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The Structure and Seasonal Dynamics of Coprophagous Scarabaeoidea (Coleoptera) Communities in Later Developmental Stages of Pine Stands in NW Poland

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ABSTRACT

The research was conducted in Człuchów Forest (Polish: Lasy Człuchowskie) in NW Poland. Eight research plots, representing later developmental stages of pine stands, were established. Five traps baited with cow dung were set in each of the plots. In total, 47389 specimens of dung beetles (coprophagous Scarabaeoidea) were collected, representing 30 species; earth-boring dung beetles (Geotrupidae) *Anoplotrupes stercorosus* and *Trypocopris vernalis* dominated in the collected material. Three communities of dung beetle were differentiated, based on the season of adult activity: spring type (characterized by high species richness and the presence of *Aphodius ater, A. fossor, A. nemoralis, A. pusillus, A. sphacelatus, A. sticticus, A. subterraneus, Heptaulacus testudinarius, Oxyomus sylvestris* and *Onthophagus nuchicornis*), summer type (characterized by much lower species richness, distinguished by the presence of *Aphodius sordidus*), and autumn type (characterized by the lowest species richness, with two characteristic species: *Aphodius contaminatus* and *A. paykulli*).

Key words: Scarabaeoidea, dung beetles, community structure, seasonal dynamics, pine stands, Poland

INTRODUCTION

The Scarabaeoidea inhabit all zoogeographic regions of the world. They are the most abundant in the tropics, and the further north the less numerous they become (species of the genus *Aphodius* have been recorded 300 km beyond the Arctic Circle) (Tesař, 1957). In Europe, the Scarabaeoidea are represented by 9 families, 142 genera and ca. 1250 species (Löbl and Smetana, 2006). In Poland, 143 species of the Scarabaeoidea have been recorded, but the actual occurrence of 21 of them is highly doubtful and should be confirmed by new records (Byk, 2012).

A dominant trophic group among the Scarabaeoidea are dung beetles. Dung beetles are encountered worldwide but they are most diversified in tropical forests and on savannahs (Hanski and Cambefort, 1991). The newest evidence of fossil faeces clearly indicate that the coprophagy of dung beetles had been connected with dinosaurs even before the mammals evolved (Chin and Gill, 1996). Dung beetles can be endocopric (e.g. genus *Aphodius*), paracopric (e.g. the genera: *Copris*, *Geotrupes* and *Onthophagus*) or telecopric (e.g. the genera: *Gymnopleurus*, *Scarabaeus* and *Sisyphus*) (Bornemissza, 1976). Endocopric species lay eggs directly into dung, paracropic species dig earth tunnels of various lengths ending with brooding chambers beneath the dung, and telecopric species separate a portion of dung and roll it into round balls which are then transported, sometimes far from the original source of the dung, to a place where the beetles dig tunnels ending with brooding chambers. Such diversified methods of dung transporting and foraging obviously result in an increased diversification of ecological processes such as nutrient recycling, soil aeration, plant seed dispersal, and reduction of parasite numbers, which provide benefits both to the ecosystem and to human activities (De Groot *et al*., 2002). Among dung beetles presently encountered in Poland there are endocopric and paracopric species (Byk, 2011a, 2012).

In natural ecosystems, dung beetles play an important role in ecosystem functioning, especially in secondary seed dispersal and the circulation of chemical elements in the environment (Nichols *et al*., 2008). Apart from that, dung beetles have been considered as practical indicators in case of disturbances in habitat functioning, especially in the case of tropical rainforests (Favila and Halffter, 1997; Davis *et al*., 2001), but also in forests growing in the temperate zone (Szwałko, 1995; Szwałko and Starzyk, 1997; Skłodowski *et al*., 1998; Klimaszewski and Strużyński, 2005; Skłodowski and Duda, 2007; Byk, 2011a, 2011b, 2012). There are several features that make dung beetles useful as bioindicators (Favila and Halffter, 1997), for instance the fact that their populations are very sensitive to changes in microclimate, vegetation structure, soil properties and abundance of food resources (Osberg *et al*., 1994; Davis, 1996; Lumaret and Iborra, 1996). Changes in dung beetle populations may refer to species abundance and diversity, but also to abundance and structure of the population (e.g. in connection with activity types, preferred food, foraging and migration routines) (Andresen, 2005). Therefore, gaining an insight into the role and species composition of dung beetles inhabiting forest areas is essential for human economy, and especially for forest management.

In Poland, the structure of dung beetle communities has been studied by Stebnicka (1976) and Breymeyer (1978) in pastures of the Pieniny mountain range, Bunalski (1996a, 1996b) in Greater Poland, by Żuk (2005) in Trzebnickie Hills and by Górz (2007) in Kraków-Częstochowa Upland. Results of the above studies indicate unequivocally that the core of dung beetle communities in Polish pastures is formed by species characteristic for open areas (praticoles) and eurytopic species.

The above studies contain premises pointing to differences between species composition of dung beetle communities inhabiting open areas and forests. The structure of forest dung beetle communities in Polish lowlands has been discussed in the study on coprophagous Scarabaeoidea inhabiting tree stands and post-agricultural and forest areas in Człuchów Forest (Szyszko, 1983), in the study devoted to the Scarabaeoidea of Białowieża Forest (Szwałko, 1995) and in studies focusing on abundance and species composition of the Geotrupidae (Byk, 2011a) and coprophagous Scarabaeidae (Byk, 2012) in the developmental cycle of tree stands in

Człuchów Forest. Those studies have shown that the core of dung beetle communities in Polish forests is composed of forest species (sylvicoles) and eurytopic species.

Bunalski (1996b) proposed a division of dung beetles into phenological-generational groups based on the period of occurrence of adults. He differentiated the following groups of dung beetles: “whole season” species, “spring-autumn” species, “spring” species, “spring-summer” species, “summer-autumn” species and “autumn” species.

It is necessary to gather more data on changes taking place in the structure of dung beetle communities inhabiting forests at different times of the vegetation season and to undertake studies on the following issues:

- abundance and species composition of dung beetle communities in later developmental stages of pine stands;

- identification of dominant species and differentiation of dung beetle communities characteristic for later pine stands in consecutive periods of the vegetation season;

- insight into the character of changes in species composition and abundance of dung beetle communities in later pine stands in the course of the vegetation season.

We noted that in later developmental stages of pine stands, species of dung beetle active in spring seem much more than those active in summer and autumn. The present study want to answer to the following questions:

- Are the numbers of dung beetle individuals and species inhabiting later developmental stages of tree stands reduced in the course of the vegetation season?

- Is this a continuous or an abrupt process, and if the latter, when does the most considerable reduction of the number of species take place?

MATERIAL AND METHODS

Człuchów Forest is situated in Poland, within the geobotanical region of Pomeranian Divide, the region of Sandar Forefields of Central Pomeranian Lake District (Polish: Kraina Sandrowych Przedpoli Pojezierzy Środkowopomorskich) and the subregion of Wałcz (Polish: Podkraina Wałecka) (Fig. 1). The region is characterized by a considerable areage of sandur lowlands with coniferous forests (*Leucobryo-Pinetum* association) and mixed forests (*Fago-Quercetum*, *Querco-Pinetum*) (Matuszkiewicz, 1993). Study sites were located in tree stands belonging to Niedźwiady Forest Inspectorate and the adjacent tree stands belonging to Osusznica Forest Inspectorate. The area was covered by a compact forest complex, mostly by coniferous forest (ca. 90%), of which fresh coniferous forest constituted ca. 80%. It comprised mainly pines with a small admixture of spruces and birches.

For purposes of the study 8 study sites were established, representative of elder stages of pine stand developmental cycle (Table 1). Five ground glycol traps baited with portions of cow dung (10 cm^3) were set in each of the study sites (Fig. 2). The size of a single portion of cow dung was based on the assumption that the amount of bait should allow to acquire knowledge about the complete species composition of the beetle community, but should neither alter the nutritional conditions within a given area nor attract individuals from beyond that area. During the study period, the total number of 40 traps functioned; in each site they were arranged in a square with 20-meter sides, and with marked diagonals (so-called “envelope”). Insects were collected at monthly intervals from April till October, in 1998 and 1999.

The average monthly temperature was recorded during trapping the coprophagous Scarabaeoidea (Fig. 3).

Table 1. Research plots established for dung beetle collection in later developmental stages of pine stands in Człuchów Forest (NW Poland).

Study site	**Forest district**	**Forest compartment**	**Stand age**	**Plant community type**
S1	Stara Brda	65k	50	*Sedo-Scleranthetea / Vaccinio-Piceetea*
S2	Stara Brda	83a	42	*Leucobryo-Pinetum*
S3	Stara Brda	88c	50	*Sedo-Scleranthetea / Vaccinio-Piceetea*
S4	Stary Most	293i	48	*Leucobryo-Pinetum*
S5	Stara Brda	63b	90	*Leucobryo-Pinetum*
S6	Stara Brda	61b	105	*Leucobryo-Pinetum*
S7	Stara Brda	91a	110	*Leucobryo-Pinetum*
S8	Pustowo	168a	90	*Leucobryo-Pinetum*

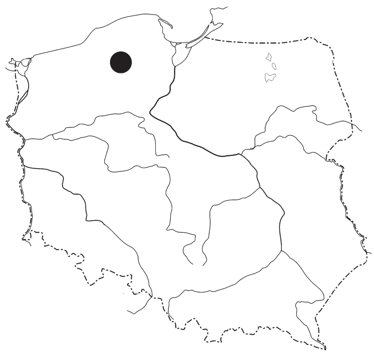

Fig. 1. Location of Człuchów Forest in Poland.

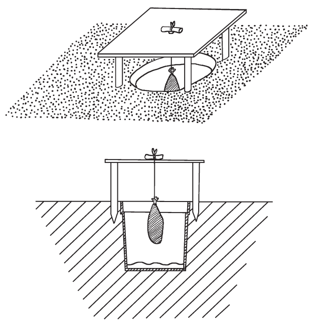

Fig. 2. A baited ground trap for collecting dung beetles in later developmental stages of pine stands in Człuchów Forest (NW Poland) (drawing by J. Piętka).

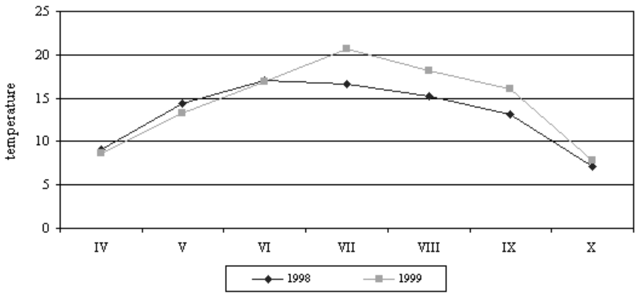

Fig. 3. Average monthly temperatures during trapping the coprophagous Scarabaeoidea in years 1998-1999.

The systematic hierarchy and nomenclature were quoted after the “Catalogue of Palearctic Coleoptera” (Löbl and Smetana 2006). While specifying the pattern of domination, the scale developed by Kasprzak and Niedbała (1981) was used: superdominants: > 30.00%, dominants: 5.01 - 30.00%, subdominants: 1.01 - 5.00% and accidental: ≤ 1.00%.

Faunistic similarity of dung beetles (coprophagous Scarabaeoidea) communities inhabiting later pine stands in various months was evaluated using hierarchical cluster analysis applying Ward’s method, and squared Euclidean distance was used as the measure of similarity. Statistical significance of noted differences in the number of species and dung beetle abundance was verified. A monthly yield of a trap was considered as a sample. The conformity of data with normal distribution was verified with the aid of Shapiro-Wilk test, and the equality of variances was verified with the aid of Levene’s test. The non-parametric Kruskal-Wallis method was utilized to test the effect of the season on the number of species and individuals of dung beetles, including earth-boring dung beetles (Geotrupidae), scarab dung beetles (Scarabaeinae) and aphodiine dung beetles (Aphodiinae). Months were treated as an independent variable whereas the number of individuals and the number of species were treated as dependent variables. Statistical analyses were performed using Statistica 10 software (StatSoft, Inc., 2011).

RESULTS

In the course of the study a total number of 47389 dung beetle individuals (representing coprophagous Scarabaeoidea) were collected; belonging to 30 species, 3 subfamilies and 2 families. The highest number of individuals was collected in June (11890), and the lowest number of individuals was collected in April (1850). In May, 6032 individuals were collected, in July - 6032, in August - 8423, in September - 8751 and in October - 2252. Over 78% of the total number of individuals were collected from June until the end of September, over 12% were collected in May, and in each of the remaining two months, April and October - less than 5%. Representatives of the family Scarabaeoidea that were collected in the largest numbers included the following: *Anoplotrupes stercorosus*, *Trypocopris vernalis*, *Aphodius rufipes*, *A. fimetarius*, *A. depressus*, *A. fasciatus*, and *Geotrupes stercorarius*. They constituted 95% of all collected individuals (Table 2).

In later pine stands of NW Poland the trappability of earth-boring dung beetles (Geotrupidae) was increasing from April till June and in the latter month was the highest. Then the trappability of earth-boring dung beetles was decreasing until August to increase again in September and dramatically drop in October. Similarly, the trappability of aphodiine dung beetles (Aphodiinae) was increasing from April till June and was the highest in the latter month. Then the trappability of aphodiine dung beetles decreased in July but in August it already increased again, to gradually decrease in the following months. As for the trappability of scarab dung beetles (Scarabaeinae), it was increasing only until May and then it was decreasing until July. In August the trappability of scarab dung beetles increased again and was the highest in that month, and then was gradually decreasing until October. Trappabilities of the Aphodiinae and the Scarabaeinae were definitely lower in comparison to trappability of the Geotrupidae. As a result, dung beetle trappability reflected the trends of earth-boring dung beetle trappability (Fig. 4).

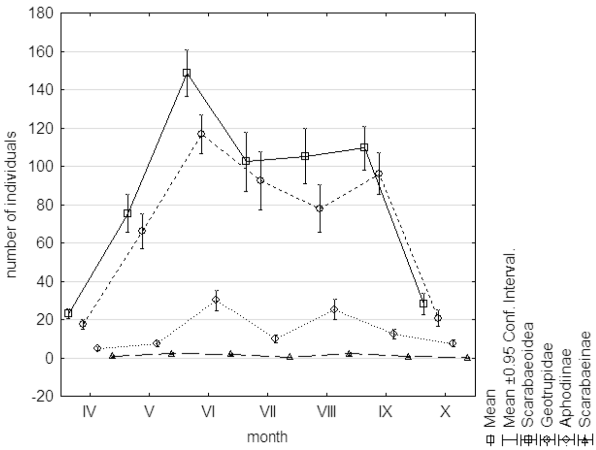

Fig. 4. The yield of a baited ground trap used for collecting dung beetles in pine stands in Człuchów Forest (NW Poland)

In later developmental stages of pine stands in NW Poland the average number of species of Geotrupidae was increasing from April until June and was the highest in the latter month. Then the average number of species of Geotrupidae dropped in July but started increasing again in August and kept increasing until September, to drop dramatically in October. The average number of species of Geotrupidae collected in September was similar to the number of species collected in June. Similarly, the average number of species of Aphodiinae was increasing from April until June and in the latter month was the highest. Then it dropped in July but started increasing again in August and then was gradually decreasing in the following months. As for the average number of species of Scarabaeinae, it was increasing only until May and was the highest in that month; then, it was decreasing until July. In August the average number of species of Scarabaeinae increased again and kept decreasing until October. The average number of the collected species of the Aphodiinae was definitely higher than that of the Geotrupidae and the Scarabaeinae. The average number of the collected species reflected the trends regarding the numbers of the collected species of Aphodiinae (Fig. 5).

Table 2. Dung beetles (coprophagous Scarabaeoidea) trapped in baited ground traps in later developmental stages of pine stands in Człuchów Forest (NW Poland) (PGG - phenological-generational group, Y - "whole season" species, Sp-Au - "spring-autumn" species, Sp - "spring" species, Sp-Su - "spring-summer" species, Su-Au - "summer-autumn" species, Au - "autumn" species).

Familia / Subfamilia / Species	PGG	Month								
		IV	V	VI	VII	VIII	IX	X	Σ	%
Geotrupidae: Geotrupinae (earth-boring dung beetles)										
Anoplotrupes stercorosus (Scriba, 1791)	Y	1120	4346	6866	5833	5192	6632	1271	**31260**	**65,96**
Geotrupes stercorarius (Linnaeus, 1758)	Y	28	248	256	69	140	160	85	**986**	**2,08**
Trypocopris vernalis (Linnaeus, 1758)	Sp-Su	235	650	2183	1483	901	869	36	**6357**	**13,41**
Typhaeus typhoeus (Linnaeus, 1758)	Sp-Au	13	39	35	2	2	29	262	**382**	**0,81**
Scarabaeidae: Aphodiinae (aphodiine dung beetles)										
Aphodius ater (DeGeer, 1774)	Sp-Su	0	3	7	0	0	0	0	**10**	**0,02**
A. coenosus (Panzer, 1798)	Sp-Su	0	60	48	14	0	0	0	**122**	**0,26**
A. contaminatus (Herbst, 1783)	Au	0	0	0	0	0	1	1	**2**	**0,00**
A. depressus (Kugelann, 1792)	Sp-Su	0	96	1079	264	90	26	0	**1555**	**3,28**
A. distinctus (O.F. Müller, 1776)	Sp-Au	96	20	1	0	0	7	49	**173**	**0,37**
A. fasciatus (A.G. Olivier, 1789)	Sp-Au	121	60	0	0	0	89	460	**730**	**1,54**
A. fimetarius (Linnaeus, 1758)	Y	33	168	480	34	778	384	62	**1939**	**4,09**
A. foetens (Fabricius, 1787)	Su-Au	0	0	17	84	72	36	0	**209**	**0,44**
A. fossor (Linnaeus, 1758)	Sp-Su	0	2	0	0	0	0	0	**2**	**0,00**
A. nemoralis Erichson, 1848	Sp-Su	4	8	0	0	0	0	0	**12**	**0,03**
A. paykulli Bedel, 1907	Sp-Au	0	0	0	0	0	0	2	**2**	**0,00**
A. prodromus (Brahm, 1790)	Sp-Au	133	132	1	0	0	29	18	**313**	**0,66**
A. pusillus (Herbst, 1789)	Sp-Su	0	12	4	0	0	0	0	**16**	**0,03**
A. rufipes (Linnaeus, 1758)	Su-Au	0	12	754	377	1010	414	3	**2570**	**5,42**
A. rufus (Moll, 1782)	Su-Au	0	0	0	4	10	9	0	**23**	**0,05**
A. sordidus (Fabricius, 1775)	Su-Au	0	0	0	0	2	0	0	**2**	**0,00**
A. sphacelatus (Panzer, 1798)	Sp-Su	0	0	3	0	0	0	0	**3**	**0,01**
A. sticticus (Panzer, 1798)	Sp-Au	2	1	0	0	0	0	0	**3**	**0,01**
A. subterraneus (Linnaeus, 1758)	Sp-Su	0	3	0	0	0	0	0	**3**	**0,01**
A. zenkeri Germar, 1813	Su-Au	0	0	0	3	58	11	0	**72**	**0,15**
Heptaulacus testudinarius (Fabricius, 1775)	Sp	0	1	0	0	0	0	0	**1**	**0,00**
Oxyomus sylvestris (Scopoli, 1763)	Sp	1	6	0	0	0	0	0	**7**	**0,01**
Scarabaeidae: Scarabaeinae (scarab dung beetles)										
Onthophagus fracticornis (Preyssler, 1790)	Y	41	113	122	13	122	47	1	**459**	**0,97**
O. nuchicornis (Linnaeus, 1758)	Sp-Su	0	3	14	0	0	0	0	**17**	**0,04**
O. ovatus (Linnaeus, 1758)	Sp-Su	5	11	7	5	9	0	0	**37**	**0,08**
O. similis (Scriba, 1790)	Sp-Su	18	38	13	6	37	8	2	**122**	**0,26**
Σ		**1850**	**6032**	**11890**	**8191**	**8423**	**8751**	**2252**	**47389**	**100,00**
%		**3,90**	**12,73**	**25,09**	**17,28**	**17,77**	**18,47**	**4,75**	**100,00**	

The analysis of faunistic similarity of coprophagous dung beetle communities in later pine stands revealed the presence of two agglomerations (Fig. 6).

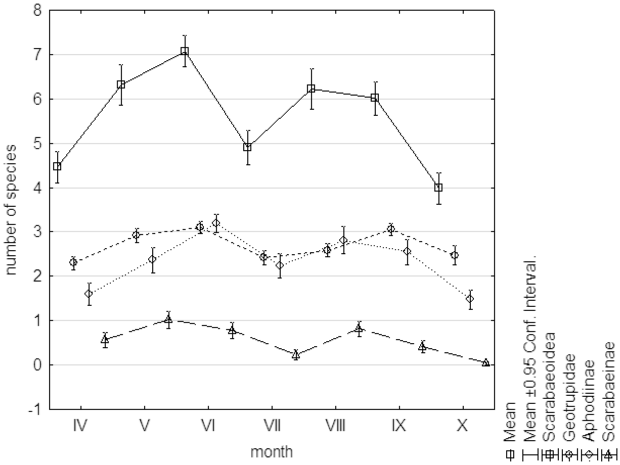

Fig. 5. The average number of dung beetles trapped in a baited ground trap in pine stands in Człuchów Forest (NW Poland).

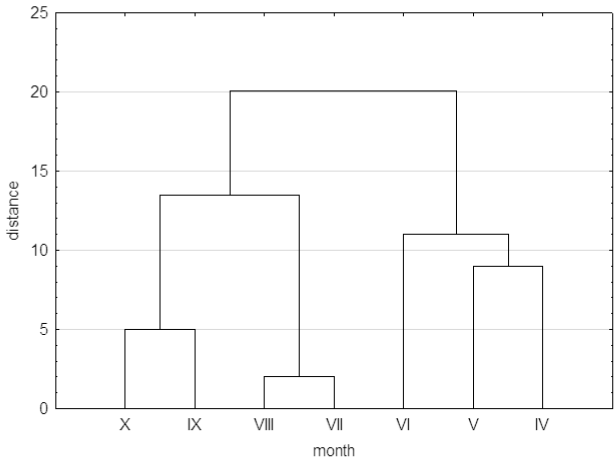

Fig. 6. Similarity dendrogram of dung beetle communities occurring in later developmental stages of pine stands in Człuchów Forest (NW Poland).

The first of those faunistic agglomerations included dung beetle communities occurring in April, May and June. They represented a spring type of dung beetle community inhabiting later developmental stages of pine stands (SpDB). The role of the superdominant was played by *Anoplotrupes stercorosus* (62.4%), whereas *Trypocopris vernalis* (15.5%) and *Aphodius depressus* (5.9%) were dominants. Subdominants were the following: *A. rufipes* (3.9%), *A. fimetarius* (3.4%), *Geotrupes* *stercorarius* (2.7%), *Onthophagus fracticornis* (1.4%) and *Aphodius prodromus* (1.3%). The core of the communities was supplemented by 17 accessory species, with 10 species specific to that agglomeration and absent from the other one, namely: *A. ater, A. fossor, A. nemoralis, A. pusillus, A. sphacelatus, A. sticticus, A. subterraneus, Heptaulacus testudinarius, Oxyomus sylvestris* and *Onthophagus nuchicornis* (Fig. 7). In that agglomeration the proportion of Geotrupidae individuals equaled 81%, while the proportions of the Aphodiinae and the Scarabaeinae amounted to 17% and 2% respectively.

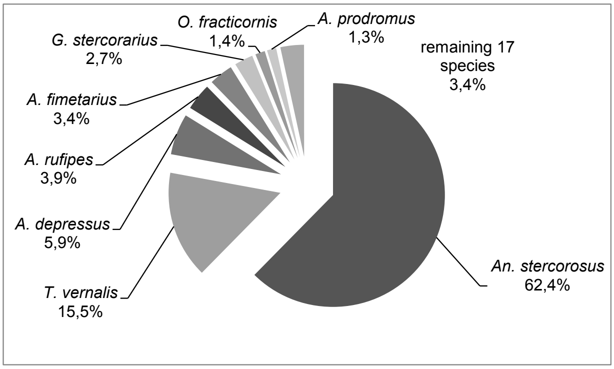

Fig. 7. Species composition of a spring dung beetle community in later developmental stages of pine stands (SpDB) in Człuchów Forest (NW Poland).

Two groups could be clearly distinguished within the second agglomeration. The first of those groups included dung beetle communities occurring in July and August, i.e. the summer type of dung beetle communities inhabiting later developmental stages of pine stands (SuDB). The second group comprised communities occurring in September and October, i.e. the autumn type of dung beetle communities inhabiting later developmental stages of pine stands (AuDB). In July and August the role of the superdominant was played by *Anoplotrupes stercorosus* (66.4%), and dominants included: *Trypocopris vernalis* (14.3%) and *Aphodius rufipes* (8.3%). The following species were subdominants: *A. fimetarius* (4.9%), *A. depressus* (2.1%) and *Geotrupes stercorarius* (1.3%). The core of that group was supplemented by 9 accessory species with just one species specific to the second agglomeration and also absent from the second group distinguished within that agglomeration, i.e. *Aphodius sordidus* (Fig. 8). In those communities the proportion of Geotrupidae individuals equaled 82%, while the proportions of the Aphodiinae and the Scarabaeinae amounted to 16.9% and 1.1% respectively. In September and October the role of the superdominant was played by *Anoplotrupes stercorosus* (71.8%). *Trypocopris vernalis* (8.2%) was a dominant, and subdominants included: *Aphodius fasciatus* (5.0%), *A. fimetarius* (4.1%), *A. rufipes* (3.8%), *Typhaeus typhoeus* (2.6%) and *Geotrupes stercorarius* (2.2%). The core of the community was supplemented with 10 accessory species, with 2 specific species, absent from both the first agglomeration and the first group of the second agglomeration: *Aphodius contaminatus* and *A. paykulli* (Fig. 9). In those communities the proportion of Geotrupidae individuals equaled 85.0%, while the proportions of the Aphodiinae and the Scarabaeinae amounted to 14.5% and 0.5% respectively.

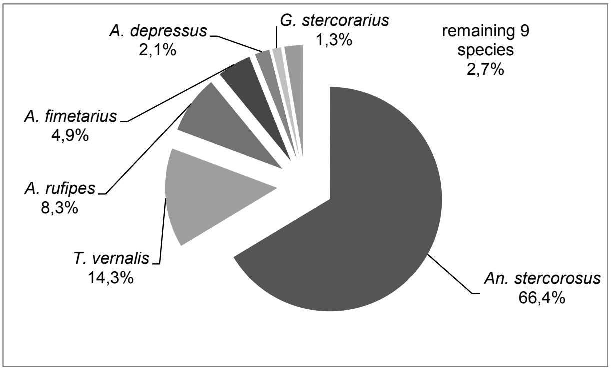

Fig. 8. Species composition of a summer dung beetle community in later developmental stages of pine stands (SuDB) in Człuchów Forest (NW Poland).

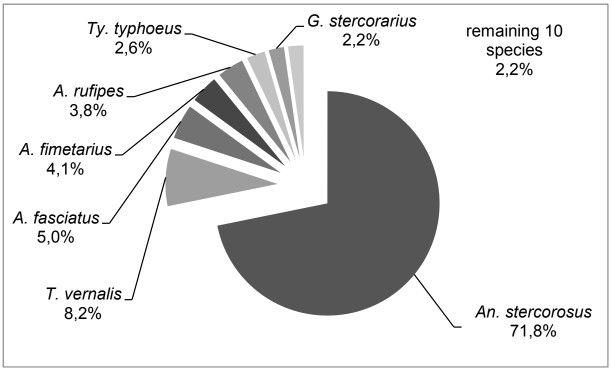

Fig. 9. Species composition of an autumn dung beetle community in later developmental stages of pine stands (AuDB) in Człuchów Forest (NW Poland).

Trappability of dung beetles was the highest in summer (M = 103.8; SE ±5.3) and the lowest in autumn (68.8 ±4.5). In spring, average trappability equaled 82.4 (±4.3) individuals. Dung beetle trappability in summer months differed significantly from dung beetle trappability in spring months ($z = 3.823$, $p < 0.001$) and autumn months ($z = 5.291$, $p < 0.001$) ($H (2, N = 560) = 29.22644$, $p < 0.001$). Similarly, Geotrupidae trappability was the highest in summer (85.1 ±4.9) and the lowest in autumn (58.4 ±4.2). In spring, average trappability equaled 66.7 (±3.5) individuals. Trappability of Geotrupidae in summer months differed in a statistically significant way from their trappability in spring months ($z = 3.180$, $p = 0.005$) and autumn months ($z = 4.570$, $p < 0.001$) ($H (2, N = 560) = 21.54627$, $p < 0.001$). Similarly, average trappability of Aphodiinae was the highest in summer (17.5 ±1.5) and the lowest in autumn (10.0 ±0.8). In spring, the average trappability of those beetles equaled 14.0 (±1.2). Average Aphodiinae trappability in summer months significantly differed from their trappability in spring months ($z = 2.428$, $p = 0.046$) and autumn months ($z = 3.069$, $p = 0.007$) (H

(2, N = 560) = 10,24455, p = 0.060). Average trappability of Scarabaeinae was the highest in spring (1.6 SE ±0.1), lower in summer (1.2 ±0.2), and the lowest in autumn (0.4 ±0.1). The trappability of Scarabaeinaein summer months differed in a statistically significant way from their trappability in summer months (z = 2.659, p = 0.024) and autumn months (z = 6.545, p < 0.001); furthermore, Scarabaeinae trappability in summer months differed significantly also from their trappability in autumn months (z = 3.547, p = 0.002) (H (2, N = 560) = 54,45615, p < 0.001) (Fig. 10).

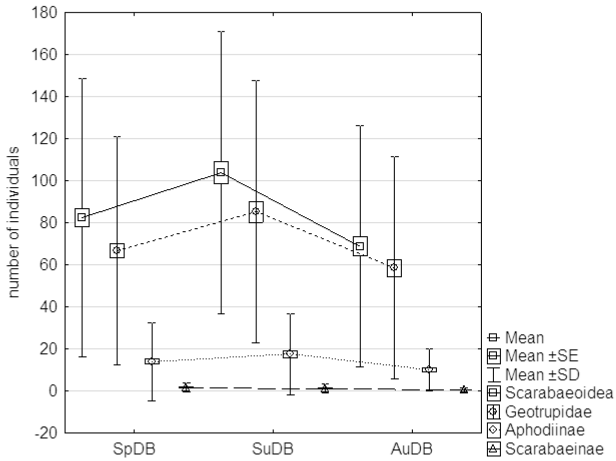

Fig. 10. The average monthly number of dung beetle individuals trapped in a baited ground trap in later developmental stages of pine stands of Człuchów Forest (NW Poland)) (SpDB - spring community of dung beetles in later developmental stages of pine stands, SuDB - summer community of dung beetles in later developmental stages of pine stands, AuDB - autumn community of dung beetles in later developmental stages of pine stands).

An average monthly number of trapped dung beetle species was the highest in spring (M = 5.9; SE ±0.1) and the lowest in autumn (5.0 ±0.2). In summer, the average monthly number of collected species amounted to 5.6 (±0.2). An average monthly number of dung beetle species collected in autumn months differed in a statistically significant way from the number of species collected in summer months (z = 2.611, p = 0.028) and spring months (z = 4.426, p < 0.001) (H (2, N = 560) = 20.09703, p < 0.001). An average monthly number of trapped Geotrupidae species was similar in spring and in autumn (2.8 ±0.1) but lower in summer (2.5 ±0.1). An average monthly number of Geotrupidae species collected in summer months differed significantly from their average number collected in spring months (z = 2.927, p = 0.011) and autumn months (z = 3.119, p = 0.006) (H (2, N = 560) = 14,18360, p < 0.001). An average monthly number of trapped Aphodiinae species was the highest in summer (2.5 ±0.1) and the lowest in autumn (2.0 ±0.1). In spring, the average number of collected Aphodiinaespecies amounted to 2.4 (±0.1). An average monthly number of Aphodiinae species collected in autumn months differed significantly from their number collected in summer months (z = 3.708, p < 0.001) and spring months (z = 3.111, p = 0.006) (H (2, N = 560) = 16.22600, p < 0.001). An average monthly number of trapped

Scarabaeinae species was the highest in spring (0.8 ±0.1), lower in summer (0.5 ±0.1), and the lowest in autumn (0.2 ±0.1). An average monthly number of Scarabaeinae species collected in spring months differed significantly from their number collected in summer months ($z = 2.785$, $p = 0.017$) and autumn months ($z = 6.402$, $p < 0.001$); similarly, average monthly number of Scarabaeinae species collected in summer months differed significantly from their number collected in autumn months ($z = 3.301$, $p = 0.003$) ($H (2, N = 560) = 53.42553$, $p < 0.001$) (Fig. 11).

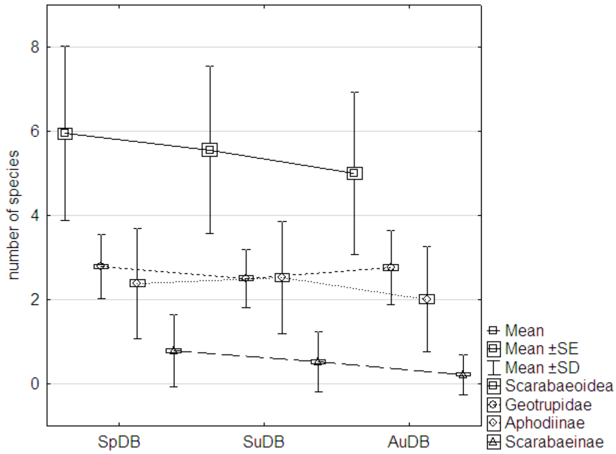

Fig. 11. The average monthly number of dung beetle species trapped in a baited ground trap in later developmental stages of pine stands in Człuchów Forest (NW Poland) (SpDB - spring community of dung beetles in later developmental stages of pine stands, SuDB - summer community of dung beetles in later developmental stages of pine stands, AuDB - autumn community of dung beetles in later developmental stages of pine stands).

DISCUSSION

The average number of species and abundance of dung beetle (coprophagous Scarabaeoidea) communities inhabiting later developmental stages of pine stands in NW Poland was the highest in June and dramatically dropped in July, to increase again August. The increasing and decreasing trends observed in the respective months could also be noted in the case of aphodiine dung beetles (Aphodiinae), whereas in the case of earth-boring dung beetles (Geotrupidae) a drop in abundance could also be observed in August. According to Finn *et al*. (1999) biomass of the *Aphodius* species was highest in late summer in the Ireland. A dramatic drop of the average number of species and community abundance in July took place also in the case of scarab dung beetles (Scarabaeinae), however, they were the most abundant in August and the average number of their species was the highest in May and June. However, the highest number of species were recorded in May (23), June (18) and September (16).

In July, the average number of species and individuals became reduced by over 30% in comparison to June. This mean that the change was abrupt rather than gradual.

In July, as a result of high temperatures, and due to the cumulative effect of high temperatures in May and June (Fig. 3), microclimatic conditions under the canopy of later pine stands changed considerably. Humidity decreased while air temperature increased, which seriously affected the nutritional value and availability of food, as well as the soil structure. Fast and excessive drying out of animal faeces, vegetation cover and soil made it difficult for dung beetles to find wholesome food, bore tunnels and build brooding chambers.

The amount of dung buried by dung beetles is connected, first and foremost, with the body size of a female (Horgan, 2001), although such factors as soil type, its moisture (Sowig, 1995), cooperation between the female and the male (Sowig, 1996) and the physical condition of the dung also play a significant role (Worthen *et al*., 1994; Dadour and Cook, 1996; Worthen *et al*., 1998; Finn and Giller, 2000; Finn and Gittings, 2003). Also temperature has a considerable effect on the abundance and structure of dung beetle populations (Hortal *et al*., 2011). Low precipitation is another important factor for dung beetles. Seasonal character of precipitation has a large influence on their populations, resulting in a complete absence of dung beetles from deciduous forests and being responsible for the fact that their biodiversity is very low in mixed forests during a dry season (Andresen, 2005). Adults occurring in spring in pine stands, mostly those of shade-loving dung beetles, in July cannot find suitable conditions for breeding any more. In this month heliophilous species from open areas arrive in pine stands looking for shelter, while umbrophilous species inhabiting forest areas reduce their activity, hide or finish swarming, lay eggs and die. Rebuilding of abundance and species richness of dung beetle communities in later pine stands begins as the temperatures drop in the second half of August and in September. As a result, an average number of species increases again by over 25% in August and the abundance increases by ca. 5% in September. In summary, the hypothesis about a gradual reduction of the numbers of dung beetle individuals and species inhabiting pine stands during the whole vegetation season should be rejected. The change has an abrupt character and takes place in July. In this month “spring” and “spring-summer” species are replaced by “summer-autumn” species, and later also by “autumn” species.

Presented results indicate significant differences with respect to abundance, species richness and species composition of dung beetle communities inhabiting pine stands of NW Poland in various periods of the vegetation season. Dung beetles inhabiting those pine stands form significantly more abundant communities in summer than in spring and autumn respectively. Similarly, the numbers of earth-boring and Aphodiinae are significantly higher in summer than in spring and autumn. As for Scarabaeinae, they are significantly more abundant in spring than in summer, and more abundant in summer than in autumn. At the same time, dung beetles form communities characterized by significantly higher species richness in spring and summer than in autumn. Similarly, species richness of Aphodiinae and Scarabaeinae communities is significantly higher in summer than in autumn. As for Geotrupidae communities, their species richness is equally high in spring and in autumn, but significantly lower in summer.

In the course of the vegetation season, later developmental stages of pine stands in NW Poland are inhabited by three types of dung beetle communities differing with respect to their structures. Spring dung beetle community inhabits pine forests in April, May and June, summer community inhabits them in July and August, whereas an autumn community inhabits them in September and October. In all these communities, the Geotrupidae constitute over 80%, the Aphodiinae constitute less than 20%, and the Scarabaeinae constitute less than 5%. The dominant role of Geotrupidae in dung beetle communities inhabiting forest areas has also been indicated by monitoring studies conducted in Człuchów Forest (Szyszko, 1983) and in Białowieża Forest (Szwałko, 1995). In open areas of Central Europe the abundance of the Geotrupidae decreases as they are being replaced by species of Scarabaeidae (Aphodiinae and Scarabaeinae) (Sowig and Wassmer, 1994; Wassmer, 1995; Bunalski, 1996a, 1996b; Górz, 2007). The further south, the more thermophilous species occur among European dung beetles inhabiting both open areas and forests; those species belong to the family Scarabaeidae and mostly represent the following genera: *Onthophagus*, *Gymnopleurus*, *Sisyphus* and *Scarabaeus* (Balthasar, 1964). Simultaneously, the abundance of species representing the Geotrupidae is decreasing (Byk, 2012). According to Hortal *et al*. (2011), representatives of the tribes Onitini and Scarabaeini have not developed mechanisms of adaptation to low temperatures that would enable them to colonize northern Europe or survive under the climatic conditions of that region. In La Mandria Park in NE Italy, which is a mosaic of open and forest areas, in communities of coprophagous Scarabaeoidea, the proportion of the Scarabaeidae amounts to 94.0% (including 32.5% Aphodiinae), whereas the Geotrupidae constitute just 6% (Barbero *et al.*, 1999).

In the spring, summer and autumn communities of dung beetles inhabiting pine stands in NW Poland the role of the superdominant was played by *Anoplotrupes stercorosus*, and the role of the dominant was played by *Trypocopris vernalis.* The proportion of *A. stercorosus* was the lowest in the spring community and the highest in the autumn community, whereas the proportion of *T. vernalis* was the highest in the spring community and the lowest in the autumn community. According to Klimaszewski and Szyszko (2000), average trappability of *T. vernalis* in forest areas was negatively correlated with forest cover. Szyszko (1983) noted that in pine forests *A. stercorosus* was the most abundant species among those representing the superfamily Scarabaeoidea, and Byk (2011a) noted that the poletimber stage and the mature stands were the developmental stages of pine stands in which this species was the most abundant. *A. stercorosus* frequently inhabits pine forests growing on post-agricultural land and in forest areas. However, it is more abundant in tree stands growing on post-agricultural land. Inhabiting tree stands growing on such land it bores earth tunnels and buries feaces of wild animals and shed leaves, in this way changing the properties of post-agricultural soils and accelerating the process of forming the soils of a forest type (Byk, 2004; Byk and Semkiw, 2010; Byk, 2011b). One of the above authors has found *A. stercorosus* larvae as far as 50 m from the edge of a tree stand.

The spring community was characterized by high species richness. In spring, the following species were frequent or abundant in the forest habitat: *Aphodius depressus*, *A. rufipes, A. fimetarius, A. prodromus, Geotrupes stercorarius* and *Onthophagus fracticornis.* There were definitely fewer species in the summer community. Species that were both frequent or abundant in summer included: *Aphodius rufipes, A. fimetarius, A. depressus* and *Geotrupes stercorarius*. The species richness of the autumn community was equally low. Frequent and numerous species occurring in spring included: *Aphodius fasciatus, A. fimetarius, A. rufipes, Typhaeus typhoeus* and *Geotrupes stercorarius*.

The spring community was distinguished by the presence of species that were absent from the remaining communities. They were the following: *Aphodius ater, A. fossor, A. nemoralis, A. pusillus, A. sphacelatus, A. sticticus, A. subterraneus, Heptaulacus testudinarius, Oxyomus sylvestris* and *Onthophagus nuchicornis.* In the summer community there was only one exclusive species, namely *Aphodius sordidus*, species with a statistically significant preference for the dusk-night period (Kamiński *et al*., 2015), whereas in the autumn community there were two such species: *A. contaminatus* and *A. paykulli*.

Even though *Anoplotrupes stercorosus* and *Trypocopris vernalis* are the most abundant dung beetle species in later developmental stages of pine stands of the surroundings of Człuchów (Szyszko, 1983; Byk, 2011a), a vast majority of species represents the genus *Aphodius*. According to Hanski (1986), this is the result of optimal adaptation of the Aphodiidnae to climatic conditions of Central Europe. Dung beetles from the genus *Aphodius* are the dominating coprophagous beetles in northern Europe and generally play a fundamental part in the removal of faeces, recycling of organic substances and providing plants with nutrients (Fry and Lonsdale, 1991; Hutton and Giller, 2003). The following species of the genus *Aphodius* are closely associated with forest environment: *A. depressus* and *A. fasciatus* (Szwałko, 1995; Żuk, 2005; Bunalski, 2006; Górz, 2007; Byk, 2012), *A. nemoralis* (Szwałko, 1995; Bunalski, 2006; Górz, 2007; Byk, 2012), *A. sticticus* (Landin, 1961; Szwałko, 1995; Wassmer, 1995; Żuk, 2005; Bunalski, 2006; Górz, 2007; Byk, 2012) and *A. zenkeri* (Wassmer *et al*., 1994; Wassmer, 1995; Szwałko, 1995; Byk, 2012). The presence of the eurytopic *A. rufipes* in this group has been indicated by Rainio (1966), Hanski and Koskela (1977), Wassmer (1995) and Byk (2012). Also results obtained in the present study indicate that the above species are closely associated with the microclimate under the canopy of tree stands.

CONCLUSIONS

The structure of dung beetle communities in pine stands in NW Poland changes in the course of the vegetation season. The culmination of the process takes place in July, when a dramatic drop of the number of both individuals and species occurs. This is probably due to fast and excessive drying out of animal faeces, vegetation cover and soil, that makes it difficult for dung beetles to find wholesome food, bore tunnels and build brooding chambers. Due to low humidity and high temperatures during that month, a number of “spring” and “spring-summer” species disappear from the community while the conditions are still unsuitable for the occurrence of “summer-autumn” and “autumn” species”.

Dung beetle (coprophagous Scarabaeoidea) communities inhabiting later developmental stages of pine stands of NW Poland are dominated by earth-boring dung beetles (Geotrupidae). The proportion of individuals representing Aphodiinae and Scarabaeinae dung beetles amounts to less than ¼ of the total. *Anoplotrupes stercorosus* plays the role of the superdominant in those communities, and *Trypocopris vernalis* is a dominant species.

During the vegetation season, later pine stands in NW Poland are inhabited by three dung beetle communities, defined on the basis of the season of adult ativity and differing with respect to their structure and species composition. The spring dung beetle community is characterized by high species richness and the presence of *Aphodius ater, A. fossor, A. nemoralis, A. pusillus, A. sphacelatus, A. sticticus, A. subterraneus, Heptaulacus testudinarius, Oxyomus sylvestris* and *Onthophagus nuchicornis.* The summer dung beetle community is characterized by lower species richness and distinguished by the presence of *Aphodius sordidus.* The autumn dung beetle community is also characterized by low species richness and by the presence of two species specific only to that community: *Aphodius contaminatus* and *A. paykulli*.

REFERENCES

Andresen, E., 2005, Effects of Season and Vegetation Type on Community Organization of Dung Beetles in a Tropical Dry Forest. *Biotropica*, 37(2): 291-300.

Balthasar, V., 1964, *Monographie der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region. Band 3. Aphodiidae*. Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prag, 652.

Barbero, E., Palestrini, C., Rolando, A., 1999, Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). *Journal of Insect Conservation,* 3: 75-84.

Bornemissza, G. F., 1976, The Australian dung beetle project: 1965-1975. *Australian Meat Research Committee Review,* 30: 1-32.

Breymeyer, A., 1978, Analysis of the trophic structure of some grassland ecosystems. *Polish Ecological Studies,* 4: 55-128. It is not

Bunalski, M., 1996a, Żuki koprofagiczne (Coleoptera, Scarabaeoidea) okolic Szamotuł. Cz. I. Analiza faunistyczna [Coprophagous beetles (Coleoptera, Scarabaeoidea) of the Szamotuły area. Part I. Faunistic analisys]. *Wiadomości Entomologiczne,* 15(3): 139-146. [in Polish, abstract in English]

Bunalski, M., 1996b, Żuki koprofagiczne (Coleoptera, Scarabaeoidea) okolic Szamotuł. Cz. II [Coprophagous beetles (Coleoptera, Scarabaeoidea) of the Szamotuły area. Part II]. *Wiadomości Entomologiczne,* 15(4): 217-224. [in Polish, abstract in English]

Bunalski, M., 2006, Żuki (Coleoptera: Scarabaeoidea) wschodnich rubieży Polski. Studium faunistyczno-ekologiczne części północnej i środkowej [Lamellicorn beetles (Coleoptera: Scarabaeoidea) of eastern border of Poland. A faunistic-and-ecological study of the northern and central part]. *Rozprawy Naukowe,* 376: 1-133. [in Polish, abstract in English]

Byk, A., 2004, Zmiany liczebności żuka leśnego *Anoplotrupes stercorosus* (Hartm.) pod wpływem zalesień [The effect of afforestations on population dynamics of *Anoplotrupes stercorosus* (Hartm.)]. *Sylwan,* 148(3): 28-34. [in Polish, abstract in English]

Byk, A., 2011a, Abundance and composition of Geotrupidae (Coleoptera: Scarabaeoidea) in the developmental cycle of pine stands in Człuchów Forest (NW Poland). *Baltic Journal of Coleopterology,* 11(2): 171-186.

Byk, A., 2011b, Wpływ sposobu przygotowania gleby na zgrupowania chrząszczy (Coleoptera) występujące na uprawach leśnych założonych na gruntach porolnych [Effect of soil preparation on beetle (Coleoptera) assemblages occurring in the forest plantations established on former farmland]. *Sylwan,* 155(9): 622-632. [in Polish, abstract in English]

Byk, A., 2012, Abundance and composition of coprophagous Scarabaeidae (Coleoptera: Scarabaeoidea) in the developmental cycle of pine stands in Człuchów Forest (NW Poland). *Baltic Journal of Coleopterology,* 12(2): 127-144.

Byk, A., Semkiw, P., 2010, Habitat preferences of the forest dung beetle *Anoplotrupes stercorosus* (Scriba, 1791) (Coleoptera: Geotrupidae) in the Białowieża Forest. *Acta Scientiarum Polonorum Silvarum Colendarum Ratio et Industria Lignaria,* 9(3-4): 17-28.

Chin, K., Gill, B. D., 1996, Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaios,* 11: 280-285.

Dadour, I. R., Cook, D. F. 1996, Survival and reproduction in the scarabaeine dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae) on dung produced by cattle on grain diets in feedlots. *Environmental Entomology,* 25: 1026-1031.

Davis, A. J., Holloway, J. D., Huijbregts, H., Kirk-Spriggs, A. H., Sutton, S. L., 2001, Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology,* 38: 593-616.

Davis, A. L. V., 1996, Community organization of dung beetles (Coleoptera: Scarabaeidae): Differences in body size and functional group structure between habitats. *African Journal of Ecology,* 34: 258-275.

De Groot, R. S., Wilson, M. A., Boumans, R. M. J., 2002, A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics,* 41: 393-408.

Favila, M. E., Halffter, G., 1997, The use of indicator groups for measuring biodiversity as related to community structure and function. *Acta Zoologica Mexicana, Nueva Serie,* 72: 1-25.

Finn, J. A., Giller, P. S., 2000, Patch size and colonisation patterns: an experimental analysis using north temperate coprophagous dung beetles. *Ecography,* 23: 315-327.

Finn, J. A., Gittings, T., 2003, A review of competition in north temperate dung beetle communities. *Ecological Entomology,* 28: 1-13.

Finn, J. A., Gittings, T., Giller, P. S., 1999, Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. *Ecological Entomology,* 24: 24-36.

Fry, R., Lonsdale, D., 1991, *Grassland habitats. In:* Fry, R., Lonsdale, D. (Eds.). Habitat Conservation for Insects - A Neglected Green Issue. The Amateur Entomologists' Society, Middlesex, 93-115.

Górz, A., 2007, Changes in the coprofagous beetle fauna of the Scarabaeoidea (Coleoptera) superfamily on the Krakow-Czestochowa Upland. *Polish Journal of Entomology,* 76: 199-206.

Hanski, I., 1986, Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Oecologica,* 7(2): 171-187.

Hanski, I., Cambefort, Y., 1991, *Dung Beetle Ecology*. Princeton University Press, Princeton, 520.

Hanski, I., Koskela, H., 1977, Niche relations among dung-inhabiting beetles. *Oecologia,* 28: 203-231.

Horgan, F. G., 2001, Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. *European Journal of Soil Biology,* 37: 103-111.

Hortal, J., Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., Rangel, T. F., Hawkins, B. A., Lobo, J. M., 2011, Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters,* 14: 741-748.

Hutton, S. A., Giller, P. S., 2003, The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Applied Ecology,* 40: 994-1007.

Kamiński, M. J., Byk, A., Tykarski, P., 2015. Seasonal and Diel Activity of Dung Beetles (Coleoptera: Scarabaeoidea) Attracted to European Bison Dung in Białowieża Primeval Forest, Poland. *The Coleopterists Bulletin,* 69: 1-8.

Kasprzak, K., Niedbała, W., 1981, *Wskaźniki biocenotyczne stosowane przy porządkowaniu i analizie danych w badaniach ilościowych [Biocenotic indicators applied to order and analyze data in quantitative analysis]. In:* Górny, M., Grűm, L. (Eds.). Metody stosowane w zoologii gleby [Methods applied in soil zoology]. PWN, Warszawa, 397-409. [in Polish]

Klimaszewski, K., Strużyński, W., 2005, *Some population characteristics of Anoplotrupes stercorosus (Hartmann in Scriba, 1791) in relation to forest habitat and soil quality. In:* Skłodowski, J., Huruk, S., Barševskis, A., Tarasiuk, S. (Eds.). Protection of Coleoptera the Baltic Sea Region. Warsaw Agricultural University Press, Warsaw, 179-184.

Klimaszewski, K., Szyszko, J., 2000, Żukowate (Coleoptera, Scarabaeidae) negatywnych drzewostanów sosnowych [Dung beetles (Coleoptera, Scarabaeidae) in pine stands of low quality]. *Sylwan,* 10: 39-43. [in Polish, abstract in English]

Landin, B. O., 1961, Ecological studies on dung-beetles (Col. Scarabaeidae). *Opuscula Entomologica Supplementa,* 19: 1-227.

Löbl, I., Smetana, A., 2006, *Catalogue of Palaearctic Coleoptera, Vol. 3.* Apollo Books, Stenstrup, 690.

Lumaret, J. P., Iborra, O., 1996, Separation of trophic niches by dung beetles (Coleoptera, Scarabaeoidea) in overlapping habitats. *Pedobiologia,* 40: 392-404.

Matuszkiewicz, J. M., 1993, Krajobrazy roślinne i regiony geobotaniczne Polski [Vegetation landscape and geobotanical regions of Poland]. *Prace Geograficzne,* 158: 5-107. [in Polish]

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E., 2008, Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation,* 141: 1461-1474.

Osberg, D. C., Doube, B. M., Hanrahan, S. A., 1994, Habitat specificity in African dung beetles: The effect of soil type on the survival of dung beetle immatures (Coleoptera Scarabaeidae). *Tropical Zoology,* 7: 1-10.

Rainio, M., 1966, Abundance and phenology of some coprophagous beetles in different kinds of dung. *Annales Zoologici Fennici,* 3: 88-98.

Skłodowski, J., Byk, A., Malinowska, A., Spała, S., Błędowski, J., 1998, Występowanie przedstawicieli rodzaju żuk (*Geotrupes* Latreille) na zrębie z pozostawionymi kępami sosen [Occurrence of representatives of the *Geotrupes* Latreille genus on a clearcut with remaining groups of Pine trees]. *Sylwan,* 11: 37-42. [in Polish, abstract in English]

Skłodowski, J., Duda, T., 2007, *Zmiany długości żuka leśnego Anoplotrupes stercorosus w drzewostanach zniszczonych przez huragan i w drzewostanach kontrolnych [Dynamics of body length of the dung beetle Anoplotrupes stercorosus in the hurricane destroyed stands and in the control stands]. In:* Skłodowski, J. (Ed.). Monitoring zooindykacyjny pohuraganowych zniszczeń ekosystemów leśnych Puszczy Piskiej [Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest]. Wydawnictwo SGGW, Warszawa, 107-111. [in Polish]

Sowig, P., 1995, Habitat selection and offspring survival rate in three paracoprid dung beetles: The influence of soil type and soil moisture. *Ecography,* 18: 147-154.

Sowig, P., 1996, Duration and benefits of biparental brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae). *Ecological Entomology,* 21: 81-86.

Sowig, P., Wassmer, T., 1994, Resource Partitioning in Coprophagous Beetles from Sheep Dung: Phenology and Microhabitat Preferences. *Zoologische Jahrbucher, Systematik,* 121: 171-192.

StatSoft, Inc., 2011, STATISTICA (data analysis software system), version 10.

Stebnicka, Z., 1976, Żukowate (Coleoptera, Scarabaeidae) Pienin [Scarab beetles (Coleoptera, Scarabaeidae) of the Pieniny Mountains]. *Fragmenta Faunistica,* 21: 331-351. [in Polish]

Szyszko, J., 1983, *Scarabaeidae. In:* Szujecki, A. (Ed.). The process of forest soil macrofauna formation after afforestation of farmland. Warsaw Agricultural University Press, Warsaw, 112-116.

Szwałko, P., 1995, Chrząszcze żukowate (Coleoptera: Scarabaeoidea) Puszczy Białowieskiej w aspekcie dotychczasowych badań monitoringowych na terenie północno-wschodniej Polski [Scarabaeoidea (Coleoptera) of the Białowieża Primeval Forest in the aspect of the results obtained so far in the monitoring study in NE Poland]. *Prace IBL, Ser. A,* 794: 108-128. [in Polish, abstract in English]

Szwałko, P., Starzyk, J. R., 1997, *Zmiany liczebności wybranych gatunków Carabidae i Geotrupidae (Coleoptera) w drzewostanach objętych zwalczaniem brudnicy mniszki Lymantria monacha (L.) [Changes in the abundance of selected species of Carabidae and Geotrupidae (Coleoptera) in tree stands where black arches Lymantria monacha (L.) undergoes eradication treatment]. In:* Mazur, S. (Ed.). Waloryzacja ekosystemów leśnych metodami zooindykacyjnymi [Valorization of forest ecosystems by methods of zooindication]. Fundacja „Rozwój SGGW", Warszawa, 140-156. [in Polish]

Tesař, Z., 1957, *Brouci listorozí.* Fauna ČSR. Československá Akademie Věd, Praha, 326. [in Czech]

Wassmer, T., 1995, Selection of the spatial habitat of coprophagous beetles in the Kaiserstuhl area near Freiburg (SW - Germany). *Acta Ecologica,* 16(4): 461-478.

Wassmer, T., Himmelsbach, W., Himmelsbach, R., 1994. Dungbewohnende Blatthornkäfer (Scarabaeoidea) und Wasserkäfer (Hydrophilidae) aus dem Hessental bei Schelingen im Kaiserstuhl. *Mitteilungen des Badischen Landesvereins fur Naturkunde und Naturschutz,* 16(1): 75-83.

Worthen, W. B., Jones, M. T., Jetton, R. M., 1998, Community structure and environmental stress: desiccation promotes nestedness in mycophagous fly communities. *Oikos,* 81: 45-54.

Worthen, W. B., Mayrose, S., Wilson, R. G., 1994, Complex interactions between biotic and abiotic factors: effects on mycophagous fly communities. *Oikos,* 69: 277-286.

Żuk, K. 2005, Koprofagiczne żukowate (Coleoptere: Scarabaeoidea) pastwiska w Jarach na Wzgórzach Trzebnickich [Coprophagous beetles (Coleoptera: Scarabaeoidea) of a pasture in Jary in Wzgórza Trzebnickie Hills]. *Wiadomości Entomologiczne,* 24(3): 153-164. [in Polish, abstract in English]

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