



# Body mass distributions along successional gradients in epigeic carabid beetle fauna (Coleoptera: Carabidae)

ARMIN SCHREINER<sup>1</sup>  
ADAM KWIATKOWSKI<sup>2</sup>  
JAN SZYSZKO<sup>3</sup>  
AXEL SCHWERK<sup>3</sup>

<sup>1</sup> Am Schultenbrink 50, 45549 Sprockhövel, Germany

<sup>2</sup> Horodnianska 1, 16-020 Czarna Białostocka, Poland

<sup>3</sup> Laboratory of Evaluation and Assessment of Natural Resources, Warsaw University of Life Sciences – SGGW, Nowoursynowska Street 166 02-787 Warsaw, Poland

## Correspondence:

Axel Schwerk

E-mail: aschwerk@yahoo.de

## Nonstandard abbreviations

MIB: Mean individual biomass of Carabidae

**Key words:** MIB, succession, forest, post-industrial area, bioindication

Received December 14, 2015.

Revised May 11, 2016.

Accepted May 16, 2016.

## Abstract

**Background and purpose:** Body mass distributions may be related to the stage of succession of a habitat and provide with information for assessing successional processes. Therefore, body mass distributions of carabid assemblages were studied in three research areas, which were post-industrial areas near the city of Bełchatów (Central Poland) planted with different tree and shrub species, moist and wet forest stands in the Puszcza Knyszyńska forest (Northeastern Poland), and beech stands in the Ruhr valley (Western Germany) in order to analyze the changes in body mass distributions within single assemblages along successional gradients.

**Materials and Methods:** For each carabid assemblage, the mean individual biomass (MIB) as well as MIB standard deviation (SD) and coefficient of variation (CV) were calculated. SD and CV were plotted against the age of study sites and MIB values, respectively. Analyses of Covariance (ANCOVA) were carried out with SD and CV as dependent variables and the age of study sites and MIB as covariates.

**Results:** SD was low at young stages of succession, but increased rapidly and plateaued at advanced stages in beech but not in wet forest stands. Accordingly, CV was low at very young stages of succession, showing a rapid increase and subsequent decrease in the beech stands, whereas in the wet stands it stayed on a constant level. ANCOVA revealed significant differences in SD and CV between the research areas and significant changes with age or MIB, but, with the exception of CV as dependent variable and MIB as covariate, interactions were also significant.

**Conclusions:** The results of the study suggest that data on body mass distributions within single carabid assemblages may be useful in the assessment and comparison of successional stages and processes between different habitat types.

## INTRODUCTION

The biomass and body size of organisms have been linked to several ecological factors (e.g. 1, 2, 3, 4, 5). Lindenmayer *et al.* (6) classified species which provide much of the biomass or number of species in an area as being potential indicators of environmental conditions. Accordingly, Koivula (7) called such species “dominance indicators”. In this context, he also discussed the indicatory potential of changes in carabid body size or biomass linked to ecological processes.

Carabid beetles have been used in ecological research in different habitat types such as primeval forests, mountain ranges, or brownfields (*e.g.* 8, 9, 10). In some of these studies, the body size of the beetles or their body mass, respectively, has been analyzed, indicating that either small carabids of low body mass or large carabids of high body mass may dominate in an assemblage, depending on the environmental conditions given. It has been shown that average body size in carabid assemblages decreased with increasing disturbance (*e.g.* 11). Cárdenas & Hidalgo (12) used mean body mass differences in order to assess environmental recovery processes. Several studies deal with the mean individual biomass of Carabidae (MIB) as indicator of the stage of succession of a habitat (*e.g.* 13, 14, 15). MIB is based on the observation that in carabid assemblages smaller open-habitat species are replaced by larger forest species with ongoing succession of a habitat (13, 16). Yet, reanalyzing size trends in carabids at an abandoned fertilizer factory in Germany (17), Lövei & Magura (18) showed that, dividing carabid beetles into different functional groups with respect to their foraging strategy, the size trends indicate group-specific differences.

However, the same MIB value may result from different body mass distributions within a carabid assemblage. On the one hand, the species and individuals might cover a wide range of body masses and therefore the MIB variation may be high, whereas, on the other hand, their body masses might be fairly homogenous, resulting in a low variation of MIB. Just as assumed for the MIB value itself, the underlying body mass distributions may be related to the habitat or certain habitat characteristics. Since MIB is related to the stage of succession the body mass distribution may be, too, and may provide with additional information for assessing successional processes. Hence, the aim of this work was to study potential changes in body mass distribution patterns of epigeic carabid beetles in relation to successional stages.

In order to characterize the body mass distribution patterns we calculated the standard deviation (SD) for our samples. Since the standard deviation to a certain extent depends on the mean value we also calculated the coefficient of variation (CV), i.e. SD divided by mean.

For characterization of the successional stage we also used two measures. Generally, we may assume that succession progresses with increasing age of a study site after renaturation or afforestation. However, depending on environmental conditions, succession may proceed faster or slower. For example, in many post-industrial areas (primary) succession is delayed (19, 20, 21). Therefore, we used the age of study sites along with the MIB as an indicator of the stage of succession.

We analyzed study sites of different age in selected research areas, which were post-industrial areas located close to the city of Bełchatów (Central Poland) (22), wet forests in the Puszcza Knyszyńska (Northeastern Poland) (23),

and beech forests in the Ruhr valley (Western Germany) (24). We wanted to study the changes of SD and CV along the successional gradient as measured by the age and particularly MIB of study sites, and their potential differences between the research areas. We also wanted to test whether or not any interaction between the research area and age or MIB exists with respect to SD or CV.

## METHODS

### Research areas and field methods

A detailed description of the study sites in the three research areas is provided in Table 1.

From the industrial activity at Bełchatów of brown coal mining and electricity production two heaps of waste material originated: A heap of ashes produced by the power station, on which three sites of different age since renaturation with tree and shrub species were sampled, and a heap of stony material produced during the mining process, on which four sites (pine stands) of different age were sampled from 2004 to 2011. On each site, 3 pitfall traps were installed. Since in some samples the number of individuals was very low, data of each two consecutive years were pooled for each study site, resulting in 28 samples with an age-of-site range of 3–27 years (Appendix 1).

Puszcza Knyszyńska is one of the biggest forest complexes in Poland with an overall area of about 114,000 ha. Here, 24 study sites in wet and humid forest habitats were selected. The sampling period was 2006–2008 with 3 pitfall traps installed on each site. Since at individual study sites the traps were temporarily flooded in some years due to strong fluctuations of the water level the data of all 3 years of study were pooled for each study site, resulting in 24 samples with an age-of-site range of 3–127 years, with age defined as the age of the respective study site in 2007 (Appendix 1).

In the Ruhr valley in Western Germany, 14 sites in afforested beech forests were selected for inventory. With 3 pitfall traps on each study site, sampling was carried out in the years 2009 and 2010, resulting in 28 samples (age-of-site range from 1 to 166 years, Appendix 1).

Pitfall traps were containers topped with a funnel (upper diameter of about 10 cm) set flush with the soil surface. A roof was suspended a few cm above the funnel and ethylene glycol was used as a killing agent and preservative. Sampling times covered mid/late-April (beginning of May in 2010) to mid/late-October at Bełchatów, mid-May to late-September in Puszcza Knyszyńska, and mid-April to mid-November (2009) and early-April to mid-October (2010) in the Ruhr valley. Despite differences in exposure of the traps the main peaks of carabid activity were covered by the sampling periods in each research area.

Determination of collected individuals was carried out according to the nomenclature of Freude *et al.* (25).

**Tab. 1:** Description of the study sites in the research areas Bełchatów (BE), Puszcza Knyszyńska (PK), and Rubr valley (RV).

Study site	Description
BE1	Plantation on ash heap, dominated by robinia ( <i>Robinia pseudoacacia</i> ), sea buckthorn ( <i>Hippophæ rhamnoides</i> ), and Siberian peashrub ( <i>Caragana arborescens</i> ), about 8 years old in 2004
BE2	Plantation on ash heap, dominated by birch ( <i>Betula</i> sp.) and pine ( <i>Pinus sylvestris</i> ), about 10 years old in 2004
BE3	Plantation on ash heap, dominated by robinia ( <i>Robinia pseudoacacia</i> ) and sea buckthorn ( <i>Hippophæ rhamnoides</i> ), about 12 years old in 2004
BE4	Pine ( <i>Pinus sylvestris</i> ) plantation on spoil heap, 3 years old in 2004
BE5	Pine ( <i>Pinus sylvestris</i> ) plantation on spoil heap, 10 years old in 2004
BE6	Pine ( <i>Pinus sylvestris</i> ) plantation on spoil heap, 14 years old in 2004
BE7	Pine ( <i>Pinus sylvestris</i> ) plantation on spoil heap, 21 years old in 2004
PK1	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ), 3 years old in 2007
PK2	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ), birch ( <i>Betula pubescens</i> ), and oak ( <i>Quercus robur</i> ), 3 years old in 2007
PK3	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ) and oak ( <i>Quercus robur</i> ), 3 years old in 2007
PK4	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ), sporadically oak ( <i>Quercus robur</i> ), 4 years old in 2007
PK5	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ) and ash ( <i>Fraxinus excelsior</i> ), 7 years old in 2007
PK6	Black alder ( <i>Alnus glutinosa</i> ) and spruce ( <i>Picea abies</i> ) stand, with ash ( <i>Fraxinus excelsior</i> ) and oak ( <i>Quercus robur</i> ), 8 years old in 2007
PK7	Oak ( <i>Quercus robur</i> ) and black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ) and ash ( <i>Fraxinus excelsior</i> ), 13 years old in 2007
PK8	Mixed stand with black alder ( <i>Alnus glutinosa</i> ), oak ( <i>Quercus robur</i> ), hornbeam ( <i>Carpinus betulus</i> ), and birch ( <i>Betula pubescens</i> ), sporadically pine ( <i>Pinus sylvestris</i> ), 22 years old in 2007
PK9	Black alder ( <i>Alnus glutinosa</i> ) stand with birch ( <i>Betula pubescens</i> ), 26 years old in 2007
PK10	Black alder ( <i>Alnus glutinosa</i> ) stand with birch ( <i>Betula pubescens</i> ), ash ( <i>Fraxinus excelsior</i> ), and spruce ( <i>Picea abies</i> ), 28 years old in 2007
PK11	Black alder ( <i>Alnus glutinosa</i> ) and birch ( <i>Betula pubescens</i> ) stand with spruce ( <i>Picea abies</i> ) and ash ( <i>Fraxinus excelsior</i> ), 29 years old in 2007
PK12	Black alder ( <i>Alnus glutinosa</i> ) stand with birch ( <i>Betula pubescens</i> ), 46 years old in 2007
PK13	Birch ( <i>Betula pubescens</i> ) and black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ), 46 years old in 2007
PK14	Spruce ( <i>Picea abies</i> ) stand with pine ( <i>Pinus sylvestris</i> ) and black alder ( <i>Alnus glutinosa</i> ), sporadically oak ( <i>Quercus robur</i> ) and birch ( <i>Betula pubescens</i> ), 68 years old in 2007
PK15	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ) and birch ( <i>Betula pubescens</i> ), 73 years old in 2007
PK16	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ), sporadically birch ( <i>Betula pubescens</i> ) and ash ( <i>Fraxinus excelsior</i> ), 78 years old in 2007
PK17	Spruce ( <i>Picea abies</i> ) and black alder ( <i>Alnus glutinosa</i> ) stand with birch ( <i>Betula pubescens</i> ) and ash ( <i>Fraxinus excelsior</i> ), sporadically aspen ( <i>Populus tremula</i> ) and lime ( <i>Tilia cordata</i> ), 81 years old in 2007
PK18	Black alder ( <i>Alnus glutinosa</i> ) stand with spruce ( <i>Picea abies</i> ) and birch ( <i>Betula pubescens</i> ), sporadically pine ( <i>Pinus sylvestris</i> ), 83 years old in 2007
PK19	Spruce ( <i>Picea abies</i> ) stand with birch ( <i>Betula pubescens</i> ), pine ( <i>Pinus sylvestris</i> ), and aspen ( <i>Populus tremula</i> ), 91 years old in 2007
PK20	Black alder ( <i>Alnus glutinosa</i> ) and spruce ( <i>Picea abies</i> ) stand with birch ( <i>Betula pubescens</i> ) and ash ( <i>Fraxinus excelsior</i> ), 93 years old in 2007
PK21	Spruce ( <i>Picea abies</i> ) stand with black alder ( <i>Alnus glutinosa</i> ), sporadically pine ( <i>Pinus sylvestris</i> ), 93 years old in 2007
PK22	Spruce ( <i>Picea abies</i> ) stand with pine ( <i>Pinus sylvestris</i> ) and black alder ( <i>Alnus glutinosa</i> ), sporadically birch ( <i>Betula pubescens</i> ) and ash ( <i>Fraxinus excelsior</i> ), 101 years old in 2007
PK23	Spruce ( <i>Picea abies</i> ) stand with black alder ( <i>Alnus glutinosa</i> ) and birch ( <i>Betula pubescens</i> ), sporadically aspen ( <i>Populus tremula</i> ) and ash ( <i>Fraxinus excelsior</i> ), 103 years old in 2007
PK24	Black alder ( <i>Alnus glutinosa</i> ) stand with few spruce ( <i>Picea abies</i> ), 127 years old in 2007
RV1	Beech ( <i>Fagus sylvatica</i> ) stand with larch ( <i>Larix</i> sp.) and cherry ( <i>Prunus</i> sp.), 1 year old in 2009
RV2	Beech ( <i>Fagus sylvatica</i> ) stand with 5 % cherry ( <i>Prunus</i> sp.), 1 year old in 2009
RV3	Beech ( <i>Fagus sylvatica</i> ) stand, 3 years old in 2009
RV4	Beech ( <i>Fagus sylvatica</i> ) stand, 4 years old in 2009
RV5	Beech ( <i>Fagus sylvatica</i> ) stand, 13 years old in 2009
RV6	Beech ( <i>Fagus sylvatica</i> ) stand, 20 years old in 2009
RV7	Beech ( <i>Fagus sylvatica</i> ) stand with 10 % larch ( <i>Larix</i> sp.), 26 years old in 2009
RV8	Beech ( <i>Fagus sylvatica</i> ) stand with larch ( <i>Larix</i> sp.) and cherry ( <i>Prunus</i> sp.), 28 years old in 2009
RV9	Beech ( <i>Fagus sylvatica</i> ) stand with 10 % larch ( <i>Larix</i> sp.), 52 years old in 2009
RV10	Beech ( <i>Fagus sylvatica</i> ) stand with 10 % oak ( <i>Quercus</i> sp.), 26 years old in 2009
RV11	Beech ( <i>Fagus sylvatica</i> ) stand, 146 years old with 10-year-old byplants in 2009
RV12	Beech ( <i>Fagus sylvatica</i> ) stand, 146 years old in 2009
RV13	Beech ( <i>Fagus sylvatica</i> ) stand with 10 % oak ( <i>Quercus</i> sp.), 152 years old in 2009
RV14	Beech ( <i>Fagus sylvatica</i> ) stand, 165 years old in 2009

**Tab. 2:** ANCOVA results of SD and CV. Area – research area, age – age of study sites, MIB – mean individual biomass of Carabidae.

Dep. var.	Factor	df	F	p
SD	Area	2	59.672	0.000
	Age	1	14.604	0.001
	Area * Age	2	10.798	0.000
SD	Area	2	36.188	0.000
	MIB	1	79.630	0.000
	Area * MIB	2	36.214	0.000
CV	Area	2	18.587	0.000
	Age	1	5.277	0.031
	Area * Age	2	5.731	0.008
CV	Area	2	30.571	0.000
	MIB	1	30.880	0.000

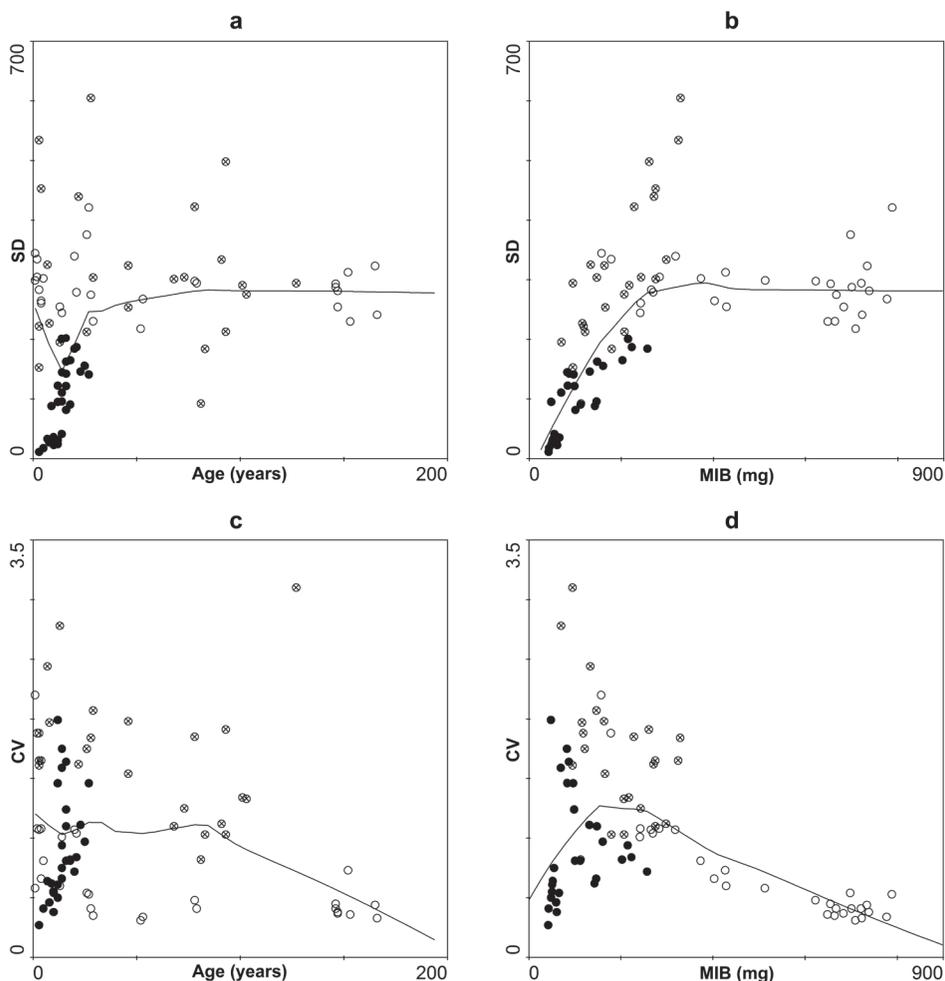
**Statistical methods**

For each sample, the mean individual biomass (MIB), standard deviation (SD), and coefficient of variation (CV) were calculated.

MIB values were calculated by dividing the biomass of all carabids in a sample by the number of specimens caught. Biomass values for the species recorded were those cited by Szyszko (13) or obtained using the equation by Szyszko (26) which describes the relationship between the body length of a single carabid individual (x) and its biomass (y):

$$\ln y = -8.92804283 + 2.55549621 \times \ln x$$

SD and CV were plotted against the age of study sites and MIB, respectively. Robust fitted locally weighted scatterplot smoothing (LOESS) models were applied in order to generate response curves to the data sets, using



**Fig. 1:** SD and CV for all study sites (●, Betchatów; ⊗, Puszcza Knyszyńska; ○, Rubr valley) plotted against age of study sites and MIB, respectively, with LOESS curves drawn for (a) SD and age of study sites (LOESS: residual standard error = 102.3536, multiple R-squared = 0.296), (b) SD and MIB (LOESS: residual standard error = 67.2909, multiple R-squared = 0.604), (c) CV and age of study sites (LOESS: residual standard error = 0.6149, multiple R-squared = 0.057), and (d) CV and MIB (LOESS: residual standard error = 0.4806, multiple R-squared = 0.337).

CanoDraw for Windows 4.14 (27). We used a local linear model and a span value of 0.67. Predictors were not conditionally parametric and we normalized the scale for two predictors.

In order to study the potential influence of the research area, repeated-measures analyses of covariance (ANCOVA) were carried out using IBM SPSS Statistics v. 22, with SD and CV as dependent variables and second-order effects of age and MIB as covariates. The initial models included interactions with the covariate, but all non-significant interactions were removed from the final model.

## RESULTS

Altogether, 22,786 carabid individuals were collected. In the research area Bełchatów the number of individuals amounted to 3,550, with individuals per sample ranging from 29 to 621. In the research area Puszcza Knyszyńska 8,903 individuals were collected (61 to 1,353 individuals per sample) while in the Ruhr valley the number of individuals was 10,333 (42 to 866 individuals per sample; Appendix 1).

When SD is plotted against the age of study sites (Fig. 1a) and MIB (Fig. 1b), respectively, for the study sites at Bełchatów an increase is visible in both cases. For the study sites of Puszcza Knyszyńska SD values are generally high and show no trend when plotted against the age of study sites, but increase when plotted against MIB. The study sites of the Ruhr valley show no trend in both cases. For this research area SD values are also high, but variation in SD values is low compared to the values elaborated for Puszcza Knyszyńska. Taking into account all three research areas, SD plotted against the age of study sites results in a LOESS curve which drops sharply until about 15 years are reached on the age axis, followed by a steep increase until an age of about 25 years is reached. From then on, the curve shows almost horizontal progression. However, when plotting SD against MIB, the LOESS curve shows a steep increase for low MIB values while it flattens and continues horizontally from MIB values of about 300 mg.

CV plotted against age (Fig. 1c) shows an increase with very high values at an age of about 15 years for the study sites at Bełchatów. When plotted against MIB (Fig. 1d), for this research area CV shows a clear increase with MIB values up to about 100 mg, but with higher values for MIB a slight decrease is visible. For the study sites in Puszcza Knyszyńska the CV values are in general very high. Plotted against both the age of study sites and MIB they describe an arch which reaches the lowest values at an age of about 80 years and a MIB of about 260 mg, respectively. For the study sites in the Ruhr valley the CV values show high variation for young study sites and low variation for older ones. When plotted against MIB, the values drop steadily. Taking into account all three re-

search areas, CV plotted against the age of study sites leads to horizontal progression of the LOESS curve until an age of about 80 years is reached, whereas, when CV is plotted against MIB, an increase until about 150 mg are reached on the MIB axis, followed by a slight decrease which becomes more pronounced from about 250 mg, can be discerned.

With age of study sites as covariate, ANCOVA revealed significant differences of both SD and CV between the research areas. SD and CV changed significantly with increasing age of sites. Yet, for both SD and CV, a significant interaction between the research area and age of sites was detected (Tab. 2). When using MIB as covariate, significant differences of both SD and CV were again detected between the research areas. Both changed significantly with increasing MIB. However, whereas a significant interaction between the research area and MIB existed with respect to SD, no significant interaction was revealed with respect to CV (Tab. 2).

## DISCUSSION

To our knowledge, changes in SD and CV of body mass distributions in carabid assemblages have not been studied in detail up to now. Studying differences between the mean and median body length in populations of *Carabus arvensis*, *Carabus violaceus*, and *Pterostichus niger*, Garbalińska & Skłodowski (28) concluded that particular species may show different patterns of body size adaptation to hurricane-induced habitat changes. Schreiner & Schwerk (29) analyzed possible changes in SD of elytra length of the species *Carabus violaceus* and *Carabus problematicus* in the beech stands of the Ruhr valley, but neither for males nor for females a significant correlation between SD and age of stands could be detected. Having analyzed the current data with LOESS models and ANCOVA we can indeed state that body mass distributions change along successional gradients and that differences in the changes between the research areas exist. However, with the exception of CV as dependent variable and MIB as covariate, there were significant interactions between research area and succession.

Data on the age of study sites as an indicator of succession show a much higher scatter than data on MIB, which is underscored by lower multiple R-squares for both SD and CV. Particularly high variability can be observed in Puszcza Knyszyńska and young study sites in the Ruhr valley. In Puszcza Knyszyńska, this may be due to a general lack of succession processes as already indicated by the fact that MIB does not correlate with the age of study sites (23). The strong habitat dynamics may be caused by fluctuating water conditions. Soil conditions and forestry methods might also play a role (30). In the Ruhr valley, our results may originate from a high variability of initial degradation levels. As a matter of fact, MIB values for

young study sites in the research area Ruhr valley range from about 150 mg up to more than 500 mg (24).

It is evident that very low as well as very high MIB values are accompanied by comparatively low values for SD and CV. Therefore, SD and CV in a medium MIB range, i.e. at medium stages of succession, are particularly interesting. In this context, MIB values of about 150–250 mg seem to mark a decisive moment. This is when the SD curve flattens and the CV curve shows a maximum. This MIB range may represent a transition coenoses between carabid assemblages of open areas and those of advanced stages of succession. Here, changes in soil conditions may be an important factor since studies have shown that the distribution of woodland carabids may depend on the soil water holding capacity, soil trophic status, and soil acidity (31) or litter layer (32, 33). However, studying native beech forests and spruce plantations, Magura *et al.* (34) reported that also canopy closure has an influence on changes in carabid assemblages during forestry cycles.

Depending on the speed of succession, the described MIB range of a possible transition coenosis may be reached on individual study sites at a different age. Accordingly, the highest CV on the study sites at Bełchatów was observed for sites with an age of about 12–16 years, whereas in the Ruhr valley it was already reached on sites of a by far younger age. Interestingly, the CV peaks approximate the inflexion points of curves based on a logistic model of succession on the study sites in these areas (35, 24), i.e. the moment of maximum speed of succession.

Significant differences between the research areas were indicated by the results of ANCOVA. However, in three cases significant interaction was revealed and thus the response to the groups (research areas) should not be interpreted as an overall or average main effect (36). Accordingly, a significant difference between the research areas can be approved without reservation only for CV plotted against MIB. In all other cases we may merely assume a difference in response to the age of study sites or MIB between the research areas.

Management of successional stages is an important task with respect to biodiversity conservation, for instance on post-industrial areas (*e.g.* 14, 37) or in connection with construction projects (38). Diversification of successional stages is an important feature determining landscape structure (39). Habitat diversity, landscape structure, and land-use intensity have been proven to affect diversity patterns in different arthropod groups in temperate European agricultural landscapes (40). Hence, a variety of succession indicators is needed in order to manage sensitive habitats and landscapes effectively. Data on body mass distributions within single carabid assemblages may be useful in the assessment and comparison of successional stages and processes in different habitat types.

## Acknowledgements

The authors thank Rikjan Vermeulen and an anonymous reviewer for their valuable comments on an earlier version of the manuscript and Karsten Hannig for confirming the determination of beetles. This paper is communication No. 474 of the Laboratory of Evaluation and Assessment of Natural Resources, Warsaw University of Life Sciences – SGGW.

## REFERENCES

1. HESPENHEIDE H A 1973 Ecological inferences from morphological data. *Ann Rev Ecol Syst* 4: 213–229
2. CZECHOWSKI W 1980 Influence of the manner of managing park areas and their situation on the formation of the communities of carabid beetles (Coleoptera, Carabidae). *Fragm Faun* 25: 199–219
3. RINK U 1990 Struktur und Phänologie der Fauna von Laufkäfern (Coleoptera, Carabidae) in immissionsbelasteten Kiefernbeständen des Berliner Grunewaldes. *Zool Beitr N F* 33: 265–294
4. SZYSZKO J, VERMEULEN H J W, DEN BOER PJ 1996 Survival and reproduction in relation to habitat quality and food availability for *Pterostichus oblongopunctatus* F. (Carabidae, Col.). *Acta Jul* 71: 25–40
5. TENHUMBERG B, TYRE A J, ROITBERG B 2000 Stochastic variation in food availability influences weight and age at maturity. *J Theor Biol* 202: 257–272 <http://dx.doi.org/10.1006/jtbi.1999.1049>
6. LINDENMAYER D B, MARGULES C R, BOTKIN D B 2000 Indicators of biodiversity for ecologically sustainable forest management. *Conserv Biol* 14: 941–950
7. KOIVULA M J 2011 Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys* 100: 287–317. <http://dx.doi.org/10.3897/zookeys.100.1533>
8. SKŁODOWSKI J J W 2006 Anthropogenic transformation of ground beetle assemblages (Coleoptera: Carabidae) in Białowieża Forest, Poland: from primeval forests to managed woodlands of various ages. *Entomol Fenn* 17: 296–314
9. PIZZOLOTTO R, GOBBI M, BRANDMAYR P 2014 Changes in ground beetle assemblages above and below the treeline of the Dolomites after almost 30 years (1980/2009). *Ecol Evol* 4: 1284–1294. <http://dx.doi.org/10.1002/ece3.927>
10. HODECEK J, KURAST,ŠIPOŠ J, DOLNÝ A 2015 Post-industrial areas as successional habitats: Long-term changes of functional diversity in beetle communities. *Basic Appl Ecol* 16: 629–640. <http://dx.doi.org/10.1016/j.baae.2015.06.004>
11. BLAKE S, FOSTER G N, 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
12. CÁRDENAS A M, & HIDALGO J M 2007 Application of the mean individual biomass (MIB) of ground beetles (Coleoptera, Carabidae) to assess the recovery process of the Guadamar Green Corridor (southern Iberian Peninsula). *Biodivers Conserv* 16: 4131–4146 <http://dx.doi.org/10.1007/s10531-007-9211-5>
13. 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, p 96
14. SCHWERK A, SZYSZKO J 2008 Patterns of succession and conservation value of post-industrial areas in central Poland based on carabid fauna (Coleoptera: Carabidae). In: Penev L, Erwin T, Assmann T (eds) Back to the roots and back to the future. Towards a new synthesis between taxonomic, ecological and biogeographical approaches in Carabidology. Pensoft Publishers, Sofia, Moscow, p 469–481

15. ŠERIĆ JELASKA L, DUMBOVIĆ V, KUČINIĆ M 2011 Carabid beetle diversity and mean individual biomass in beech forests of various ages. *ZooKeys* 100: 393-405. <http://dx.doi.org/10.3897/zookeys.100.1536>
16. SZYSZKO J, VERMEULEN H J W, KLIMASZEWSKI K, ABS M, SCHWERK A 2000 Mean Individual Biomass (MIB) of 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, p 288-294
17. BRAUN S D, JONEST H, PERNER J 2004 Shifting average body size during regeneration after pollution – a case study using ground beetle assemblages. *Ecol Entomol* 29: 543-554
18. LÖVEI G L, MAGURA T 2006 Body size changes in ground beetle assemblages – a reanalysis of Braun *et al.*(2004)'s data. *Ecol Entomol* 31: 411-414
19. PARMENTER R R, MACMAHON J A 1987 Early successional patterns of arthropod recolonization on reclaimed strip mines in southwestern Wyoming: the ground-dwelling beetle fauna (Coleoptera). *Environ Entomol* 16: 168-175 <http://dx.doi.org/10.1093/ee/16.1.168>
20. PFLUG W (ed) 1998 Braunkohlentagebau und Rekultivierung. Landschaftsökologie – Folgenutzung – Naturschutz. Springer Verlag, Berlin, Heidelberg, New York, p 1068 <http://dx.doi.org/10.1007/978-3-642-58846-4>
21. SCHWERK A, SZYSZKO J 2011 Model of succession in degraded areas based on carabid beetles (Coleoptera, Carabidae). *ZooKeys* 100: 319-332. <http://zookeys.pensoft.net/articles.php?id=2395>
22. SCHWERK A 2014 Changes in carabid beetle fauna (Coleoptera: Carabidae) along successional gradients in post-industrial areas in Central Poland. *Eur J Entomol* 111: 677-685. doi: 10.14411/eje.2014.076 <http://dx.doi.org/10.14411/eje.2014.076>
23. KWIATKOWSKI A 2011 Assemblages of carabid beetles (Coleoptera: Carabidae) in humid forest habitats of different stage of succession in the Puszcza Knyszyńska Forest (northeastern Poland). *ZooKeys* 100: 447-459. doi: 10.3897/zookeys.100.1539 <http://dx.doi.org/10.3897/zookeys.100.1539>
24. SCHREINER A 2012 Succession development in forest habitats of the Ruhr valley (Germany) in consideration of ecological aspects and biotope conservation using the example of epigeic carabid beetles (Coleoptera: Carabidae) as compared to Polish habitats. Dissertation, Warsaw University of Life Sciences –SGGW, Warsaw, p 112
25. FREUDE H, HARDE K-W, LOHSE G A, KLAUSNITZER B 2004 Die Käfer Mitteleuropas. Bd. 2, Adepthaga 1, Carabidae (Laufkäfer). 2. (erweiterte) Aufl., Spektrum, Heidelberg/Berlin, p 521
26. 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, p 10-16
27. TER BRAAK C J F, ŠMILAUER P 2002 CANOCO reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, p 499
28. GARBALIŃSKA P, SKŁODOWSKI J 2008 Body size differentiation in selected carabid species inhabiting Puszcza Piska forest stands disturbed by the hurricane. *Baltic J Coleopterol* 8: 101-114
29. SCHREINER A, SCHWERK A 2011 Standard deviation of carabid size in Western Germany forest succession – a complex picture. *Baltic J Coleopterol* 11: 25-31
30. SKŁODOWSKI J J W 1995 Soil fertilization and acidification effect on the rate of development of epigeic carabid (Coleoptera, Carabidae) communities in a Scots pine forest plantation. *Fol. For. est. Pol. ser. A* 37: 21-46
31. BAGUETTE M 1993 Habitat selection of carabid beetle in deciduous woodlands of southern Belgium. *Pedobiol* 37: 365-378
32. GUILLEMAIN M, LOREAU M, DAUFRESNEY T 1997 Relationships between the regional distributions of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. *Acta Oecol* 18: 465-483 [http://dx.doi.org/10.1016/S1146-609X\(97\)80035-5](http://dx.doi.org/10.1016/S1146-609X(97)80035-5)
33. KOIVULA M, PUNTTILA P, HAILA Y, NIEMELÄ J 1999 Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22: 424-435
34. MAGURA T, TÓTHMÉRÉSZ B, ELEK Z 2003 Diversity and composition of carabids during a forestry cycle. *Biodivers Conserv* 12: 73-85 <http://dx.doi.org/10.1023/A:1021289509500>
35. SCHWERKA 2008 Model of the rate of succession of epigeic carabid beetles (Coleoptera: Carabidae) on degraded areas. Instytut Badawczy Leśnictwa, Sękocin Stary, p 71
36. ENGQVIST L 2005: The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim Behav* 70: 967-971 <http://dx.doi.org/10.1016/j.anbehav.2005.01.016>
37. TROPEK R, KADLECT, KARESOVA P, SPITZER L, KOCAREK P, MALENOVSKY I, BANAR P, TUF I H, HEJDA M, KONVICKA M 2010 Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *J Appl Ecol* 47: 139-147. <http://dx.doi.org/10.1111/j.1365-2664.2009.01746.x>
38. DYMITRYSZYN I 2014 The effect of the construction and renovation of a highway bypass in Central Poland on the carabid beetle fauna (Coleoptera: Carabidae). *Eur J Entomol* 111: 655-662. <http://dx.doi.org/10.14411/eje.2014.081>
39. SZYSZKO J, SCHWERK A, MALCZYK J 2011 Animals as indicator of carbon sequestration and valuable landscapes. *ZooKeys* 100: 565-573. <http://dx.doi.org/10.3897/zookeys.100.1547>
40. HENDRICKX F, MAELFAIT J-P, VAN WINGERDEN W, SCHWEIGER O, SPEELMANS M, AVIRON I, AUGENSTEIN I, BILLETTER R, BAILEY D, BUKACEK R, BUREL F, DIEKÖTTER T, DIRKSEN J, HERZOG F, LIRA J, ROUBALOVA M, VANDOMME V, BUGTER R 2007 How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J Appl Ecol* 44: 340-351

**Appendix 1:** Information on individual samples with respect to study year(s), age of site, number of carabid individuals (*n*), mean individual biomass of Carabidae (MIB), standard deviation (SD), and coefficient of variation (CV). Age of site refers to each first year (study sites at Bełchatów) and to the year 2007 (study sites in Puszcza Knyszyńska), respectively. BE – Bełchatów, PK – Puszcza Knyszyńska, RV – Ruhr valley.

Study site	Study year(s)	Age of site	n	MIB	SD	CV
BE1	2004/05	8	621	59.18	27.40	0.46
BE1	2006/07	10	170	65.79	35.57	0.54
BE1	2008/09	12	59	83.98	122.67	1.46
BE1	2010/11	14	120	146.49	96.07	0.66
BE2	2004/05	10	281	60.84	22.88	0.38
BE2	2006/07	12	99	50.78	31.04	0.61
BE2	2008/09	14	59	69.53	110.63	1.59
BE2	2010/11	16	58	98.33	121.91	1.24
BE3	2004/05	12	174	47.91	95.26	1.99
BE3	2006/07	14	63	82.81	144.87	1.75
BE3	2008/09	16	60	87.12	142.52	1.64
BE3	2010/11	18	66	111.44	90.49	0.81
BE4	2004/05	3	165	42.22	11.37	0.27
BE4	2006/07	5	245	43.19	17.70	0.41
BE4	2008/09	7	348	52.28	33.24	0.64
BE4	2010/11	9	103	142.69	88.38	0.62
BE5	2004/05	10	50	50.62	27.85	0.55
BE5	2006/07	12	59	48.78	24.37	0.50
BE5	2008/09	14	37	55.05	41.43	0.75
BE5	2010/11	16	42	100.50	81.68	0.81
BE6	2004/05	14	98	214.62	200.99	0.94
BE6	2006/07	16	29	147.66	162.79	1.10
BE6	2008/09	18	83	202.70	165.26	0.82
BE6	2010/11	20	97	256.97	184.63	0.72
BE7	2004/05	21	117	222.84	187.20	0.84
BE7	2006/07	23	118	131.84	146.26	1.11
BE7	2008/09	25	88	160.36	155.65	0.97
BE7	2010/11	27	41	96.66	141.07	1.46
PK1	2006-08	3	259	118.22	222.20	1.88
PK2	2006-08	3	168	95.19	152.99	1.61
PK3	2006-08	3	148	324.32	534.07	1.65
PK4	2006-08	4	129	274.64	452.98	1.65
PK5	2006-08	7	81	133.43	325.33	2.44
PK6	2006-08	8	61	115.43	227.14	1.97
PK7	2006-08	13	451	70.32	195.44	2.78
PK8	2006-08	22	281	271.13	439.68	1.62
PK9	2006-08	26	159	121.67	212.80	1.75

PK10	2006-08	28	116	328.44	604.75	1.84
PK11	2006-08	29	165	146.63	303.98	2.07
PK12	2006-08	46	310	163.51	324.14	1.98
PK13	2006-08	46	326	165.27	253.86	1.54
PK14	2006-08	68	554	274.84	301.20	1.10
PK15	2006-08	73	272	242.83	304.38	1.25
PK16	2006-08	78	442	227.86	422.55	1.85
PK17	2006-08	81	297	112.59	92.45	0.82
PK18	2006-08	83	413	179.32	184.21	1.03
PK19	2006-08	91	549	298.01	333.85	1.12
PK20	2006-08	93	222	260.60	498.18	1.91
PK21	2006-08	93	1353	206.82	212.86	1.03
PK22	2006-08	101	730	217.42	290.94	1.34
PK23	2006-08	103	1206	206.58	275.67	1.33
PK24	2006-08	127	211	95.06	294.37	3.10
RV1	2009	1	744	156.88	344.55	2.20
RV1	2010	2	376	178.23	334.75	1.88
RV2	2009	1	129	512.40	298.98	0.58
RV2	2010	2	206	283.02	304.81	1.08
RV3	2009	3	163	265.18	283.42	1.07
RV3	2010	4	205	242.03	261.03	1.08
RV4	2009	4	139	402.37	264.62	0.66
RV4	2010	5	42	372.83	302.43	0.81
RV5	2009	13	125	428.34	254.89	0.60
RV5	2010	14	78	241.12	244.61	1.01
RV6	2009	20	866	317.90	339.71	1.07
RV6	2010	21	589	269.24	279.22	1.04
RV7	2009	26	352	697.41	375.52	0.54
RV7	2010	27	292	788.10	421.09	0.53
RV8	2009	28	699	666.67	274.78	0.41
RV8	2010	29	494	663.55	230.55	0.35
RV9	2009	52	277	708.53	217.97	0.31
RV9	2010	53	353	776.67	267.63	0.34
RV10	2009	78	477	622.06	297.77	0.48
RV10	2010	79	373	721.09	294.26	0.41
RV11	2009	146	586	654.30	293.36	0.45
RV11	2010	147	862	683.01	254.29	0.37
RV12	2009	146	442	700.24	287.68	0.41
RV12	2010	147	476	737.95	281.58	0.38
RV13	2009	152	273	426.19	312.55	0.73
RV13	2010	153	321	648.13	230.28	0.36
RV14	2009	165	264	733.63	323.09	0.44
RV14	2010	166	130	722.70	241.34	0.33