<0.001	Intercept	1	58.693	<0.001
Year	1	0.805	0.369	Year	1	0.299	0.584
Stand	2	17.011	<0.001	Stand	2	49.098	<0.001
Year × Stand	2	0.924	0.336	Year × Stand	2	0.160	0.689
<b>Large zoophages</b>				<b>Hemizoophages</b>			
Intercept	1	209.990	<0.001	Intercept	1	391.765	<0.001
Year	1	3.225	0.072	Year	1	23.967	<0.001
Stand	2	159.017	<0.001	Stand	2	419.020	<0.001
Year × Stand	2	3.088	0.079	Year × Stand	2	23.883	<0.001
<b>Open area species</b>				<b>Forest species</b>			
Intercept	1	275.346	<0.001	Intercept	1	230.0215	<0.001
Year	1	13.600	<0.001	Year	1	14.8381	<0.001
Stand	2	294.895	<0.001	Stand	2	172.5620	<0.001
Year × Stand	2	13.757	<0.001	Year × Stand	2	14.7929	<0.001
<b>Hygrophilous</b>				<b>Xerophilous</b>			
Intercept	1	148.543	<0.001	Intercept	1	3.754602	0.050
Year	1	20.562	<0.001	Year	1	5.492001	0.019
Stand	2	127.475	<0.001	Stand	2	1.633743	0.201
Year × Stand	2	21.667	<0.001	Year × Stand	2	5.378584	0.020
<b>Winged species</b>				<b>Wingless</b>			
Intercept	1	252.325	<0.001	Intercept	1	222.307	<0.001
Year	1	2.250	0.134	Year	1	6.678	0.010
Stand	2	16.477	<0.001	Stand	2	169.351	<0.001
Year × Stand	2	1.635	0.441	Year × Stand	2	6.466	0.010

**Fig. 1** Chao2 index ( $\pm$ SE) (a) and average abundance ( $\pm$ SE) (b) of carabid beetles in the pine stands with one story (S), understory (SU) and two stories (D); different letters above the bars mean  $p < 0.05$





**Fig. 2** Percentage of large zoophages (a), hemizoophages (b), open area species (c) and forest species (d) ( $\pm$  SE) of carabid beetles in the pine stands with one story (S), understory (SU) and two stories (D); different letters above the bars mean  $p < 0.05$

species (Table 2, Figs. 2b, c, 3c). The percentage shares of xerophilous species in the carabid assemblages were the same in all stand types.

### Carabids and environmental variables

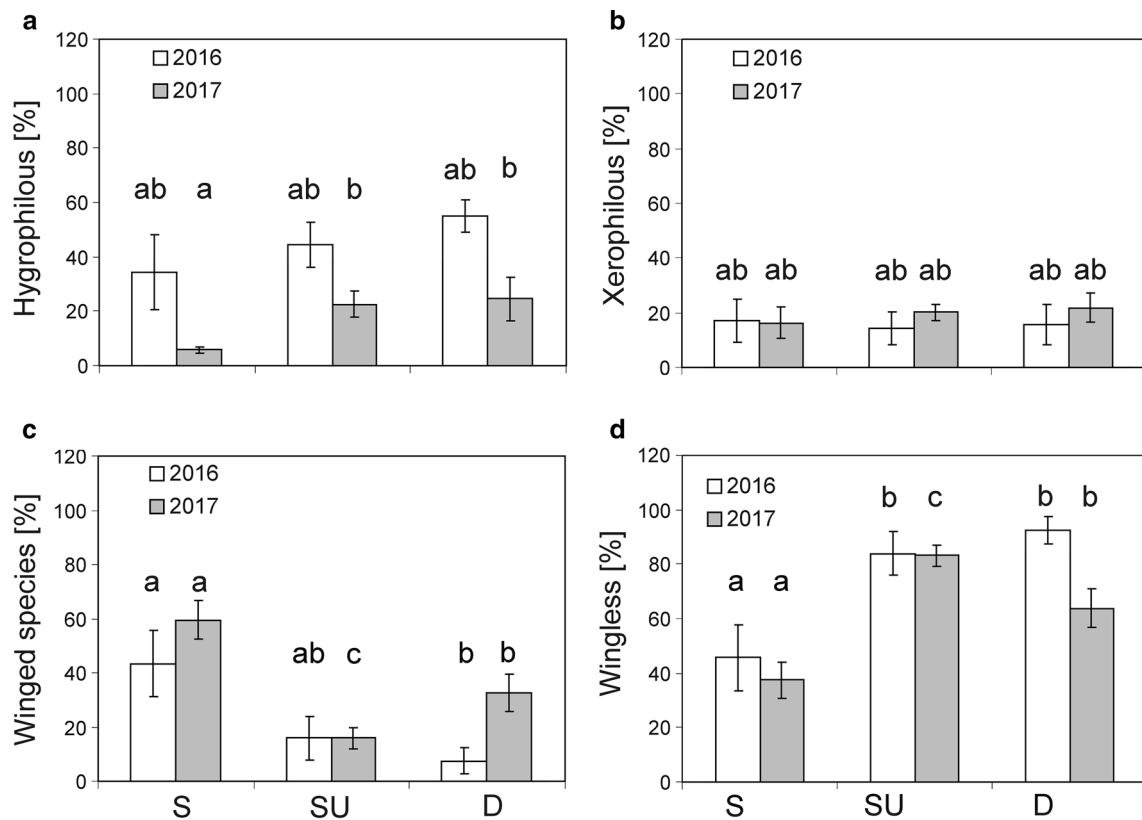
The first and second axis in the RDA diagram explained, respectively, 74.7% and 14.5% of the variance in the species–environment data and 50.7% and 60.6% of the species data (Table 3, Fig. 4). The first RDA axis separated the carabid assemblages inhabiting the one-storied stands from the assemblages inhabiting the one-storied stands with understory and the two-storied stands, which suggests a gradient associated with the vertical structure of the stands. The first axis was correlated with the percentage share of pine needles in the litter layer ( $-0.85$ ) and the second-story cover ( $0.60$ ). The second axis was correlated with the understory ( $0.73$ ) and with litter and soil humidity ( $0.62$ ).

The part of the first RDA axis which the one-storied stands were correlated with was correlated with *Notiophilus aesthuans*, *Pterostichus strenuus*, *Notiophilus germinyi*, *Amara lunicollis* and *A. communis* and the half of the axis which the two-storied stands (DW2 and DW1) were correlated with was correlated with the large zoophages

*Pterostichus niger*, *Carabus hortensis*, *Cychrus caraboides*, *Pterostichus melanarius* and the hemizoophage *Harpalus quadripunctatus*. The second axis (the part correlated with the stands with understory (PD1–PD3)) was associated with the large forest zoophages *Carabus nemoralis*, *Carabus violaceus*, *Carabus auronitens* and *Carabus glabratus*.

### Characteristic species

The IndVal analysis detected four ground beetle species which were characteristic for the assemblages inhabiting the one-storied and two-storied stands (Table 4). Four species with significant IndVal values were detected. They included *Amara communis* and *Amara lunicollis*, which preferred the one-storied pine stands. The remaining two species (*Abax carinatus* and *Pterostichus oblongopunctatus*) showed preference for the two-storied stands.



**Fig. 3** Percentage of hygrophilous species (a), xerophilous species (b), long-winged species (c) and wingless species (d) of carabid beetles in the pine stands with one story (S), understory (SU) and two stories (D); different letters above the bars mean  $p < 0.05$

**Table 3** The resulting summary table of RDA analysis

Axes	1	2	3	4	Total variance
Eigenvalues	0.507	0.099	0.057	0.016	1.000
Species–environment correlations	0.912	0.790	0.903	0.555	
Cumulative percentage variance of species data	50.7	60.6	66.3	67.9	
of species–environment relation	74.7	89.2	97.7	100.0	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.679

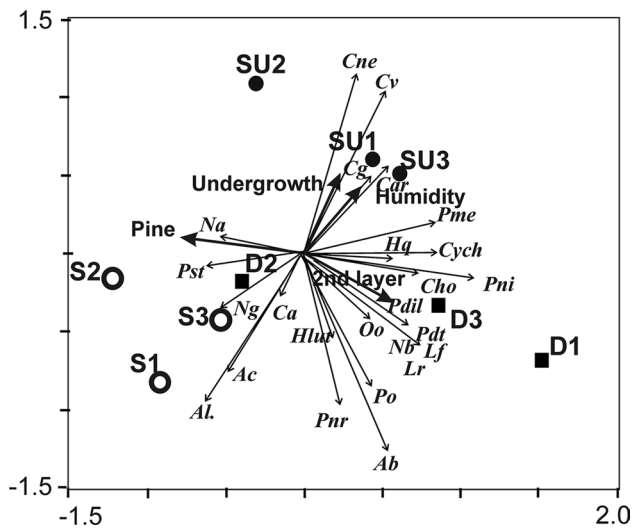
## Discussion

### Carabids in the three pine stand types

The silvicultural cycle of pine stands begins with the clear-cut, plowing the land and planting the saplings. After ca. 100 years the cycle ends with the cutting down of the trees. Over ca. 10 years, the canopy of the young pine plantation closes. In the following years, the dense canopy layer moves upwards and the organic material that falls from the canopy becomes the litter layer. Early plantations with an open canopy are inhabited by small non-forest species which

are usually winged hemizoophages. After canopy closure, increasing numbers of large wingless predatory species begin to occur, which dominate in assemblages inhabiting 20- to 30-year-old stands (Szyszko 1983; Šerić Jelaska et al. 2011). Therefore, it was assumed that late-successional fauna would dominate in the tree stands under study and achieve the highest percentage share in the two-storied stands.

Our results support this assumption. Late-successional fauna, such as large zoophages, forest species, hygrophilous species, and wingless species, reached the highest percentage shares in the assemblages inhabiting the two-storied stands and the lowest in the assemblages inhabiting



**Fig. 4** RDA analysis for the data from 2016 (a) and 2017 (b) in the pine stands with one story (S), understory (SU) and two stories (D) (numbers 1–3 indicate the replication of the plot). Stands and habitat indicators: first, second, understory—% cover of the first, second story and understory, respectively, Litter and Humus—thickness of the litter layer and the humus layer, Temperature and Humidity—temperature and humidity of the humus, Pine, Birch, Oak—contribution of pine, birch and oak leaves to the litter layer (for abbreviations of carabid species names see table in appendix)

**Table 4** IndVal analysis of carabid species in different study treatments: single layer pine stands—S, double layer stands—D—Holm's correction

Species	IndVal	P	Holm	Study variant
<i>Amara lunicollis</i>	0.90	0.039	0.016	S
<i>Amara communis</i>	0.69	0.037	0.016	S
<i>Abax carinatus</i>	0.66	0.034	0.016	D
<i>Pterostichus oblongopunctatus</i>	0.56	0.029	0.016	D

the one-storied stands. It was connected with higher litter humidity and more shade in the two-storied tree stands in comparison with the one-storied ones. Habitat conditions in mature stands and in large continuous stands are preferred by late-successional species (Szyszko 1983; Szujecki et al. 1983; Šerić Jelaska and Durbešić 2009; Skłodowski 2017). On the contrary, in the one-storied pine stands which were lighter and where there was less humus humidity, higher percentage shares of early-successional species: (hemizoo-phages, open area species and long-winged species) were observed. It probably resulted from the carabid response to the greater access to light. It has been noted that carabid catches reflect tree density, and generalist catches indicate that tree density is an important determinant of the assemblage structure (Koivula 2002). According to another study that corroborated our results, oak and beech stands

(uneven-aged, and mature) were mainly inhabited by typical forest species, and even-aged conifer stands mainly supported ubiquitous species (du Bus de Warnaffe and Lebrun 2004).

Only the percentage shares of xerophilous species were very low in the carabid assemblages inhabiting all three tree stand types. This was probably due to the absence of large gaps in the stands, which possibly contributed to the increase in ground temperature.

The richness of carabid assemblages was the highest in the one-storied stands and the lowest in the two-storied stands. As carabid diversity is higher in younger stands than in older stands (Szyszko 1983; Magura et al. 2015), it may be pointed out, by analogy, that one-storied pine stands represent an earlier stage of successional development than stands with understory or a second story. Similarly, carabid diversity is higher in transitional ecotone habitats than in the middle of the stand (Magura 2017; Magura et al. 2017). According to Humphrey et al. (1999) and Jukes et al. (2001), high spruce canopy cover and soil organic matter indicated lower carabid diversity and species richness. Evidence to the contrary was provided by Szyszko (1974, 1991), who noted that the understory in even-aged pine stands did not affect the numbers of carabid species and individuals. Nevertheless, forest specialist species diversity is lower in early phases of reforestation when the canopy is open than in later phases, after the canopy closure (Nagy et al. 2016). According to the results of the present study, the presence of both an understory and a second story significantly increased carabid abundance.

### Carabids and environmental variables

Redundancy analysis separated the carabid assemblages inhabiting the one-storied pine stands from those inhabiting the stands with understory and the two-storied stands, pointing to considerable environmental differences. The factors associated by redundancy analysis with carabid assemblages inhabiting one-storied stands included higher percentage content of pine needles in the litter layer. Moor type litter with high pine needle content had higher thickness in the one-storied stands, as opposed to moder- or mull-type litter with low conifer needle content in the two-storied stands. The thickness of the humus and litter layer indicates slow decomposition of organic matter, which is more characteristic for the acidic soil of pine stands in comparison with the stands with an admixture of deciduous trees. The lower moist level of humus in one-storied stands may also contribute to slowing down biological processes, resulting with the accumulation and considerable thickness of the litter layer. Such conditions are less favorable for forest carabid species than the conditions provided by the stands with the admixture of deciduous species.



Redundancy analysis correlated increased humus humidity with the pine stands with understory. In those pine stands, both humus and litter layer were thicker than in the one-story pine stands. The litter layer, composed of oak and birch leaves and of pine needles, represented the moder type, which pointed to high activity of such organisms as mites, springtails, etc., participating in organic matter decomposition. In turn, their presence entailed the presence of predators specializing in hunting litter organisms. In particular, the occurrence of forest carabid species—photophobic and hygrophilous ones—depends on the composition and thickness of the litter layer and humus (Niemelä and Halme 1992; Koivula et al. 1999; Koivula 2001; Magura et al. 2001). As the qualitative increase in leafy components in the litter is accompanied by an increased percentage share of forest fauna in carabid assemblages (Guillemain et al. 1997), the results of the present study validate the rationale for the introduction of an understory, and the introduction of a second story in one-storied stands. That conclusion corroborates the results of the research on the consequences of introducing deciduous admixtures or the second story in pine stands (Andrzejczyk and Drozdowski 2007; Andrzejczyk et al. 2011). Uneven-aged management is recommended during the reforestation procedure, because it is less intensive and might be less harmful than even-aged stand management (Debnár et al. 2016).

Redundancy analysis correlated environmental variables of pine stands with understory and a second story with the occurrence of large forest species (*Carabus glabratus*, *Carabus violaceus*, *Carabus hortensis*, *Abax carinatus*, *Cychrus caraboides*, *Carabus auronitens*, and *Pterostichus niger*) and small forest species (*Pterostichus oblongopunctatus*, and *Oxypselaphus obscurus*), including those that specialize in hunting springtails (*Leistus ferrugineus*, *Leistus rufescens* and *Notiophilus biguttatus*) (Bauer 1981, 1985). Our observations appear accurate: for instance, Baguette (1993) connected the habitats of *Carabus nemoralis* with the presence of mull plant litter and the habitats of *Pterostichus oblongopunctatus* with the presence of moder plant litter. Similar plant litter preferences were observed in *Carabus hortensis* (Schjotz-Christiansen 1968; Turin 2000).

### Characteristic species

It came as a considerable surprise that in both years of the study, indicator species analysis identified the early-successional hemizoophage *Amara lunicollis*, strongly associated with open habitats, clear-cut areas and young pine silvicultures (Szyszko 1983, Szujecki et al. 1983), as a characteristic species for the one-storied pine stands. As the study focused

on mature stands, it had been expected that the characteristic species would be a forest specialist. The identification of *Amara lunicollis* and *Amara communis* as the characteristic species for the one-storied pine stands suggests their poor condition, which might have been caused excessive accumulation of anthropogenic nitrogen. According to Magura et al. (2017), and Magura and Lövei (2018), not many open-habitat and generalist species enter into the forest, so the finding of *A. lunicollis* as a characteristic species for the one-storied pine stands all the more validates the rationale for modifying such stands through enrichment with deciduous shrub and tree species.

The introduction of understory, and especially a second, deciduous, story in pine stands has been validated (though only in the second year) by the identification of two forest species, namely, *Pterostichus oblongopunctatus* and *Abax carinatus*, by indicator species analysis. As *P. oblongopunctatus* is associated with leafy litter (Baguette 1993), *Abax carinatus* probably has similar litter preferences. Habitat conditions in the one-storied pine stands differed from those in the other stand types. Redundancy analysis suggested a less rich litter layer composition and warmer humus in them, which might indicate that the habitat was not very favorable for forest species, but good for, e.g., hemizoophages, such as *Amara lunicollis* and *Amara communis*, as indicated by indicator species analysis.

### Implications for forest management

Our results validate the rationale for modifying one-storied pine stands by enriching them with deciduous species introduced into the understory or a second story. It seems that such modification is especially advisable in pine stands (or in other coniferous stands) that now grow under conditions considerably different from optimal ones (too low soil and air humidity, too much nitrogen accumulation). Pine stands growing in such conditions deteriorate as has been demonstrated in the present paper by the reduced proportion of late-successional fauna in such stands in comparison with the stands where broad-leaved tree species were introduced, and in particular by the identification of a hemizoophage as a characteristic species. Modification of one-storied pine stands by introducing an understory or a second story should improve their functioning.

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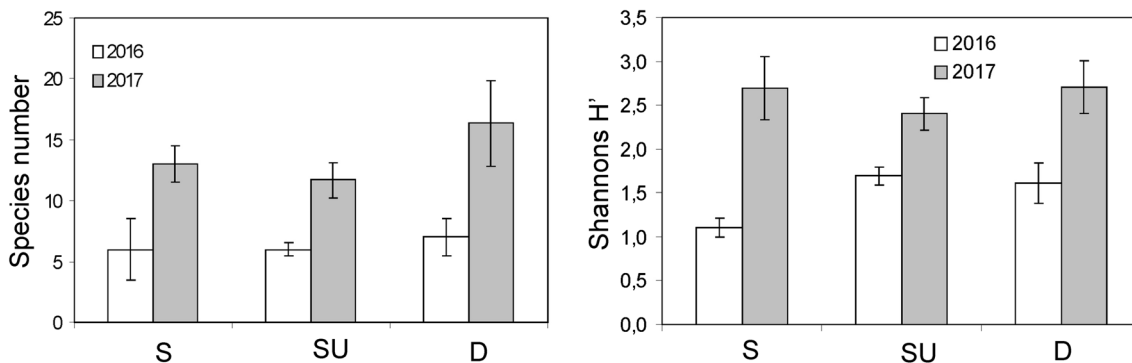
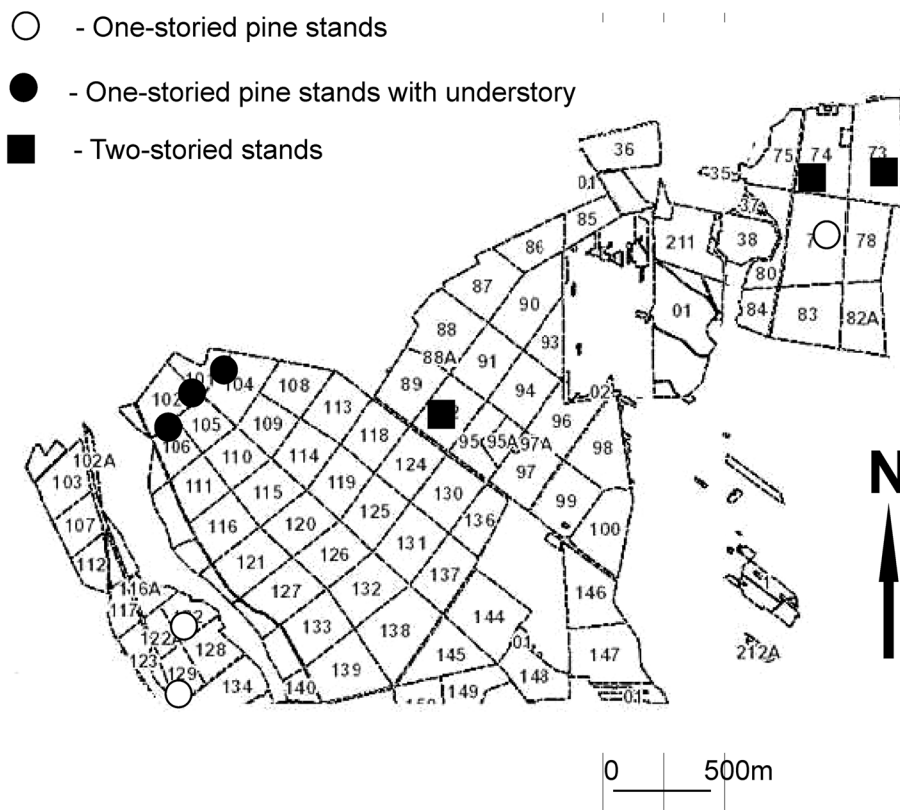
## Appendix

Carabids caught in the pine stands with one story (S), under-story (SU) and two stories (D), with abbreviations of the species names used in the RDA analysis and their ecological traits: column T: *hz* hemizoophages, *lz* large zoophages, and *sz* small zoophages; column E: *o* open-habitat species, *g* generalist species, *f* forest species; column H: *x* xerophilous species, *m* mesophilous species, and *h* hygrophilous species; column W: *wl* wingless species, *wp* wing-polymorphic, and *w* winged species.

Species	Abbreviation	T	E	H	W	S	SU	D
<i>Abax carinatus</i> (Duftschmid, 1812)	Ab	sz	f	m	wl	+	+	+
<i>Oxypselaphus obscurus</i> (Herbst, 1784)	Oo	sz	f	h	wp	-	-	+
<i>Amara communis</i> (Panzer, 1797)	Ac	hz	o	m	w	+	+	+
<i>A. lunicollis</i> (Schiodte, 1837)	Al	hz	g	m	w	+	-	+
<i>Badister bullatus</i> (Schränk von Paula, 1798)	Bd	sz	g	m	w	-	-	+
<i>Carabus arcensis</i> Herbst, 1784	Car	lz	f	x	wl	+	+	+
<i>Carabus auronitens</i> Fabricius, 1792	Ca	lz	f	m	wl	+	+	+

Species	Abbreviation	T	E	H	W	S	SU	D
<i>C. glabratus</i> Paykull, 1790	Cg	lz	f	m	wl	+	+	+
<i>C. hortensis</i> Linnaeus, 1758	Cho	lz	f	m	wl	+	+	+
<i>C. nemoralis</i> O.F.Müller, 1764	Cne	lz	f	m	wl	+	+	+
<i>C. violaceus</i> Linnaeus, 1758	Cv	lz	f	m	wl	+	+	+
<i>Cychrus caraboides</i> (Linnaeus, 1758)	Cych	lz	f	m	wl	+	+	+
<i>Harpalus latus</i> (Linnaeus, 1758)	Hl	hz	g	m	w	-	-	+
<i>H. luteicornis</i> (Duftschmid, 1812)	Hlut	hz	o	m	w	+	-	+
<i>H. neglectus</i> Serville, 1821	Hn	hz	o	x	w	-	-	+
<i>H. quadripunctatus</i> Dejean, 1829	Hq	hz	f	m	w	+	+	+
<i>H. rubripes</i> (Duftschmid, 1812)	Hrb	hz	g	x	w	+	+	+
<i>Leistus ferrugineus</i> (Linnaeus, 1758)	Lf	sz	f	m	wp	-	-	+
<i>L. rufomarginatus</i> (Duftschmid, 1812)	Lr	sz	f	m	wp	-	-	+
<i>Notiophilus aestuans</i> Dejean, 1826	Na	sz	o	m	w	+	+	-
<i>N. biguttatus</i> (Fabricius, 1799)	Nb	sz	f	m	wp	-	-	+
<i>N. germinyi</i> Fauvel in Grenier, 1863	Ng	sz	g	x	wp	+	-	+
<i>Pterostichus aethiops</i> (Panzer, 1797)	Pae	lz	o	m	w	+	+	+
<i>P. diligens</i> (Sturm, 1824)	Pdil	sz	f	h	wp	-	-	+
<i>P. melanarius</i> (Illiger, 1798)	Pme	lz	f	h	wl	-	+	+
<i>P. niger</i> (Schaller, 1783)	Pni	sz	g	h	w	+	+	+

**Fig. 5** Map of Chojnów Forest Inspectorate and Chojnów Forest District, where research plots were established in 3 different treatments: in pine stands with one story (S), understory (SU) and two stories (D); the numbers 1–3 refer to replications of the treatments



**Fig. 6** Species number ( $\pm$ SE) and Shannon's  $H$  index ( $\pm$ SE) of carabid beetles in the pine stands with one story (S), understory (SU) and two stories (D); no statistical difference

Species	Abbreviation	T	E	H	W	S	SU	D
<i>P. nigrita</i> (Paykull, 1790)	Pnr	sz	f	m	w	+	-	+
<i>P. oblongopunctatus</i> (Fabricius, 1787)	Po	sz	f	h	wp	+	+	+
<i>P. strenuus</i> (Panzer, 1797)	Pst	sz	g	h	wp	+	-	-

See Figs. 5, 6.

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