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Abundance and composition of coprophagous Scarabaeidae (Coleoptera: Scarabaeoidea) in the developmental cycle of pine stands in Człuchów Forest (NW Poland)

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The aim of the study was to gain knowledge about changes in abundance and species composition of Scarabaeidae in pine stands. Beetles were collected in baited traps in Człuchów Forest, Pomeranian Lake District (Lasy Człuchowskie, Pojezierze Pomorskie) in 1998-1999. In total, 18,207 specimens were collected, representing 36 species. It has been discovered that the structure of coprophagous Scarabaeidae communities inhabiting pine stands changes in the course of the forest developmental cycle. Brownfield adjoining to a forest, clear-cut areas and plantations are inhabited by heliophilous communities of coprophagous Scarabaeidae, with dominant species such as *Aphodius fimetarius, A. coenosus, A. distinctus, A. prodromus, Onthophagus nuchicornis* and *O. fracticornis*. Thicket stage, pole timber stage, and the mature stand are inhabited by umbrophilous coprophagous Scarabaeidae communities characteristic of pine stands, with dominant species such as *Aphodius rufipes, A. fimetarius, A. depressus, A. fasciatus* and *Onthophagus fracticornis*. At thicket stage both the number of species and abundance of coprophagous Scarabaeidae are dramatically reduced in comparison to other developmental stages. Moreover, a fundamental change in species composition is observed.

Key words: Coprophagous, Scarabaeidae, *Aphodius*, community structure, pine stands, Poland

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INTRODUCTION

Scarabaeidae inhabit all zoogeographical regions of the world. Although a majority of species live in the tropical zone, some species of the genus *Aphodius* Illiger, 1798 spread north to the border of permafrost and have even been recorded 300 km beyond the Arctic Circle (Tesař 1957). In Europe, Scarabaeidae are represented by 13 subfamilies, 113 genera, and ca. 1,150 species (Löbl & Smetana 2006). Within the territory of Poland 143 Scarabaeoidea species have been recorded so far, of which the presence of 21 is highly questionable and ought to be confirmed by new records. In the process of evolution, the representatives of Scarabaeidae have become adapted to diverse nourishment, feeding on both plants and animals. Among the Scarabaeidae there are

phyllophagous and rhizophagous species, some of which are dangerous pests, as well as creophagous and coprophagous species. However, coprophagy as the type of nutritional specialisation dominates among the Scarabaeidae. Coprophagous Scarabaeidae can be endocoprids (e.g. genus *Aphodius*), paracoprids (*Onthophagus* Latreille, 1802, *Copris* Geoffroy, 1762), or telecoprids (*Gymnopleurus* Illiger, 1803, *Scarabaeus* Linnaeus, 1758 and *Sisyphus* Latreille, 1807) (Bornemissza 1976). Endocopric species lay eggs directly in faeces while paracopric species dig tunnels of various lengths in the ground under the faeces. These tunnels end in brood chambers where the beetles store portions of the faeces they had rolled into balls and on which the larvae are going to feed.

In world literature, a number of studies can be found which discuss the complex character of the relationship between coprophages and the environment (Rainio 1966, Desiere 1973, Koskela & Hanski 1977, Grosfilley & Buisson 1982, Henry & Prelle 1986, Hanski & Cambefort 1991, Lobo 1993, Sowig & Wassmer 1994, Wassmer 1995, Mittal & Bhati 1998). A clear majority of works analysing the structure of coprophagous Scarabaeidae communities describe areas located far away from Poland, such as meadows and forests in Australia, the northern part of South America, and the southern part of Africa. In Europe, Breymeyer & Zachareva-Stoilowa (1983) conducted research on the structure of coprophagous Scarabaeidae communities of mountain pastures in Bulgaria, Wassmer et al. (1994) and Wassmer (1995) investigated the same topic with reference to pastures in South-Western Germany, Barbero et al. (1999) focussed on the northern part of Italy, and, finally, Hutton and Giller (2003) investigated Southern Ireland.

Information on ecological requirements of species representing the family Scarabaeidae encountered in Poland are either scattered across various publications or featured in larger studies focussing on the superfamily Scarabaeoidea (Hildt 1896, Stebnicka 1976a, Burakowski et al. 1983, Bunalski 1999). In Poland, the structure of coprophagous Scarabaeoidea communities inhabiting pastures has been investigated by Breymeyer (1974) - in the Pieniny Mountains, Stebnicka (1976b), Bunalski (1996a, b) - in Greater Poland, Żuk (2005) - in Trzebnickie Hills, and Górz (2007) - in Kraków-Częstochowa Upland. The results of these studies clearly indicate that the core of coprophagous Scarabaeoidea communities inhabiting Polish pastures are composed of species characteristic for open areas and eurytopic species of the genus *Aphodius*: *A. distinctus* (O. F. Müller, 1776), *A. erraticus* (Linnaeus, 1758), *A. fimetarius* (Linnaeus, 1758), *A. haemorrhoidalis* (Linnaeus, 1758), *A. prodromus* (Brahm, 1790), *A. pusillus* (Herbst, 1789), *A. rufus* (Moll, 1782), *A. rufipes* (Linnaeus, 1758), *A. sphacelatus* (Panzer, 1798) and *A. subterraneus* (Linnaeus, 1758). In the above mentioned studies some habitats were observed suggesting the existence of differences in species composition of coprophagous Scarabaeoidea communities between open areas and forests. Similarly, Breymeyer (1978), Rembiałkowska (1980), and Rojewski (1980), pointing out the importance of coprophagous Scarabaeoidea in meadow and forest ecosystems, draw attention to the presence of pasture and forest species. In a comprehensive study on the biology and ecology of genus *Onthophagus*, Goljan (1953) points out that the presence of coprophagous beetles mainly depends on the ground type and climate conditions, and not on the type of faeces.

Knowledge on the function of coprophagous Scarabaeidae in forest environments, as well as on their ecological requirements, is still insufficient. The structure of coprophagous Scarabaeidae communities in Polish lowlands has been discussed in only two studies. One of these investigated the structure of Scarabaeidae communities inhabiting tree stands in post-agricultural and forest areas in Człuchów Forest (Szyszko 1983) and the other was devoted to the Scarabaeoidea of Białowieża Primaeveal Forest (Szwałko 1995). Hence there is a need for obtaining more extensive knowledge on Scarabaeidae communities inhabiting forest areas, including the following issues:

– Abundance and species composition of coprophagous Scarabaeidae communities

inhabiting pine stands;
- Dominant species and coprophagous Scarabaeidae communities characteristic for particular stages of the pine stand developmental cycle;
- Character of changes in species composition and abundance of Scarabaeidae communities in the course of tree stand development.

In general, coprophagous Scarabaeidae can be divided into species characteristic of open areas (praticoles), forest species (silvicoles), and eurytopic species. There are few species of coprophagous Scarabaeidae inhabiting Polish lowlands and being tightly connected with forest environment: *Aphodius borealis* Gyllenhal, 1827, A. *fasciatus* (A. G. Olivier, 1789), *A. nemoralis* Erichson, 1848, *A. sticticus* (Panzer, 1798), and *A. zenkeri* Germar, 1813 (Stebnicka 1976a, Burakowski et al. 1983, Szwałko 1995, Żuk 2005, Bunalski 2006, Górz 2007). The small number of species found in compact tree stands in comparison to open areas seems to suggest that the number of species present in the course of the tree stand developmental cycle should be gradually diminishing as a stand matures. Hence the following exploratory questions arise:
- Does the number of coprophagous Scarabaeidae species inhabiting afforested post-agricultural lands and renewed forest areas gradually decrease as the renewed tree stands mature?
- If so, is this a continuous process or does it take place by leaps, and if the latter is the case, at which stage does the most significant reduction in the number of species occur?

MATERIAL AND METHODS

Człuchów Forest (Polish: Lasy Człuchowskie) is situated within the geobotanical region of Pomeranian Divide, the syntaxonomical region of Sandar Forefields of Central Pomeranian Lake District (Polish: Kraina Sandrowych Przedpoli Pojezierzy Środkowopomorskich), and the syntaxonomical subregion of Wałcz (Polish: Podkraina Wałecka) (Fig. 1).

The region is characterised by a considerable area of sandur lowlands, with the landscape of coniferous forests and mixed forests with the association of *Leucobryo-Pinetum* characteristic of coniferous forests and the associations of *Fago-Quercetum* and *Querco-Pinetum* characteristic of mixed forests (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 ca. 80% was fresh coniferous forest. The coniferous forest comprised mainly pine with a small admixture of spruce and birch (Forest Management Plan... 1992).

Twenty study sites were established, selected as to represent a sequence of successive stages of the pine stand developmental cycle, i.e. land before afforestation (brownfield adjoining to a forest, clear-cut), forest plantation, thicket, pole timber and mature stand (Tab. 1).

In each of the study sites 5 ground traps were placed, baited with portions of cow manure (10 cm^3) (Fig. 2). The size of a single portion of cow

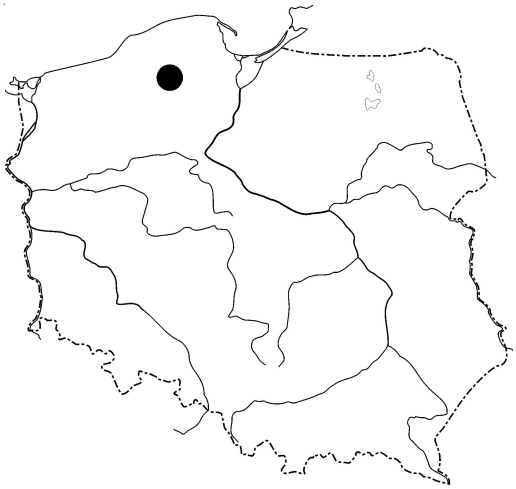

Fig. 1. Location of Człuchów Forest within the territory of Poland

Table 1. Study sites established for collecting coprophagous Scarabaeidae in pine stands in Człuchów Forest, 1998-1999

Symbol of study site	Forest district	Forest compartment	Stand age	Stage of pine stand developmental cycle	Plant community type
LBA1	Stara Brda	–	–	land before afforestation (fallow land)	*Sedo-Scleranthetea*
LBA2	Stara Brda	–	–	land before afforestation (fallow land)	*Molinio-Arrhenatheretea*
LBA3	Brzeźno	249d	–	land before afforestation (clear-cut area)	*Epilobio-Senecionetum silvatici*
LBA4	Pustowo	169h	–	land before afforestation (clear-cut area)	*Epilobio-Senecionetum silvatici*
FP1	Pustowo	118b	2	forest plantation	*Epilobio-Senecionetum silvatici*
FP2	Stara Brda	92j	2	forest plantation	*Epilobio-Senecionetum silvatici*
FP3	Stary Most	293a	4	forest plantation	*Sedo-Scleranthetea*
FP4	Stara Brda	88a	2	forest plantation	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T1	Pustowo	139f	12	thicket stage	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T2	Stara Brda	60f	11	thicket stage	*Leucobryo-Pinetum*
T3	Stara Brda	66j	12	thicket stage	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T4	Stara Brda	63k	11	thicket stage	*Epilobio-Senecionetum silvatici*
P1	Stara Brda	65k	50	pole timber stage	*Sedo-Scleranthetea / Vaccinio-Piceetea*
P2	Stara Brda	83a	42	pole timber stage	*Leucobryo-Pinetum*
P3	Stara Brda	88c	50	pole timber stage	*Sedo-Scleranthetea / Vaccinio-Piceetea*
P4	Stary Most	293i	48	pole timber stage	*Leucobryo-Pinetum*
MS1	Stara Brda	63b	90	mature stand	*Leucobryo-Pinetum*
MS2	Stara Brda	61b	105	mature stand	*Leucobryo-Pinetum*
MS3	Stara Brda	91a	110	mature stand	*Leucobryo-Pinetum*
MS4	Pustowo	168a	90	mature stand	*Leucobryo-Pinetum*

manure was specified on the assumption that the amount of bait should allow to acquire knowledge about the complete species composition of a particular beetle community, but should neither alter the nutritional conditions within a given area nor attract individuals from beyond this area. The total number of 100 traps functioned throughout the complete study period; in each site they were arranged in a square with 20-meter side length and marked diagonals (so-called "en-

velope"). Insects were collected at monthly intervals from April until October 1998 and 1999.

Systematic hierarchy and species denomination followed the "Catalogue of Palearctic Coleoptera" (Löbl & Smetana 2006). The score of Kasprzak & Niedbała (1981) was used for the specification of dominance patterns: superdominants – > 30.00%, dominants – 5.01 – 30.00%, subdominants – 1.01 – 5.00% and accidental species – ⩽1.00%.

The evaluation of dependence of Scarabaeidae on selected environmental gradients was conducted by implementing the PCA method of the program CANOCO 4.0 (Ter Braak & Smilauer 1997). The standard settings were used in the analysis of the PCA. The choice of study sites allowed for connecting particular Scarabaeidae communities either to the gradient of forest succession or the environmental gradient connected with the height of the tree stands. PCA analysis was performed after having checked the gradient length by DCA; since it was lower than 3 units, the performance of linear analysis was advisable. The faunistic similarity of Scarabaeidae communities at various stages of the forest developmental cycle was calculated by means of cluster analysis using Ward's method, and Euclidean distance was used to measure the similarity. The statistical significance of differences discovered in the number of Scarabaeidae species and abundance of individuals, also in the abundance of selected species, was determined. Statistical analysis was performed with the help of the program Statistica 9.1 (StatSoft, Inc. 2010). Normal distribution of data was verified by the Shapiro-Wilk test, and the equality of variances by Levene's test. The non-parametric Kruskal-Wallis method was employed to test the phases of the forest developmental cycle (land before afforestation, plantation, thicket, pole timber, mature stand) with respect to the number of Scarabaeoidea species and number of individuals (Scarabaeidae, *Aphodius coenosus, A. depressus, A. distinctus, A. fasciatus, A. fimetarius, A. prodromus, A. rufipes, Onthophagus fracticornis,* and *O. nuchicornis*). Each stage of the forest developmental cycle was treated as an independent variable while the number of individuals and the number of species were treated as dependent variables. The total number of individuals caught in a single trap in the course of one season of the study was treated as one sample.

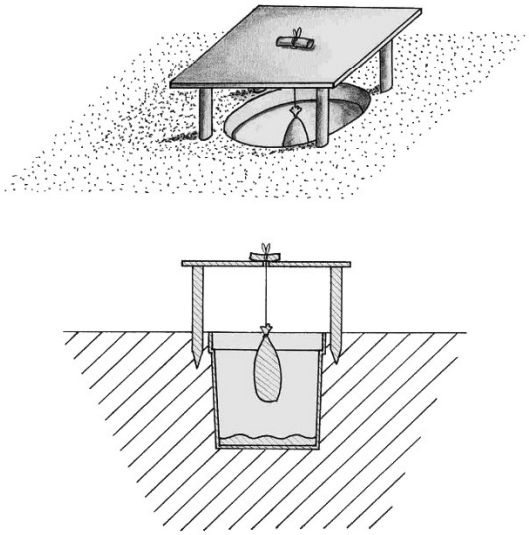

Fig. 2. Baited ground trap for collecting Scarabaeidae in pine stands in Człuchów Forest, 1998-1999 (drawing by J. Piętka).

RESULTS

In the course of the study, 18,207 specimens of coprophagous Scarabaeidae were collected, representing 36 species. In 1998, the number of collected specimens was 6,573, and, in 1999, 11,634. The highest number of individuals was collected on land before afforestation (i.e. 4,576) while the lowest number of individuals was collected at the thicket stage (i.e. 1,065). As many as 4,162 specimens were collected at the plantation stage, whereas 3,847 specimens were collected at the pole timber stage, and 4,557 in mature stands. The first two stages of the pine stand developmental cycle yielded 48.0% of the total number of collected specimens while the thicket stage yielded merely 5.8%. The final two stages of the forest developmental cycle, namely pole timber stage and mature stand, yielded 46.2%. The rep-

resentatives of the Scarabaeidae family which were collected in greatest numbers in pine stands of Człuchów Forest included the following: *Aphodius fimetarius* (Linnaeus, 1758), *A. rufipes* (Linnaeus, 1758), *A. coenosus* (Panzer, 1798), *A. depressus* (Kugelann, 1792), *A. distinctus* (O. F. Müller, 1776), *Onthophagus fracticornis* (Preyssler, 1790), and *Aphodius prodromus* (Brahm, 1790). These species constituted 81.4% of the total number of collected specimens (Tab. 2).

The mean number of coprophagous Scarabaeidae species collected per trap during one season of research conducted at particular stages of the forest developmental cycle was highest in plantations (10.45 ± 0.33) and lowest at the thicket stage (5.50 ± 0.28). At the remaining stages of the pine stand developmental cycle the numbers of collected species were similar. They amounted to 9.07 ± 0.42 on land before afforestation, 9.03 ± 0.24 in mature stands, and 8.40 ± 0.31 at the pole timber stage. These results confirmed the difference between the number of coprophagous Scarabaeidae species collected at the thicket stage and the remaining developmental stages of pine stands (Fig. 3).

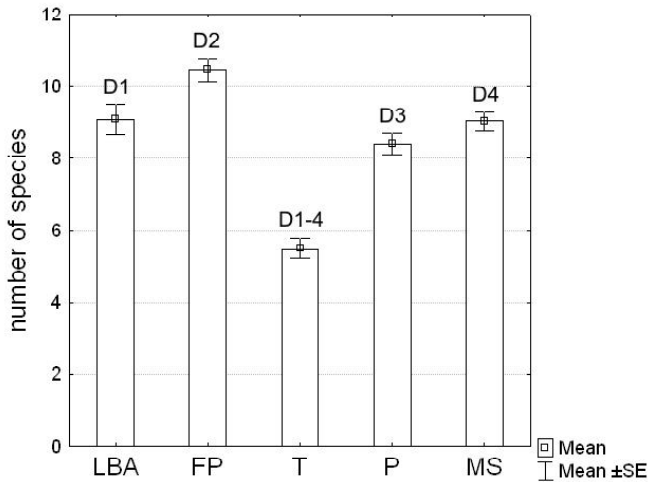

Fig. 3. Mean number of coprophagous Scarabaeidae species collected per trap during one season in pine stands in Człuchów Forest (MS - mature stand, P - pole timber stage, T - thicket stage, FP - forest plantation, LBA - land before afforestation, SE - standard error, D - significance level $p<0.001$)

The mean number of coprophagous Scarabaeidae individuals collected per trap during one season of research conducted in pine stands in Człuchów Forest was highest on the land before afforestation (114.4 ± 13.2) and lowest at the thicket stage (26.6 ± 1.8). In mature stands the number of collected individuals amounted to 113.9 ± 8.3 as compared to 104.1 ± 8.8 at the plantation stage and 96.2 ± 6.4 at the pole timber stage. Similar to the species level the results matched the difference between the number of coprophagous Scarabaeidae individuals collected at the thicket stage and the remaining developmental stages of pine stands (Fig. 4).

Analysis of faunistic similarity of coprophagous Scarabaeidae communities inhabiting pine stands helped to distinguish two faunistic agglomerations (Fig. 5). One of these agglomerations encompassed coprophagous Scarabaeidae communities inhabiting land before afforestation and plantations. The dominant species in these communities were: *Aphodius fimetarius* (22.2%), *A. coenosus* (21.2%), *A. distinctus* (15.8%), *Onthophagus nuchicornis* (9.8%), *O. fracticornis* (9.7%), and *Aphodius prodromus* (6.7%). Subdominant species comprised: *Onthophagus ovatus* (4.3%), *O. similis* (2.8%), *Aphodius rufipes* (1.6%), *A. foetens* (1.5%) and *A. subterraneus* (1.1%). The core of these communities, as described above, was supplemented by 22 accessory species, among which 9 species in particular were absent from the other agglomeration: *Aphodius erraticus, A. granarius, A. haemorrhoidalis, A. luridus, A. merdarius, Rhyssemus germanus, Copris lunaris, Onthophagus coenobita,* and *O. joannae* (Fig. 6). The other agglomeration encompassed communities inhabiting the thicket stage, pole timber stage, and mature stands, with *Aphodius rufipes* (31.6%) in the role of a superdominant species and *A. fimetarius* (23.0%), *A. depressus* (17.3%), *A. fasciatus*

Table 2. Scarabaeidae collected in baited ground traps in pine stands in Człuchów Forest, 1998-1999

Species		Land before afforestation	Forest plantation	Thicket stage	Pole timber stage	Mature stand	Σ	%
Aphodius ater (DeGeer, 1774)	A.at	3	1	0	5	5	**14**	**0,08**
A. coenosus (Panzer, 1798)	A.coe	1148	704	0	14	108	**1974**	**10.84**
A. contaminatus (Herbst, 1783)	A.con	0	1	0	1	1	**3**	**0.02**
A. depressus (Kugelann, 1792)	A.de	38	4	82	629	926	**1679**	**9.22**
A. distinctus (O. F. Müller, 1776)	A.di	593	785	29	60	113	**1580**	**8.68**
A. erraticus (Linnaeus, 1758)	A.er	1	21	0	0	0	**22**	**0.12**
A. fasciatus (A. G. Olivier, 1789)	A.fa	32	27	107	461	269	**896**	**4.92**
A. fimetarius (Linnaeus, 1758)	A.fi	777	1167	240	1119	820	**4123**	**22.65**
A. foetens (Fabricius, 1787)	A.foe	63	72	14	110	99	**358**	**1.97**
A. fossor (Linnaeus, 1758)	A.fos	2	0	0	0	2	**4**	**0.02**
A. granarius (Linnaeus, 1767)	A.gr	0	16	0	0	0	**16**	**0.09**
A. haemorrhoidalis (Linnaeus, 1758)	A.ha	15	1	0	0	0	**16**	**0.09**
A. luridus (Fabricius, 1775)	A.lu	1	0	0	0	0	**1**	**0.01**
A. merdarius (Fabricius, 1775)	A.me	0	2	0	0	0	**2**	**0.01**
A. nemoralis Erichson, 1848	A.ne	0	0	0	6	6	**12**	**0.07**
A. paykulli Bedel, 1907	A.pa	0	7	0	2	0	**9**	**0.05**
A. prodromus (Brahm, 1790)	A.pr	369	219	51	94	219	**952**	**5.23**
A. pusillus (Herbst, 1789)	A.pu	8	9	0	8	8	**33**	**0.18**
A. rufipes (Linnaeus, 1758)	A.rufi	66	78	424	973	1597	**3138**	**17.24**
A. rufus (Moll, 1782)	A.rufu	2	3	5	4	19	**33**	**0.18**
A. sordidus (Fabricius, 1775)	A.so	8	3	0	2	0	**13**	**0.07**
A. sphacelatus (Panzer, 1798)	A.sp	0	2	0	3	0	**5**	**0.03**
A. sticticus (Panzer, 1798)	A.st	0	0	0	0	3	**3**	**0.02**
A. subterraneus (Linnaeus, 1758)	A.su	30	69	0	3	0	**102**	**0.56**
A. zenkeri Germar, 1813	A.ze	0	0	12	15	57	**84**	**0.46**
Heptaulacus testudinarius (Fabricius, 1775)	H.te	3	6	3	1	0	**13**	**0.07**
Oxyomus sylvestris (Scopoli, 1763)	Ox.sy	0	8	0	4	3	**15**	**0.08**
Rhyssemus germanus (Linnaeus, 1767)	R.ge	0	1	0	0	0	**1**	**0.01**
Copris lunaris (Linnaeus, 1758)	C.lu	0	1	0	0	0	**1**	**0.01**
Onthophagus coenobita (Herbst, 1783)	O.co	17	0	0	0	0	**17**	**0.09**
O. fracticornis (Preyssler, 1790)	O.fr	515	336	67	229	230	**1377**	**7.56**
O. joannae Goljan, 1953	O.jo	1	0	0	0	0	**1**	**0.01**
O. nuchicornis (Linnaeus, 1758)	O.nu	474	384	6	5	12	**881**	**4.84**
O. ovatus (Linnaeus, 1758)	O.ov	254	125	12	34	3	**428**	**2.35**
O. similis (Scriba, 1790)	O.si	147	96	11	65	57	**376**	**2.07**
O. taurus (Schreber, 1759)	O.t	9	14	2	0	0	**25**	**0.14**
Σ		**4576**	**4162**	**1065**	**3847**	**4557**	**18207**	**100.00**
%		**25.13**	**22.86**	**5.85**	**21.13**	**25.03**	**100.00**	

(8.8%), and *Onthophagus fracticornis* (5.6%) as dominant ones. Subdominant species comprised: *Aphodius prodromus* (3.8%), *A. foetens* (2.4%), *A. distinctus* (2.1%), *Onthophagus similis* (1.4%), and *Aphodius coenosus* (1.3%). The core of these communities now was supplemented by 17 accessory species, among which 3 species were absent from the first agglomeration: *Aphodius nemoralis, A. zenkeri*, and *A. sticticus* (Fig. 7). Within this agglomeration two groups were differentiated, one of which encompassed the community inhabiting the thicket stage while the other

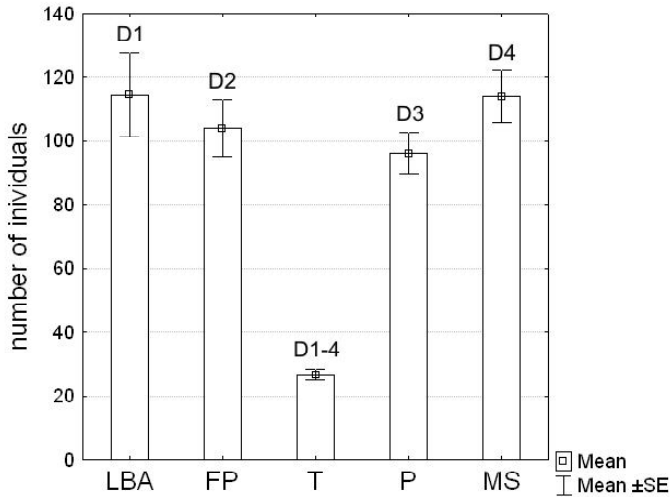

Fig. 4. Mean number of coprophagous Scarabaeidae individuals collected per trap during one season in pine stands in Człuchów Forest (legend as in Fig. 3).

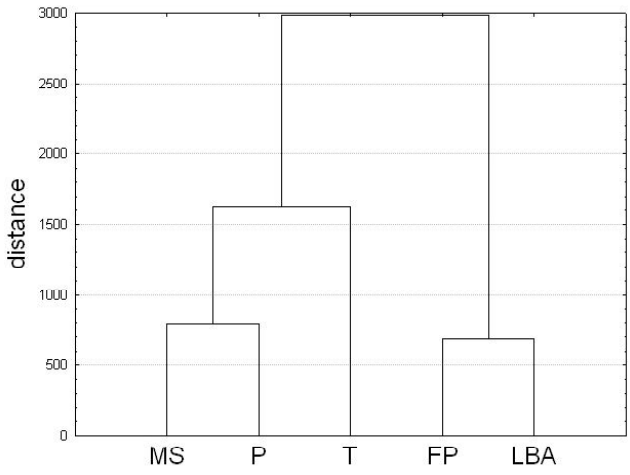

Fig. 5. Dendrogram of similarity of coprophagous Scarabaeidae communities inhabiting various phases of the developmental cycle of pine stands in Człuchów Forest (MS – mature stand, P – pole timber stage, T – thicket stage, FP – forest plantation, LBA – land before afforestation)

encompassed the communities of coprophagous Scarabaeidae inhabiting the pole timber stage and mature stands.

In coprophagous Scarabaeidae communities inhabiting land before afforestation and plantations as well as older stages of the pine stand development cycle, two species were dominant: *Aphodius fimetarius* and *Onthophagus fracticornis*. The mean number of *Aphodius fimetarius* individuals collected per trap in the course of one research season was highest at the plantation stage (29.2 ± 3.1) and lowest at the pole timber stage (6.0 ± 0.1). At each of the remaining stages of the pine stand developmental cycle the number of individuals of this species was similar. At the plantation stage it was 7.1 ± 1.1, in mature stands 3.7 ± 0.6, and at the pole timber stage 3.5 ± 0.5. There were confirmed differences between the number of individuals of *A. fimetarius* and *O. fracticornis* collected at the thicket stage and at the remaining stages of the pine stand developmental cycle (Fig. 8).

Solely in coprophagous Scarabaeidae communities inhabiting land before afforestation and plantations the dominant species were: *Aphodius coenosus, A. distinctus, A. prodromus,* and *Onthophagus nuchicornis*. The mean number of *Aphodius coenosus* individuals collected per trap in the course of one research season was very high at younger stages of the pine stand developmental cycle, amounting to 28.7 ± 6.2 on land before afforestation and 17,6 ± 3.9 in plantations. In mature stands the number of collected individuals of this species was 2.7 ± 0.6, and at the pole timber stage 0.4 ± 0.1. The species was not encountered at the thicket stage. The differences between the number of collected specimens of *A. coenosus* on land before afforestation and in plantations and the number of specimens collected at the pole timber stage were statistically significant. *Aphodius distinctus* was collected in high numbers in plantations (19.6 ± 3.0) and on land before afforestation (14.8 ± 1.8). At the

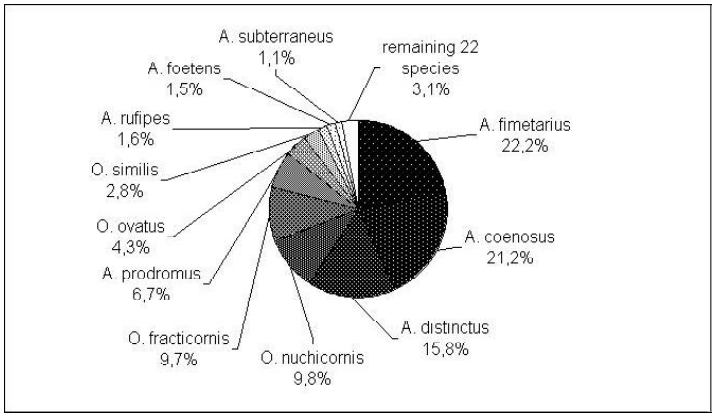

Fig. 6. Percentage of coprophagous Scarabaeidae inhabiting land before afforestation and pine plantations in Człuchów Forest

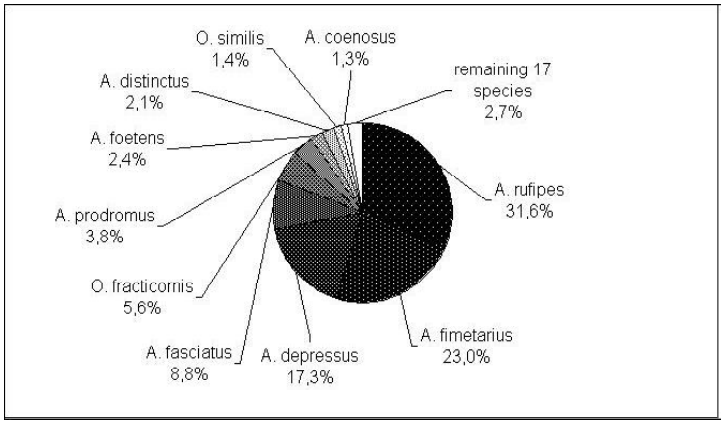

Fig. 7. Percentage of coprophagous Scarabaeidae inhabiting thicket stage, pole timber stage, and mature pine stands in Człuchów Forest

remaining stages of the forest developmental cycle the number of collected specimens of this species was very low. It was 2.8 ± 0.9 in mature stands and 1.5 ± 0.5 at the pole timber stage, whereas at the thicket stage it was merely 0.7 ± 0.3. Similarly, the number of collected specimens of *Onthophagus nuchicornis* was high on land before afforestation (11.9 ± 1.6) and in plantations (9.6 ± 1.1). At the remaining stages of the pine stand developmental cycle the number of individuals of this species was very low. In mature stands it amounted to 0.3 ± 0.2, at the thicket stage 0.2 ± 0.1, and at the pole timber stage 0.1 ± 0.06. Differences between the number of collected specimens of *A. distinctus* and *O. nuchicornis* were not statistically significant regarding land before afforestation and plantations as compared to the three older developmental stages of pine stands. The number of collected specimens of *Aphodius prodromus* was highest on land before afforestation (9.2 ± 1.5) and lowest in mature stands (5.5 ± 1.0) and plantations (5.5 ± 0.7). Moreover, it was also clearly lower in pine stands with dense crowns, at the pole timber stage (2.4 ± 0.5) and the thicket stage (1.3 ± 0.3). Statistical significance was reached regarding the difference between the number of collected specimens of *A. prodromus* at younger stages, i.e. land before afforestation and plantations, and older stages, i.e. thicket and pole timber stages (Fig. 8).

Solely in coprophagous Scarabaeidae communities inhabiting the thicket, pole timber, and mature stands the dominant species were: *Aphodius rufipes*, *A. depressus,* and *A. fasciatus*. On the one hand, the mean number of *Aphodius rufipes* specimens collected per trap in the course of one research season was high in the older developmental stages of pine stands. It amounted to 39.9 ± 4.2 in mature stands as compared to 10.6 ± 1.3 at the thicket stage. On the other hand, the number of individuals of this species was low in plantations (2.0 ± 0.3) and on land before afforestation (1.7 ± 0.3). There was a confirmed difference between the number of individuals of *A. rufipes* collected at the thicket stage as compared to the remaining stages of the pine stand developmental cycle. Such difference was also seen between the pole timber stage and the two earliest stages (land before afforestation

and plantations) as well as between the mature stands and land before afforestation. The number of collected specimens of *Aphodius depressus* was very high at the two oldest stages of the pine stand developmental cycle, namely in mature stands and at the pole timber stage, whereas it was markedly lower at the thicket stage, in plantations, and on land before afforestation. The number of *A. depressus* individuals was clearly highest in mature stands (23.2 ± 3.2) and lowest in plantations (0.1 ± 0.07). It amounted to 15.7 ± 2.2 at the pole timber stage and 2.1 ± 0.4 at the thicket stage, whereas on land before afforestation it was 1.0 ± 0.4. The number of collected specimens of *Aphodius fasciatus* was highest at the pole timber stage (11.5 ± 1.4), whereas in mature stands and at the thicket stage it was lowest (0.8 ± 0.3 and 0.7 ± 0.2, respectively). There was a statistically significant difference between the number of specimens of *A. depressus* and *A.*

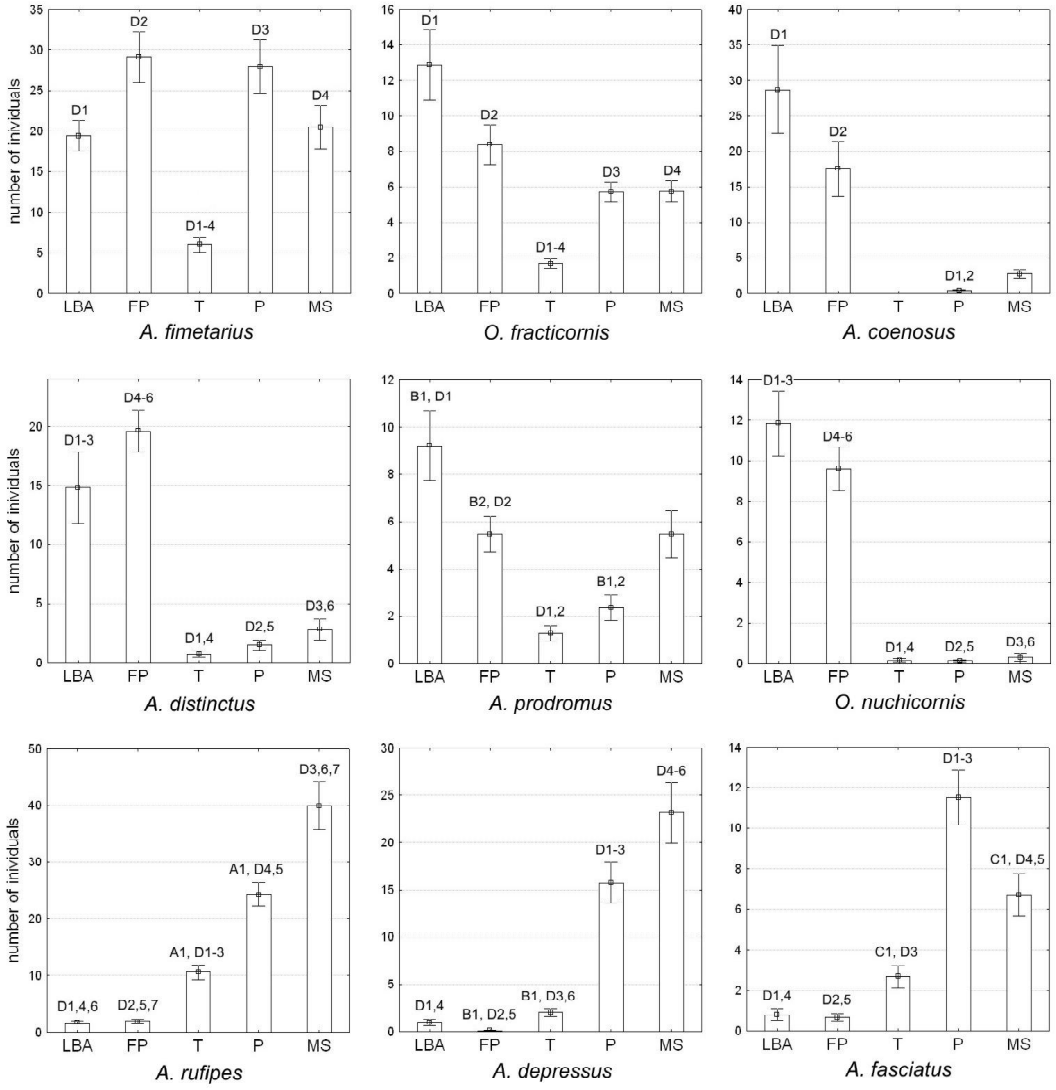

Fig. 8. Mean number of individuals of selected coprophagous Scarabaeidae collected per trap during one season in pine stands in Człuchów Forest (MS - mature stand, P - pole timber stage, T - thicket stage, FP - forest plantation, LBA - land before afforestation, SE - standard error, significance levels: A - $p<0.05$, B - $p<0.01$, C - $p<0.005$, D - $p<0.001$)

timber stage and mature stands, and the three younger stages of the pine stand developmental cycles; in the case of *A. depressus* there was also a statistically significant difference between beetle numbers of the thicket and the plantation stage (Fig. 8).

The axes of the PCA diagram describe the Eigen values as to 0.865, 0.072, 0.047, and 0.016. The cumulative percentage variance of species explains 86.5% of the variability of the first axis. On the right side of the PCA diagram there are two developmental stages: land before afforestation (LBA) and forest plantation (FP), whereas on the left side there are: pole timber stage (P), mature stands (MS), and thicket stage (T). Such arrangement suggests a succession gradient from the land before afforestation or areas at initial stages of forest development, situated on the right side of the diagram, to more mature stands situated on the left. Species of genus *Aphodius* featured on the left side of the diagram (i.e. *A. rufipes, A. zenkeri, A. fasciatus, A. depressus, A. rufus,* and *A. nemoralis*) should be considered as species associated with older tree stands characterised by the presence of a considerable degree of shade. Species of genus *Onthophagus* (*O. nuchicornis, O. ovatus, O. similes,* and *O. fracticornis*) as well as those of genus *Aphodius* featured on the right side of the diagram (i.e. *A. coenosus, A. distinctus, A. subterraneus,* and *A. sordidus*) should be considered as characteristic species of open areas, thus inhabiting brownfields, clear cuts and plantations (Fig. 9).

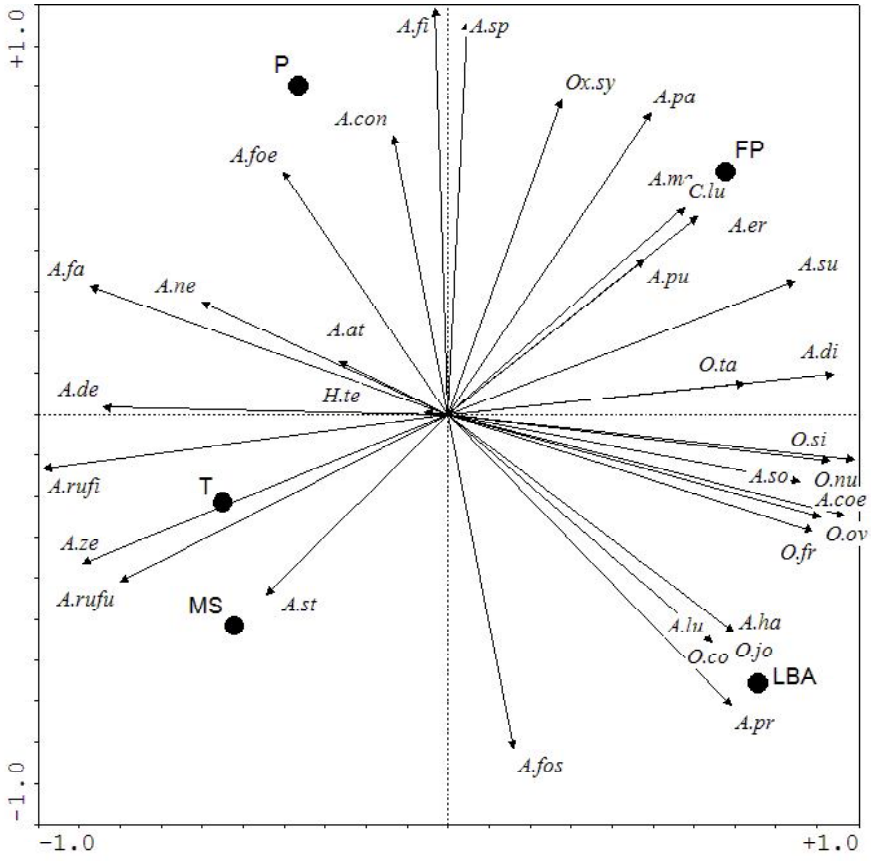

Fig. 9. Result of PCA analysis featuring Scarabaeidae communities inhabiting various stages of the pine stand developmental cycle in Człuchów Forest (legend as in Fig. 5; species abbreviations as in Tab. 2)

DISCUSSION

In pine stands of Człuchów Forest the representatives of genus *Aphodius* constitute the core of coprophagous Scarabaeidae communities. This confirms the results of research conducted in this area in the 1980s (Szyszko 1983). According to Hanski (1986), the fact results from the optimal adjustment of Aphodiinae to the climatic conditions of Central Europe. Dung beetles of genus *Aphodius* are the dominant coprophagous beetles found in temperate Northern Europe and play an essential role in the breakdown of dung and recycling of the organic matter and plant nutrients that it contains (Fry & Lonsdale 1991). On farms located in Southern Ireland, *Aphodius prodromus, A. sphacelatus, A. ater, A. rufipes,* and *A. depressus* dominate among coprophagous beetles (Hutton & Giller 2003). However, *Anoplotrupes stercorosus* (Scriba, 1791) and *Trypocopris vernalis* (Linnaeus, 1758) – species belonging to the Geotrupidae family – are the most numerous among the coprophagous representatives of the superfamily Scarabaeoidea inhabiting Człuchów Forest (Szyszko 1983, Byk 2011). In Central Europe, the abundance of coprophagous Scarabaeidae is greater in open as compared to forest areas, whereas the number of species representing the Geotrupidae family is lower (Sowig & Wassmer 1994, Wassmer 1995, Bunalski 1996a,b, Górz 2007). Similarly, considering coprophagous Scarabaeoidea, the further south in Europe the more numerous the species from the Scarabaeidae family become, both in open and forest areas, while the species from the Geotrupidae family become less numerous. In La Mandria Park in Italy the Scarabaeidae have been found to constitute 94% of the community of coprophagous Scarabaeoidea (out of which 32.5% were the Aphodiinae), whereas the Geotrupidae constituted merely 6% (Barbero et al. 1999).

The study results suggest significant differences in community abundance and species richness between the coprophagous Scarabaeidae inhabiting the thicket and the other stages of the pine stand developmental cycle. Coprophagous Scarabaeidae communities inhabiting the thicket stage are less numerous and characterised by lower species richness than the corresponding communities inhabiting land before afforestation (brownfield), land before restoration (clear cuts), as well as plantations, pole timber, and mature stands. The number of species at the time when the pine stands turn from plantation into thicket stage is reduced by nearly 50%, and the number of individuals decreases by over 70%. This means that the changes in the number of species take place by leaps rather than in a continuous manner, with the most significant reduction in numbers at the thicket stage. At the thicket stage the dense tree crowns almost entirely shade the ground, which completely changes microclimatic conditions. The coprophagous Scarabaeidae communities inhabiting tree stands up to this developmental stage comprise mainly species characteristic for open areas which, being mostly heliophilous and thermophilous, cannot find proper environmental conditions in the thicket. Furthermore, the thicket is rather slowly colonized by shade-loving forest species, and as a result the number of Scarabaeidae considerably decreases. From then on, communities comprising forest species continuously thrive and an increase in the number of species by over 50% at the pole timber stage and in mature stands can be observed as a result. Meanwhile, the number of individuals increases by more than 2.5 times. Even though the coprophagous Scarabaeidae communities inhabiting land before afforestation and plantations as well as pole timber and mature stands are similarly abundant with regard to the number of individuals and the number of species, they differ with respect to species composition. Differences in the structures of coprophagous Scarabaeidae communities inhabiting open areas and forests have been pointed out by Wassmer (1995). In the pasture that he investigated, in the part with no trees, the following species were dominant: *Aphodius granarius* (16%), *A. prodromus* (10%), *A. rufus* (8%), *A. fimetarius* (8%), *A. sticticus* (7%), *Onthophagus fracticornis* (7%), *O. ovatus* (7%), and *Oxyomus sylvestris* (5%). However, in the part of the pasture where trees grew, dominant species comprised: *Aphodius rufus* (15%), *A. sticticus* (14%), *Oxyomus sylvestris* (14%), *Aphodius fimetarius*

(9%), *A. granarius* (7%), *A. pusillus* (6%), and *Onthophagus vacca* (5%).

Analysis of the dominance structure of coprophagous Scarabaeidae communities inhabiting pine stands in Człuchów Forest resulted in the determination of two community types. One can be encountered on land before afforestation and in plantations – these are heliophilous Scarabaeidae communities inhabiting pine stands. The other type of coprophagous Scarabaeidae communities inhabits the thicket and pole timber stages as well as mature stands – these are umbrophilous Scarabaeidae communities inhabiting pine stands. A major criterion for distinguishing these two groups from each other is the replacement of species characteristic for open areas by forest species in the role of dominants. Heliophilous communities of coprophagous Scarabaeidae are characterised by the presence of the following species as dominants: *Aphodius coenosus, A. distinctus, A. fimetarius, A. prodromus, Onthophagus nuchicornis,* and *O. fracticornis.* Average participation of these species in coprophagous Scarabaeidae communities is 84.7% on land before afforestation, 86.4% in plantations, 36.9% at the thicket stage, 39.5% at the pole timber stage, and 33% in mature stands. Another characteristic feature of heliophilous communities of coprophagous Scarabaeidae is the presence of specific species not recorded at the thicket stage and older developmental stages of tree stands. These species are: *Aphodius erraticus, A. granarius, A. haemorrhoidalis, A. luridus, A. merdarius, Rhyssemus germanus, Copris lunaris, Onthophagus coenobita,* and *O. joannae*. They render the coprophagous Scarabaeidae communities of brownfields, clear cuts, and pine plantations in Człuchów Forest comparable to coprophagous Scarabaeidae communities inhabiting lowland and highland pastures of Poland. Analysing the faunistic material collected on pastures in the surroundings of Szamotuły near Poznań, Bunalski (1996a, b) has pointed out the dominant role of the representatives of the Aphodiinae subfamily in the composition of coprophagous Scarabaeoidea communities, as they constituted 28% to 99% of the total community abundance. Dominant species in the communities encountered in the neighbourhood of Szamotuły were *Aphodius fimetarius, A. distinctus, A. prodromus,* and less frequently also *A. pusillus, A. subterraneus,* and *A. haemorrhoidalis*. Similarly, while investigating the composition of coprophagous beetle communities on the pastures of Kraków-Częstochowa Upland, Górz (2007) observed that the dominant role in these communities was played by individuals of genus *Aphodius*, i.e.: *A. fimetarius, A. prodromus, A. pusillus, A. erraticus,* and less frequently also *A. haemorrhoidalis* and *A. rufus*. In addition, among the coprophagous Scarabaeoidea encountered in the Pieniny mountains the most abundant were *Aphodius fimetarius* and *A. haemorrhoidalis* (Stebnicką 1976b), and, in Trzebnickie Hills, *Aphodius prodromus, A. rufipes,* and *A. sphacelatus* (Żuk 2005).

Umbrophilous communities of coprophagous Scarabaeidae inhabiting pine stands are characterised by the presence of *Aphodius rufipes* in the role of a superdominant, and species such as *A. fimetarius, A. depressus, A. fasciatus,* and *Onthophagus fracticornis* as dominants. The mean share of these species in coprophagous Scarabaeidae communities amounted to 31.2% on land before afforestation, 38.7% in plantations, 86.4% at the thicket stage, 88.7% at the pole timber stage, and 84.3% in mature stands. *A. depressus* and *A. fasciatus* are strongly associated with the forest environment (Szwałko 1995, Żuk 2005, Bunalski 2006, Górz 2007). The preference for forest areas shown by the eurytopic species *Aphodius rufipes* has been pointed out by Rainio (1966), Hanski & Koskela (1977), and Wassmer (1995). Another characteristic feature of umbrophilous communities of coprophagous Scarabaeidae is the presence of specific species not encountered on land before afforestation and in plantations, i.e.: *Aphodius nemoralis, A. zenkeri,* and *A. sticticus.* Strong association of these species with the forest environment has also been pointed out by studies conducted in Białowieża Primeval Forest, where *Aphodius zenkeri* is not only strongly associated with the forest environment but solely encountered in

large and dense forest complexes displaying characteristic features of a primeval forest (Szwałko 1995). Wassmer et al. (1994) and Wassmer (1995) have declared forests to be the only type of environment providing proper living conditions for this species. *Aphodius nemoralis* and *A. sticticus* have been observed to settle in forest areas of the eastern border of Poland (Bunalski 2006) and Kraków-Częstochowa Upland (Górz 2007) while *A. sticticus* has also been observed to inhabit Trzebnickie Hills (Żuk 2005), the surroundings of Freiburg, Germany (Wassmer 1995), and Sweden (Landin 1961).

Significant differences in the abundance of particular species dominating at particular stages of the pine stand developmental cycle have been frequently observed. The numbers of collected specimens of *Aphodius fimetarius* and *O. fracticornis* were comparable at the initial and final stages of the pine stand developmental cycle, except for the thicket stage. The difference between the numbers of collected individuals of both species at the thicket and the remaining stages was significant. The abundance of *Aphodius coenosus* was high at the first two stages of the pine stand developmental cycle and low at the two oldest stages of forest development. No specimens of the species were collected at the thicket stage. In the case of this species the difference between the number of individuals collected on land before afforestation or in plantations and at the timber pole stage was significant. The abundance of another two species, *Aphodius distinctus* and *Onthophagus nuchicornis*, underwent similar changes, i.e. it was high at the two initial stages of the developmental cycle and low at the remaining three stages. The differences were statistically significant. Furthermore, statistical significance was revealed regarding the difference between the numbers of *Aphodius prodromus* specimens collected at the initial forest developmental stages, i.e. on land before afforestation and in plantations, and further developmental stages, i.e. thicket and pole timber stages. The species in question was collected in large numbers at the first two stages of the pine stand developmental cycle before its abundance dramatically decreased at the thicket stage but gradually rose again at the pole timber and mature stand stages. The abundance of another three species, *Aphodius rufipes*, *A. depressus*, and *A. fasciatus*, was low at the initial stages and high at the final developmental stages of pine stands. A difference between the number of specimens of *Aphodius rufipes* collected at the thicket stage and the remaining stages of the pine stand developmental cycle was confirmed. A statistically significant difference was also revealed between the abundance of this species at the stages of pole timber and mature stand and the stages of land before afforestation and plantation. A significant difference in the abundance of *Aphodius depressus* and *A. fasciatus* was seen between the stages of pole timber and mature stand and the first three stages of the pine stand developmental cycle. In the case of *Aphodius depressus* also the difference between thicket stage and plantation stage numbers was statistically significant.

In conclusion, the hypothesis of a gradual reduction of the number of coprophagous Scarabaeidae species in the course of pine stand maturing had to be abandoned. A reduction of the number of species, as well as individuals, of coprophagous Scarabaeidae inhabiting forest areas takes place abruptly at the thicket stage. At this stage of the pine stand developmental cycle, due to considerable shading of the ground surface, heliophilous and thermophilous species of genera *Onthophagus* and *Aphodius* retreat, being replaced by shade-loving species of genus *Aphodius*. Species characteristic for early stages of succession become replaced by species characteristic for later stages of succession. As a result, at the thicket stage the species composition and community structure are being reshaped, changing from those typical of the early stages of the forest developmental cycle to those typical of later stages. Such restructuring allows for an abrupt rise in abundance of coprophagous Scarabaeidae under microclimatic conditions characteristic for more mature tree stands. Considerable differences in species composition of communities inhabiting plantations, thicket and mature stands are also suggested by the evalua-

tion of preferences shown by particular species for particular developmental stages of tree stands conducted by means of PCA, as well as the evaluation of faunistic similarity of coprophagous Scarabaeidae communities inhabiting various stages of the forest developmental cycle by means of cluster analysis, using Ward's method. These two independent analyses have shown a considerable difference between coprophagous Scarabaeidae communities inhabiting areas with no trees and areas with trees providing shade. The presence of a group of species encountered solely in clear cuts and forest plantations (*Aphodius erraticus, A. granarius, A. haemorrhoidalis, A. merdarius, A. luridus, Onthophagus coenobita, O. joannae, Rhyssemus germanus, Copris lunaris*) among coprophagous Scarabaeidae inhabiting forest areas, as well as the absence of species encountered solely at thicket, pole timber, and mature stand stages (*Aphodius zenkeri, A. nemoralis, A. sticticus*) can prove useful in future monitoring studies. The presence of species belonging to the first of these groups, or the absence of species belonging to the second, in a beetle community inhabiting tree stands at more mature developmental stages may suggest that the tree stands in question have been thinned out excessively.

CONCLUSIONS

The number of species and abundance of coprophagous Scarabaeidae communities inhabiting pine stands abruptly decreases in the course of development from the plantation to the thicket stage and then again increases at the pole timber and mature stand stage.

Brownfields, clear cuts and plantations are inhabited by heliophilous communities of coprophagous Scarabaeidae characteristic for pine stands with *Aphodius fimetarius, A. coenosus, A. distinctus, A. prodromus, Onthophagus nuchicornis,* and *O. fracticornis* as dominant species.

Thicket, pole timber, and mature stand stages are inhabited by umbrophilous communities of coprophagous Scarabaeidae species characteristic for pine stands with *Aphodius rufipes, A. fimetarius, A. depressus, A. fasciatus,* and *Onthophagus fracticornis* as dominant species.

The structure of coprophagous Scarabaeidae communities inhabiting pine stands changes in the course of the forest developmental cycle. The process culminates at the thicket stage, when heliophilous species are replaced by umbrophilous ones and practicoles are replaced by silvicoles.

Obligatory silvicoles among coprophagous Scarabaeoidea are *Aphodius zenkeri, A. nemoralis,* and *A. fasciatus.*

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