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Increase of Mean Individual Biomass (MIB) of Carabidae (Coleoptera) in relation to succession in forest habitats *

Wzrost średniej biomasy osobniczej (SBO) biegaczowatych (Coleoptera: Carabidae) w sukcesji środowisk leśnych

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ABSTRACT: The applicability of Mean Individual Biomass (MIB) of Carabidae as an indicator of succession stage was tested on 35 forest stands in western Poland. The differences in MIB values as well as similarity indices (Jaccard index, Wainstein index) were calculated between two inventories at the study sites separated by a time span of 13 years. The hypotheses were set that (1) MIB values increase with time on the study areas and (2) the differences in MIB values are negatively correlated with the corresponding similarity indices. The results show an increase in numbers of species and individuals of big sized carabids in the total samples. MIB values increase at the vast majority (85.7%) of the individual study sites between the two inventories. The increase in MIB shows a significant negative correlation with both similarity indices. The correlation is more pronounced when using the Wainstein index. The results verify the applicability of MIB of Carabidae as an indicator of stage of succession. Based on the results we suggest MIB as a useful tool in forest research and forest management.

KEY WORDS: Coleoptera, Carabidae, MIB, monitoring, sustainable management, forestry.

Introduction

Succession is defined as a non-seasonal, directional and continuous pattern of colonisation and extinction of species populations in a given area (BEGON et al. 1991). Depending on the environmental conditions the process of succession may run faster or slower in different habitats. With respect to an ecologically sound management of ecosystems or landscapes,

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particularly with respect to their use for economic purposes, like agriculture or forestry, it is often required to establish special stages of succession (KOIVULA, NIEMELÄ 2002; DU BUS DE WARNAFFE, LEBRUN 2004; SZYSZKO 2004; LINDENMAYER et al. 2006). This may imply the facilitation or inhibition of the successional process (e.g. BRADSHAW 1983, 1984; DOBSON et al. 1997). However, to deal with such tasks means to be able to identify the stage as well as the speed of succession on the areas under consideration.

According to the definition above, the process of succession should be characterised by a change in species coenoses, because the species characteristic of young stages of succession should be substituted by the species characteristic of advanced stages of succession. With respect to carabid beetles such patterns have been demonstrated, for example, on recultivated brown coal mining sites (e.g. NEUMANN 1971; VOGEL, DUNGER 1991) or after reforestation of forests (e.g. SZYSZKO 1990; BAGUETTE, SYLVAINE 1993; MAGURA et al. 2002). Carabid beetles of young stage of succession are commonly described as comparatively small with a high power of dispersal, whereas in advanced stages of succession larger species with lower power of dispersal become dominant (e.g. SZYSZKO 1990; MAGURA et al. 2002).

Mean Individuals Biomass (MIB) of carabid fauna has been proposed as a good indicator of the stage of succession (SZYSZKO 1990; SZYSZKO et al. 2000). The calculation of MIB means the sum of biomass of all carabid individuals collected at an area under study divided by the total number of individuals. According to the observation that in habitats of advanced stage of succession carabid species with large individuals become dominant, MIB increases as the succession progresses. Even if MIB has already been applied successfully in different European countries (e.g. SZYSZKO et al. 1996; SERRANO, GALLEGO 2004; SCHWERK et al. 2006), this method does not seem to have been generally recognised up to now. Therefore, the present paper is an attempt to prove the indicatory significance of MIB. Based on the theoretical background, the following assumptions may be formulated:

(1) Comparing two inventories carried out at the study site at different times, big sized carabids should be more dominant in the later inventory. As a result MIB should increase, too.
(2) Succession may be quantified by calculating similarity indices between two inventories carried out at the study site at different times. The lower the similarity between the two inventories is, the higher the difference in the stage of succession, i.e. the faster the process of succession in the area. In the case of MIB acting as an indicator of the process of succession, the difference (increase) in MIB values on the study area between the two inventories should be the more pronounced the faster the pro-

cess of succession runs. Therefore, the difference in MIB should be negatively correlated with the calculated similarity on the area between the two inventories.

In the present study the carabid fauna of 35 forest stands is analysed comparing two inventories separated by a time interval of 13 years. Differences in MIB values as well as similarities between the two inventories are calculated for each study site. The hypotheses are tested that (1) MIB values increase with time on the study areas and (2) the differences in MIB values are negatively correlated with the corresponding similarity indices.

Material and Methods

Study sites and sampling methods

The study was carried out on sampling plots located in the Tuczno Forest District in the Regional Directorate of State Forests in Piła (western Poland). In this area a long-term study on carabid beetles at 91 forest stands of different stage of succession has been carried out since 1989. The study sites are mainly pine forests growing on poor sandy soil, but mixed forests and deciduous forests are included, too. More detailed information about the study areas is provided by RYLKE and SZYSZKO (2002) and SCHWERK and SZYSZKO (2005).

The data analysed in this study were chosen with the aim to maximise the time span between the compared samples. During the year 2003 a strong reduction in numbers of individuals was observed. In that year a chemical combat against the Nun moth – *Lymantria monacha* (L.) was carried out on a part of the study areas and a side effect on the carabid beetles at those areas cannot be excluded. Therefore, the data elaborated in the years 1989 and 2002 were analysed.

In order to be included in the analyses, the study sites were subject to two restrictions: first, in both years the number of collected carabids should not fall below 50 individuals, because with decreasing number of individuals the MIB values become inaccurate. Secondly, no clear cut should have been carried out between 1989 and 2002. Following these restrictions, 35 study sites were subjected to data analysis.

Collecting of beetles was carried out using pitfall traps following Barber (1931) with modifications. At each study site a Jar glass was sunk in the ground and a funnel with an upper diameter of about 10 cm and a lower diameter of about 1.6 cm was placed above it flush with the soil surface. A roof was installed a few centimetres above the funnel. Ethylene glycol was used as trapping fluid. The sampling time covered mid-May to mid-September. The traps were installed at the same position in both years.

Determination and nomenclature of the collected individuals was done according to FREUDE et al. (2004).

Statistical analysis

Mean individual biomass (MIB) of Carabidae was calculated to assess the successional stage of the sampling plots. MIB is calculated by dividing the biomass of all sampled carabids by the number of specimens caught. Biomass values were obtained using the formula of SZYSZKO (1983) that describes the relationship between the body length of a single carabid individual (x) and its biomass (y):

$$\ln y = -8.92804283 + 2.5554921 \times \ln x$$

For the calculations of MIB values, the biomass of the individuals caught were summed and subsequently divided by the total number of the individuals for the respective sample. Based on these data the difference in MIB values between the two observations was computed.

Changes in species composition were analysed using Jaccard's index of species similarity (JACCARD 1902). However, patterns of succession may be expressed by changes in the dominance values of the respective species, too. In order to consider both changes in species composition and chances in species dominances, the Wainstein index was computed (WAINSTEIN 1967).

The computed MIB values were tested on differences between the two inventories using the Wilcoxon test for paired samples. The absolute values of the differences in MIB between the two inventories were tested on correlation with the corresponding species similarities using the Spearman rank correlation coefficient (SACHS 1984).

Results

Table (Tab. I) presents total numbers of individuals of the species collected at the study sites in 1989 and 2002. Species characteristic of forests dominate in both years. However, an increase in species and numbers of big-sized forest species (e.g. *Carabus coriaceus*, *Carabus hortensis*, *Pterostichus niger*) as well as a decrease of small-sized species (e.g. *Leistus terminatus*, *Calathus micropterus*) and the species characteristic of open habitats (e.g. *Calathus erratus*, *Calathus melanocephalus*) can be observed. The occurrence of *Carabus intricatus* in 2002, which was not detected on the study areas in 1989, is worth mentioning.

The numbers of species, individuals and MIB values for both years as well as the differences in MIB between the two inventories and the calculated similarity values (Jaccard index, Wainstein index) are shown in table (Tab. II). MIB values increase significantly at the study sites (Wilcoxon test

for paired samples, $p < 0.001$). Solely at 5 of the 35 study sites the MIB value decreased from 1989 to 2002. At the remaining 30 study sites (85.7%) the MIB value increases, with the increase ranging from 5.9 mg to 242.3 mg.

The calculated values for similarity values range from 10.5% to 83.3% (Jaccard index) and from 0.3% to 57.6% (Wainstein index).

The relationship between the absolute values of differences in MIB between the two inventories and the similarity values are shown in figure (Fig.). For both similarity indices a significant negative correlation exists. However, this correlation is more pronounced for the Wainstein index (Spearman rank correlation coefficient $r_s = -0.645$, $p < 0.001$) when compared to the Jaccard index (Spearman rank correlation coefficient $r_s = -0.489$, $p < 0.01$).

Tab. I. Numbers of individuals of the species collected at the study sites in 1989 and 2002 ordered by theoretical biomass of a single individual. Biomass values were calculated according to SZYSZKO (1983)

Liczba osobników gatunków odłowionych w roku 1989 i 2002 (w kolejności wyznaczonej wielkością teoretycznej biomasy pojedynczego osobnika). Wartości biomasy przyjęto za SZYSZKO (1983)

Species Gatunek	Biomass Biomasa [mg]	Individuals Osobniki (1989)	Individuals Osobniki (2002)
1	2	3	4
Carabus coriaceus LINNAEUS, 1758	1742	1	80
Carabus violaceus LINNAEUS, 1758	750	366	395
Carabus intricatus LINNAEUS, 1761	700		16
Carabus hortensis LINNAEUS, 1758	548	303	420
Carabus problematicus HERBST, 1786	454	52	70
Carabus nemoralis O. F. MÜLLER, 1764	400	72	137
Carabus cancellatus ILLIGER, 1798	317	-	1
Broscus cephalothes (LINNAEUS, 1758)	281	1	-
Pterostichus niger (SCHALLER, 1783)	220	1735	2015
Carabus arvensis PAYKULL, 1790	219	29	7
Dolichus halensis (SCHALLER, 1783)	160	-	1
Harpalus rufipes (DE GEER, 1774)	126	4	2
Poecilus lepidus (LESKE, 1785)	84	48	-
Calathus fuscipes (GOEZE, 1777)	76	1	4
Amara equestris (DUFTSCHMID, 1812)	61	10	-
Harpalus solitaris DEJEAN, 1829	61	1	-

1	2	3	4
Harpalus laevipes ZETTERSTEDT, 1828	61	4	3
Pterostichus oblongopunctatus (FABRICIUS, 1787)	57	1153	1012
Poecilus versicolor (STURM, 1824)	56	2	2
Harpalus affinis (SCHRANK, 1781)	49	1	-
Calathus erratus (C. R. SAHLBERG, 1827)	46	155	10
Harpalus smaragdinus (DUFTSCHMID, 1812)	46	2	-
Harpalus latus (LINNAEUS, 1758)	45	10	5
Harpalus rufipalpis STURM, 1818	41	1	-
Leistus rufomarginatus (DUFTSCHMID, 1812)	36	1	5
Cymindis vaporarium (LINNAEUS, 1758)	27	2	-
Leistus ferrugineus (LINNAEUS, 1758)	25	103	9
Leistus terminatus (HELLWIG, 1793)	25	433	3
Amara lunicollis SCHIODTE, 1837	19	-	1
Calathus melanocephalus (LINNAEUS, 1758)	19	100	6
Calathus micropterus (DUFTSCHMID, 1812)	19	1213	359
Amara curta DEJEAN, 1828	13	1	-
Agonum fuliginosum (PANZER, 1797)	13	-	9
Pterostichus strenuus (PANZER, 1797)	13	1	1
Notiophilus aquaticus (LINNAEUS, 1758)	7	-	9
Notiophilus biguttatus (FABRICIUS, 1779)	7	1	2
Notiophilus palustris (DUFTSCHMID, 1812)	7	-	2

Discussion

The results significantly verify both hypotheses. This leads to the conclusion that MIB indeed may be used as an indicator of the stage of succession. With progress of succession the MIB values increase, expressed by an increase in numbers of species and individuals of big-sized carabids in the total samples and an increase in MIB in a vast majority of individual study sites from 1989 to 2002. The more pronounced this increase, the higher the difference in stage of succession, i.e. the faster the process of succession runs. When using the Jaccard index, the latter statement is supported rather weakly. However, the correlation becomes stronger taking into account not only the changes in species but also the changes in dominance values, i.e. using the Wainstein index. Succession may involve both aspects as described for carabid beetles after clear-cutting, for example by SZYSZKO (1990), KO-

Tab. II. Numbers of species, individuals and MIB values for both years as well as the differences in MIB between the 1989 and 2002 and calculated similarity values (Jaccard index, Wainstein index) – numbering of study sites according to RYLKE and SZYSZKO (2002)

Liczba gatunków i osobników oraz wartość SBO dla obu sezonów badawczych a także różnice w wartości SBO pomiędzy rokiem 1989 i 2002 oraz wartości podobieństwa (wskaźnik Jaccarda i wskaźnik Wainsteina) – numeracja stanowisk badawczych według RYLKE i SZYSZKO (2002)

Study site Stanowiska bad.	Number of species Liczba gatunków		Number of individuals Liczba osobników		MIB SBO [mg]		MIB diff. różnice w SBO [mg]	Jaccard Index Wsk. Jaccarda	Wainstein Index Wsk. Wainsteina
	1989	2002	1989	2002	1989	2002			
1	2	3	4	5	6	7	8	9	10
2	11	7	163	117	234.8	377.9	143.1	38.5	23.4
4	9	7	242	64	167.4	237.3	69.9	60.0	33.1
7	6	7	69	143	276.9	177.8	– 99.1	62.5	26.9
9	7	9	142	78	158.8	221.8	63.0	60.0	42.3
10	10	9	219	174	160.8	209.7	48.9	46.2	24.5
11	8	6	61	61	207.4	242.4	35	40.0	28.8
12	7	7	86	113	218.2	280.3	62.1	55.6	31.0
14	10	11	217	197	300.9	326.7	25.8	50.0	31.8
16	7	10	180	151	227.9	328.3	100.4	54.5	32.0
18	9	7	125	136	204.7	319.6	114.9	60.0	32.1
19	10	6	99	106	331.7	221.1	– 110.6	45.5	27.7
21	8	5	128	169	290.9	353.5	62.6	62.5	43.2
22	7	8	164	172	340.5	346.4	5.9	66.7	57.6
33	6	9	52	97	99.2	313.6	214.4	36.4	14.7
37	11	5	246	82	206.9	320.9	114	33.3	21.6
39	5	6	68	95	267.1	256.0	– 11.1	83.3	73.1
43	10	6	94	71	171.9	268.0	96.1	33.3	15.9
45	9	12	63	118	67.1	280.3	213.2	10.5	0.3
50	10	9	207	123	101.2	98.0	– 3.2	58.3	31.6
51	8	7	142	54	64.8	258.9	194.1	50.0	25.4
52	8	8	98	122	169.4	198.5	29.1	60.0	21.4
54	5	6	66	58	115.8	342.2	226.4	37.5	17.7
60	7	9	135	55	140.7	361.5	220.8	45.5	21.4
67	5	7	94	124	236.4	244.8	8.4	50.0	44.6

1	2	3	4	5	6	7	8	9	10
69	8	9	84	71	148.0	163.0	15.0	30.8	15.8
72	8	9	332	145	128.8	272.6	143.8	54.5	28.4
73	10	13	102	247	190.4	217.9	27.5	53.3	31.0
74	11	11	199	335	52.0	294.3	242.3	37.5	2.0
75	12	8	495	74	115.9	238.3	122.4	53.8	26.2
76	7	10	150	213	203.9	336.5	132.6	41.7	22.6
77	9	13	627	213	115.1	237.3	122.2	46.7	28.3
78	9	9	218	188	146.1	335.3	189.2	50.0	28.7
79	8	9	237	186	168.5	379.3	210.8	41.7	21.9
85	10	7	110	104	207.8	244.5	36.7	41.7	31.0
87	6	7	92	130	280.1	265.8	– 14.3	62.5	52.9

IVULA and NIEMELÄ (2002) and SKŁODOWSKI (2006). The changes in species composition as well as species' abundances after disturbance in forests are regarded as a common principle in carabids (RAINIO, NIEMELÄ 2003). However, populations of single species may fluctuate and even get extinct at local plots due to population dynamics processes independent from succession (DEN BOER 1968; HANSKI 1998).

A decrease of MIB between the two years, as observed on the five study sites, may point to a degradation of the habitat. At four of those sites a very high MIB value was already established in 1989. Moreover, at three of them the decrease in MIB is of very low value (<15 mg), so that a rather stable situation may be assumed. Accordingly, the similarity indices show comparatively high values (Tab. II).

Other factors may have an impact on body sizes in carabid coenoses, too. Of special importance for survival of a population is the dispersal power of the respective species (DEN BOER 1990a, 1990b), which is often low in big-sized carabids. This implies a possible reduction of large species in the remaining habitat patches in fragmented landscapes. MAGURA et al. (2006) observed a relation of body size distributions related to habitat alteration caused by urbanisation. With increasing habitat change caused by urbanisation a dominance of smaller carabid beetles was observed. Disturbance caused by urbanisation leads to a dominance of small-sized carabids. However, with respect to forestry practices for example, a process like clear cutting may be regarded as disturbance, which degrades the forest to an early stage of succession. Degraded habitats are characterised by small MIB (SZYSZKO et al. 2000). BLAKE et al. (1994) found greater body sizes for carabids in woodland

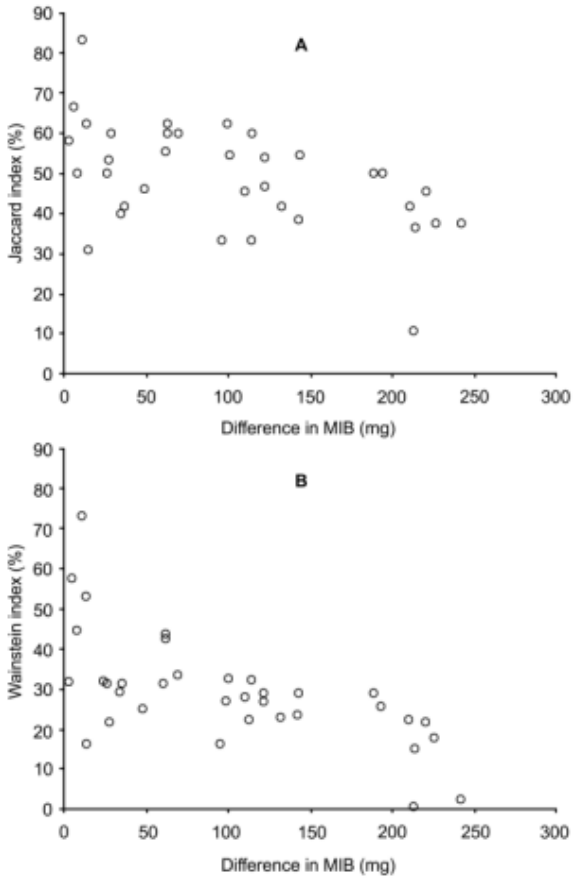

Fig. Relationship between the difference in MIB [mg] and corresponding Jaccard indices (A) (Spearman rank correlation coefficient $r_s = -0.489$, $p < 0.01$) and Wainstein indices (B) (Spearman rank correlation coefficient $r_s = -0.645$, $p < 0.001$)

Ryc. Zależność pomiędzy SBO [mg] i odpowiadającym wartościom wskaźnika Jaccarda (A) (test korelacji Spearmana $r_s = -0.489$, $p < 0.01$) oraz wartościom wskaźnika Wainsteina (B) (test korelacji Spearmana $r_s = -0.645$, $p < 0.001$)

or moorland habitats than in grassland. In the grassland areas carabid body size decreased with increasing management intensity. Management intensity was rated on a scale from 1 to 5, amongst others taking into account the age of pasture and the intensity and duration of grazing, factors of importance when concerning the stage of succession.

Rigorous monitoring is an important component of ecologically sustainable forest management (LINDENMAYER et al. 2006). In our opinion, the present study demonstrates that MIB of Carabidae can be used as indicator of

the stage of succession of a habitat. An advantage not to neglect is that identification of species is not necessary. Therefore, basic taxonomic knowledge is sufficient to elaborate the data. Moreover, using the presented formula for calculation of biomass it is possible to elaborate on MIB values from "historical" material (e.g. old publications). To conclude, MIB can be a useful tool in forest research and forest management.

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STRESZCZENIE

Mając na uwadze ekologiczny aspekt gospodarowania ekosystemami i krajobrazami winniśmy wspierać się rozpoznawaniem stadiów sukcesji środowisk oraz szybkością procesów sukcesyjnych. Proponowanym wskaźnikiem do identyfikacji stadium sukcesji środowiska jest średnia biomasa osobnicza (SBO). Jednakże, nawet jeśli fauna biegaczowatych była stosowana z powodzeniem do tego celu w różnych krajach europejskich metoda ta dotąd nie została dostatecznie rozpoznana i zweryfikowana. Artykuł jest próbą dowiedzenia znaczenia bioindykacyjnego SBO.

Zastosowanie średniej biomasy osobniczej (SBO) biegaczowatych jako wskaźnika zaawansowania sukcesji przyrodniczej było testowane na 35 powierzchniach badawczych w zachodniej części Polski. Oznaczano dla nich wartości SBO i wskaźniki podobieństwa (wskaźnik Jaccarda i wskaźnik Wainsteina) porównując ze sobą dane uzyskane podczas dwóch sezonów na przestrzeni 13 lat. Materiały do obliczeń zebrano używając po jednej pułapce chwytnej dla każdej powierzchni badawczej. W każdym roku badań lokalizacja pułapek była identyczna. Założono hipotezy, iż: (1) wartości SBO będą wzrastać w czasie na każdej powierzchni badawczej, (2) zróżnicowanie SBO jest negatywnie skorelowane z różnicami oznaczanych wskaźników podobieństwa.

Łączne wyniki dla wszystkich prób wskazują na wzrost liczby gatunków leśnych o większych rozmiarach ciała (np. *Carabus coriaceus*, *Carabus hortensis*, *Pterostichus niger*) oraz na spadek ilości gatunków o małych rozmiarach ciała jak *Leistus terminatus*, *Calathus micropterus* i gatunków charakterystycznych dla terenów otwartych (np. *Calathus erratus*, *Calathus melanocephalus*). Po porównaniu wyników uzyskanych w dwu okresach czasu, wykazano, że wartości SBO wzrastają dla znakomitej większości (85,7%) stanowisk (wartość testu Wilcoxona dla porównywanych par stanowisk $p < 0.001$). Wzrost SBO wskazuje na wyraźnie negatywną korelację z obu obliczonymi wskaźnikami podobieństwa. Korelacja jest bardziej wyraźna dla wskaźnika Wainsteina (test korelacji Spearmana $rs = -0.645$, $p < 0.001$) niż dla porównanego wskaźnika Jaccarda (test korelacji Spearmana $rs = -0.489$, $p < 0.01$).

Wyniki wyraźnie weryfikują obie hipotezy. To prowadzi do wniosku, że SBO rzeczywiście może być użyte jako wskaźnik stadium sukcesji. Przy czym, do opracowania danych wystarczająca jest tylko elementarna wiedza z zakresu taksonomii. Co więcej, używając zaprezentowanej formuły dla obliczeń biomasy możliwe jest uzyskanie retrospektywnych wartości SBO obliczonych na podstawie materiałów historycznych (np. stare publikacje). Wskaźnik SBO może być wykorzystany jako użyteczne narzędzie w badaniach z zakresu nauk leśnych i w gospodarce leśnej.

REFERENCES

BAGUETTE M., SYLVAINE G. 1993: Effects of spruce plantations on carabid beetles in southern Belgium. Pedobiol., **37**: 129-140.

BARBER H. S. 1931: Traps for cave inhabiting insects. J. Mitchel. Soc., **46**: 259-266.

BRADSHAW A. D. 1983: The reconstruction of ecosystems. J. Appl. Ecol., **20**: 1-17.

BRADSHAW A. D. 1984: Ecological principles and land reclamation practice. Landscape Plan., **11**: 35-48.

BEGON M., HARPER J. L., TOWNSEND C. R. 1991: Ökologie. Individuen, Populationen und Lebensgemeinschaften. Birkhäuser Verlag, Basel, Boston, Berlin. 1024 pp.

BLAKE S., FOSTER N. G., EYRE M. D., LUFF M. L. 1994: Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiol., **38**: 502-512.

DEN BOER P. J. 1968: Spreading of risk and stabilization of animal numbers. Acta Biotheor., **18**: 165-194.

DEN BOER P. J. 1990a: Density limits and survival of local populations in 64 carabid species with different powers of dispersal. J. Evolution. Biol., **3**: 19-48.

DEN BOER P. J. 1990b: The survival value of dispersal in terrestrial arthropods. Biol. Conserv., **54**: 175-192.

DOBSON A., BRADSHAW A. D., BAKER A. J. M. 1997: Hopes for the future: restoration ecology and conservation biology. Science, **277**: 515-522.

DU BUS DE WARNAFFE G., LEBRUN P. 2004 : Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. Biol. Conserv., **118**: 219-234.

FREUDE H., HARDE K. -W., LOHSE G. A., KLAUSNITZER B. 2004: Die Käfer Mitteleuropas. Bd. 2, Adephaga 1, Carabidae (Laufkäfer). (2. (erweiterte) Aufl.). Spektrum-Verlag, Heidelberg/Berlin. 521 pp.

HANSKI I. 1998: Metapopulation dynamics. Nature, **396**: 41-49.

JACCARD P. 1902: Lois de distribution florale dans la Zone alpine. Bull. Soc. Vaud. Sci. Nat., **38**: 69-130.

KOIVULA M., NIEMELÄ J. 2002: Boreal carabid beetles (Coleoptera, Carabidae) in managed spruce forests – a summary of Finnish case studies. Silva Fenn., **36**: 423-436.

LINDENMAYER D. B., FRANKLIN J. F., FISHER J. 2006: General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv., **131**: 433-445.

MAGURA T., ELEK Z., TÓTHMÉRÉSZ B. 2002: Impacts of non-native spruce reforestation on ground beetles. Eur. J. Soil. Biol., **38**: 291-295.

MAGURA T., TÓTHMÉRÉSZ B., LÖVEI G. 2006: Body size inequality of carabids along an urbanisation gradient. Basic Appl. Ecol., **7**: 472-482.

NEUMANN U. 1971: Die Sukzession der Bodenfauna (Carabidae [Coleoptera], Diplopoda und Isopoda) in den forstlich rekultivierten Gebieten des Rheinischen Braunkohlenreviers. Pedobiol., **11**: 193-226.

RAINIO J., NIEMELÄ J. 2003: Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers. Conserv., **12**: 487-506.

RYLKE J., SZYSZKO J. (eds.) 2002: Didactics trails for field classes on evaluation and assessment of natural resources. Warsaw Agricultural University Press, Warsaw. 167 pp.

SACHS L. 1984: Angewandte Statistik: Anwendung statistischer Methoden. (6th ed.). Springer, Berlin, Heidelberg, New York, Tokyo. 552 pp.

SCHWERK A., SAŁEK P., DUSZCZYK M., ABS M., SZYSZKO J. 2006: Variability of Carabidae in time and space in open areas. Entomol. Fennica, **17**: 258-268.

SCHWERK A., SZYSZKO J. 2005: Temporal and spatial dynamics of *Carabus hortensis* L. (Coleoptera: Carabidae) in forest stands of different stage of succession. [In:] SKŁODOWSKI J., HURUK S., BARŠEVSKIS A., TARASIUK S. (eds.): Protection of Coleoptera in the Baltic Sea Region. Warsaw Agricultural University Press, Warsaw: 161-170.

SERRANO J., Gallego D. 2004: Evaluación de la regeneración y el estado de salud de las masas forestales de Sierra Espuńa (Murcia) mediante el análisis de la biomasa media individual en coleópteros carábidos. Anales de Biología, **26**: 191-211.

SKŁODOWSKI J. 2006: Anthropogenic transformation of ground beetle assemblages (Coleoptera: Carabidae) in Białowieża Forest, Poland: from primeval forests to managed woodlands of various ages. Entomol. Fennica, **17**: 296-314.

SZYSZKO J. 1983: Methods of macrofauna investigations. [In:] SZUJECKI A., SZYZSKO J., MAZUR S., PERLIŃSKI S. (eds.): The process of forest soil macrofauna formation after afforestation of farmland. Warsaw Agricultural University Press, Warsaw: 10-16.

SZYSZKO J. 1990: Planning of prophylaxis in threatened pine forest biocoenoses based on an analysis of the fauna of epigeic Carabidae. Warsaw Agricultural University Press, Warsaw. 96 pp.

SZYSZKO J. 2004: Foundations of Poland's cultural landscape protection – conservation policy. [In:] DIETERICH M., VAN DER STRAATEN J. (eds.): Cultural landscapes and land use. Kluwer Academic Publishers, The Netherlands: 95-110.

SZYSZKO J., VERMEULEN H. J. W., DEN BOER P. J. 1996: Survival and reproduction in relation to habitat quality and food availability for *Pterostichus oblongopunctatus* F. (Carabidae, Col.). Acta Jutlandica, **71**: 25-40.

SZYSZKO J., VERMEULEN H. J. W., KLIMASZEWSKI K., ABS M., SCHWERK A. 2000: Mean individual biomass (MIB) of ground beetles (Carabidae) as an indicator of the state of the environment. [In:] BRANDMAYR P., LÖVEI G., ZETTO BRANDMAYR T., CASALE A., VIGNA TAGLIANTI A. (eds.): Natural history and applied ecology of carabid beetles. Pensoft Publishers, Sofia – Moscow: 289-294.

VOGEL J., DUNGER W. 1991: Carabiden und Staphyliniden als Besiedler rekultivierter Tagebau-Halden in Ostdeutschland. Abh. Ber. Naturkundemus. Görlitz, **65**: 1-31.

WAINSTEIN B. A. 1967: Some methods of evaluation of similarity of biocoenoses. Zool. Z., **46**: 981-986.