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Macropterous Ground Beetles (Coleoptera: Carabidae) Prevail in European Oilseed Rape Fields

Teodora M. Teofilova[*]

Institute of Biodiversity and Ecosystem Research (IBER), Bulgarian Academy of Sciences (BAS), 1 Tsar Osvoboditel Blvd., 1000 Sofia, BULGARIA
[*]Corresponding author: oberon_zoo@abv.bg

Abstract. During a research conducted in oilseed rape (*Brassica napus* L.) fields in four European countries (Bulgaria, Germany, Romania and Switzerland), species composition and ecological structure of the ground beetle (Coleoptera: Carabidae) fauna associated with the rape were studied. Field work was carried out in 2017 (2018 in Bulgaria). Pitfall traps (5 in each site) were set in each sampling site in each country. Captured beetles belonged to 179 species and 51 genera. The most diverse were genera *Harpalus* Latreille, 1802 and *Amara* Bonelli, 1810 (21 species each), followed by the genera *Carabus* Linnaeus, 1758 (15 species), *Pterostichus* Bonelli, 1810 (10 species), *Microlestes* Schmidt-Goebel, 1846 and *Poecilus* Bonelli, 1810 (9 species each), and *Brachinus* Weber, 1801 and *Ophonus* Dejean, 1821 (8 species each). In Bulgaria were found 107 species, in Germany – 68 species, in Romania – 71 species, in Switzerland – 45 species. Fourteen species were common in all countries. Macropterous species represented 65% (116 species) of all collected carabid species (in all countries). Pteridimorphic species were 20% of all (36 species), and brachypterous were only 12% (21 species). For 6 species (3%) there were no data about their wing morphology. The results were similar in each country. Macropterous species were 73% (78 species) in Bulgaria, 60% (41 species) in Germany, 68% (48 species) in Romania, and 69% (31 species) in Switzerland. Macropterous beetles prevailed in number of specimens too (79% of the specimens in all countries). The prevalence of the macropterous carabids reflects their higher mobility and adaptiveness.

Key words: carabids, agrocoenoses, ecology, Europe, wing morphology, dispersal power, flight ability.

Introduction

Wing polymorphism in carabid beetles (Coleoptera: Carabidae) is well known and relatively well studied, as constantly macropterous, constantly brachypterous or apterous as well as di- and polymorphic species are reported (Lindroth, 1949; Haeck, 1971; Den Boer, 1977; Den Boer et al., 1980; Brandmayer, 1983; Kavanaugh, 1985; Desender et al., 1986; Kromp, 1999; Kotze & O'Hara, 2003; Venn, 2016, etc.). In fact, ground beetles are probably the best studied group of animals in this respect (Kotze et al., 2011). Recently, Venn (2016) presented a review of studies on the topic.

The degree of hind wing development allows three groups to be distinguished: macropterous (winged) species have fully developed hind wings in all individuals, whereas brachypterous (wingless) species have reduced vestigial wings. In wing dimorphic

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species, some individuals have fully developed wings, others only vestigial ones (Den Boer et al., 1980; Kromp, 1999). Furthermore, wing morphology of ground beetles can vary considerably, even within the same species, and this variation suggests that the term wing-polymorphic is more appropriate than dimorphic (Desender, 1989; Venn, 2007, 2016).

The dispersal power of beetles could be estimated by measuring their wing morphology (Den Boer et al., 1980; Gutierrez & Menendez, 1997; Matalin 1994, 2003; Kotze & O'Hara, 2003; Venn 2016). The migratory component comprises mainly macropterous species, whereas the stable component comprises mainly brachypterous species and predominantly brachypterous morphs of dimorphic species (Chernov & Makarova, 2008). Good flyers, as a rule, have larger areals, and flightless beetles have smaller ranges (Kryzhanovskij, 1965). The dispersal and migration ability depends on the proportion of macropterous specimens in a given population (Lindroth, 1949) and functionality of the wing muscles (Desender, 1989), and macropterous, dimorphic and brachypterous species differ in patterns of spatial distribution and co-occurrences (Zalewski & Ulrich, 2006).

It is known that habitat type and disturbance influence wing morphology of carabids (Venn, 2016). Darlington (1943) found that full-winged species predominate among arboreal carabids due to the necessity of frequent dispersal in patchy and unstable habitats, and epigeic carabid species from stable habitats have no reason to fly, and therefore evolve brachypterous forms. A number of studies have suggested that in areas with increased disturbance the numbers of specialist, large bodied and poorly dispersing species decrease in abundance, whilst generalist, small bodied effective dispersers increase (Den Boer et al., 1980; Rushton et al., 1989; Blake et al., 1994, Niemelä et al., 2000; Grandchamp et al., 2002; Mazzei et al., 2015; Barber et al., 2017). The more stable the occupied habitats are, the more natural selection will reduce relative wing size, and the numbers of flightless species will rise (Den Boer et al., 1980; Gnetti et al., 2015). Wing morphology is also studied in relation to the trophic level of carabids, and showed that wing dimorphic species occupied higher trophic levels than winged species (Zalewki et al., 2015).

According to Holliday (1991) there may be a general pattern of ground beetle community succession, with early stages typified by small, phytophagous species with strong dispersal capability, and mature stages containing more large, flightless carnivores.

In this study the carabid diversity in oilseed rape (*Brassica napus* L.) fields in four European countries (Bulgaria, Germany, Romania and Switzerland) was researched. It aimed at establishing the composition of the carabid fauna in relation to their wing morphology.

Material and Methods

Field work was carried out in 2017 in Germany, Romania and Switzerland, and in 2018 in Bulgaria. Pitfall traps (5 in each site) with salt and 6% acetic acid saturated solution (with small amount of dishwasher detergent) as a preserving fluid were set in each sampling site in each country. The sampling periods were three in all countries and they were during the flowering, during the ripening and after the harvest of the oilseed rape. Thus, due to the specific conditions in the different countries, the periods of research were different, as well as the number of the sampling sites (Table 1). All carabids were determined to species level using the keys of Hůrka (1996), Turin et al. (2003), Luff (2007), Arndt et al. (2011). Species were classified into three groups: winged or macropterous (always possessing wings), wing dimorphic/polymorphic (only part of the population being fully winged), and brachypterous (wingless), according to the commonly accepted classification of Den Boer et al. (1980).

For the assessment of the taxonomic similarity, the classification of Zlotin (1975) was used.

Frequency of occurrence was calculated using the formula: F = (p/P).100%, where p is number of the countries where the species occur (no matter of its abundance), and P is the number of the studied countries, i.e. P = 4.

The data were processed with MS Excel and PRIMER 6 (Clarke & Gorley, 2005).

Results and Discussion

During the study altogether 37912 carabid beetles were collected. They belonged to 179 species and 51 genera (Appendix 1). The most diverse were genera *Harpalus* and *Amara* (21 species each), followed by the genera *Carabus* (15 species), *Pterostichus* (10 species), *Microlestes* and *Poecilus* (9 species each), and *Brachinus* and *Ophonus* (8 species each).

In Bulgaria were collected 5018 specimens from 107 species, in Germany – 14285 specimens from 68 species, in Romania – 7576 specimens from 71 species, in Switzerland – 11033 specimens from 45 species (Appendix 1). Fourteen species were common in all countries. It is noticeable that in countries with less species diversity there is greater abundance of established beetles, which proves the ecological effect of concentration of dominance and speaks of the presence of some catastrophic effect in the biocoenoses. This could be, for example, the intensification of the agriculture.

Macropterous species represented 65% (116 species) of all collected carabid species (in all countries). Pteridimorphic species were 20% of all (36 species), and brachypterous were only 12% (21 species). For 6 species (3%) there were no data about their wing morphology (Appendix 1, Fig. 1A). Macropterous beetles prevailed in number of specimens too (79% of the specimens in all countries) (Appendix 1, Fig. 1B).

The results were similar in each country. Macropterous species were 73% (78 species) in Bulgaria, 60% (41 species) in Germany, 68% (48 species) in Romania, and 69% (31 species) in Switzerland. Pteridimorphic species were 17% (18 species) in Bulgaria, 32% (22 species) in Germany, 15% (11 species) in Romania, and 29% (13 species) in Switzerland. Brachypterous species were less abundant in all four countries (Fig. 2).

Table 1. Number of sampling sites (Ss) and sampling periods in each country (2017 in Germany, Romania and Switzerland, and 2018 in Bulgaria).

Country	Ss	Flowering	Ripening	After the harvest
Bulgaria	10	19-22.IV – 14-16.V	14-16.V – 11-13.VI	25-27.VII – 24-26.VIII
Germany	9	4-9.V– 23-29.V	21-30.VI – 9-19.VII	16.VIII-15.IX – 4.IX-11.X
Romania	10	3-5.V – 23-24.V	13-15.VI – 5-7.VII	20-22.VIII – 9-10.IX
Switzerland	8	11-12.IV – 3-5.V	1-20.VI – 20.VI-12.VII	2-3.VIII – 22-23.VIII

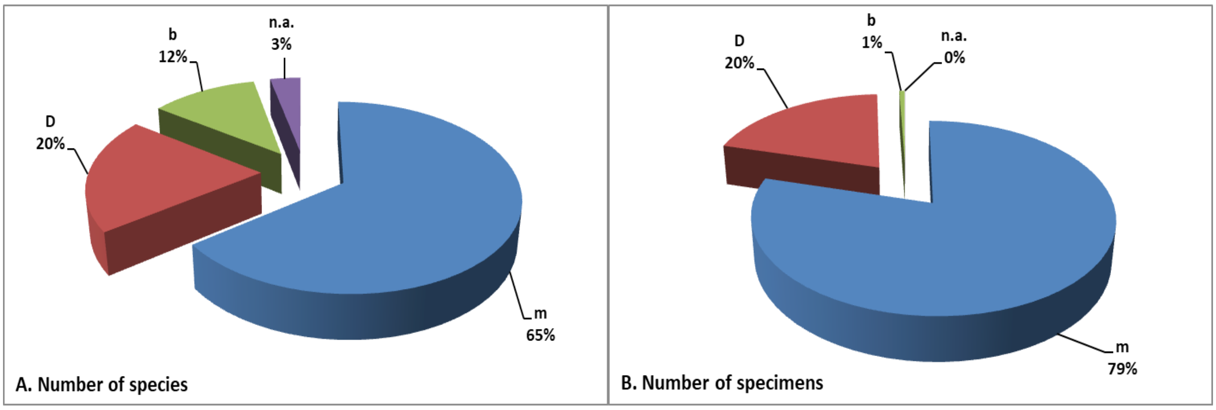


Fig. 1. Wing morphology of carabids in all countries. A. Number of species. B. Number of specimens. m – macropterous, D – wing di(poly)morphic, b – brachypterous, n.a. – no data.

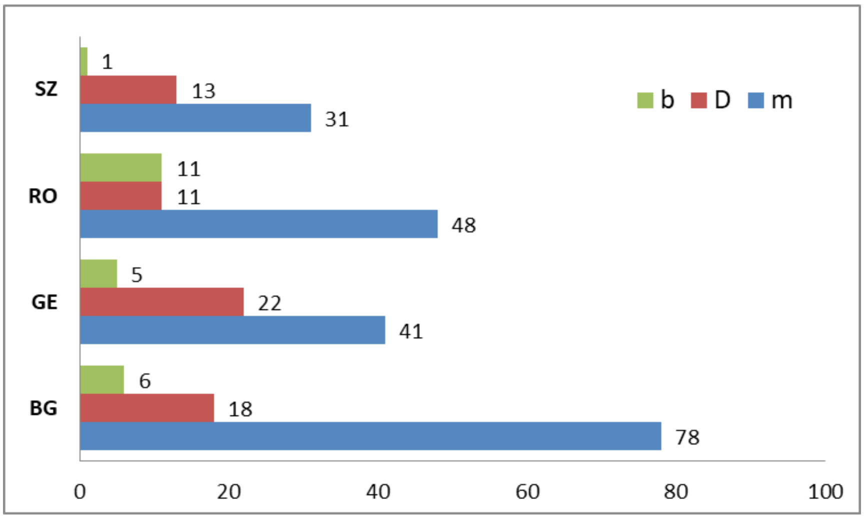


Fig. 2. Numbers of macropterous (m), di(poly)morphic (D) and brachypterous (b) species in four countries.

The prevalence of the macropterous carabids reflects their higher mobility and adaptiveness. Since macropterous wings are mainly used for dispersal flights, winged species seem normally especially abundant in scattered or disturbed habitats, e.g. cultural land. On the other hand, brachypterous species often are stenotopic (e.g. forest) inhabitants with a low dispersal ability (Kryzhanovskij, 1965; Kromp, 1999; Chernov & Makarova, 2008). Carabid communities in earliest stages of restoration of grasslands were also numerically dominated by small, winged species (Barber et al., 2017). In contrast, all species collected in high numbers in spruce forests were brachypterous (Gnetti et al., 2015).

Our results are in accordance with Gray's hypothesis, that the proportion of flight capable pioneer species should increase with increasing disturbance, and the proportion of flightless species should decrease (Gray, 1989), as it was also suggested by Magura et al. (2010). Gobbi & Fontaneto (2008) also found that short winged, large and predatory species were negatively related to human impact. Habitats with a high degree of disturbance have a lower proportion of brachypterous carabids, as those species are sensitive to unstable and variable conditions, such as in agroecosystems. Similarly, measuring the potential flight ability of carabids, Venn (2007) found that the proportion of macropterous individuals was greater, and the wing-length of brachypterous individuals was longer in the populations of disturbed sites. Ground beetle species able to fly were better represented (72%) in the younger, disturbed and less stable riparian alder stand in the study of Mazzei et al. (2015). Similar results were obtained in urban park grasslands under different mowing regimes by Venn & Rokala (2005) and in urban golf courses by Saarikivi et al. (2010).

It is considered (Lindroth, 1992; den Boer, 1971; Venn, 2007) that the proportion of macropterous individuals is indicative of the age and stability of the population. A stable and long established population should contain almost exclusively brachypterous individuals, as dispersal ability is not advantageous in these circumstances, which is not the case in our study. Such results were obtained by Kavanaugh (1985), who found 73% brachypterous carabid taxa in an Alpine habitat. During the last decades, many typical natural habitats were destroyed or declined in whole Europe, particularly in lowlands, where extensive lands were transformed into agrolandscapes. That is why brachypterous, large and specialist ground beetles are declining too (Kotze & O'Hara, 2003).

Comparing two riparian alder forests subject to different disturbance factors, Mazzei et al. (2015) also found that the younger stand is a less stable environment with fewer brachypterous species. Young sites were typified by small, macropterous, phytophagous species, while older sites contained larger species more likely to be flightless and carnivorous, in a study in restored grasslands (Barber et al., 2017). Across a coastal heathland successional gradient winged and phytophagous species predominated in the earliest successional stages too (Schirmel et al., 2012). Woodcock et al. (2012) showed that flightless beetle species and those relying on a more limited food breadth took longer to colonize early successional habitats, which explains their smaller presence in the studied rape fields.

The similarity between four countries (Fig. 3), calculated on the basis of the abundance of all macropterous, dimorphic, brachypterous and not determined species, showed that Bulgarian sample significantly distinguishes from the other countries and separates from them on a very low level of similarity, according to Zlotin (1975). Romania also distinguishes from Germany and Switzerland on an average level of similarity. The last two countries seem grouped, although their similarity is not very high. This is in accordance with the established similar ratios between the species diversity and abundance in these countries.

In relation of their frequency of occurrence, carabid species were separated in four classes (see Appendix 1): with occurrence of 25% (occurring in only one country), 50% (occurring in two countries), 75% (occurring in three countries) and 100% (constant species, occurring in all countries). Most of the species were with occurrence of 25% (Fig. 4), which is normal given the fact that every country has its own set of species. It is, however, notable that the brachypterous species where mainly in the class of the "local" species, and only two of them had occurrence of 50%. This showed the lower dispersal power of those species, in contrast of the findings of Zalewski & Ulrich (2006), where the macropterous species occupied fewer sites than dimorphic and brachypterous species. Common species with occurrence of 100% in our study where mostly winged, as only one species was dimorphic.

According to the abundance of the macropterous, dimorphic and brachypterous species, our study showed that the most abundant were common (F = 100%) macropterous species (Fig. 5). They totally predominated over all other species, which once again confirmed the already established trend for concentration of domination. This concentration is resulting from the extremely high abundances of *Poecilus cupreus* in Switzerland, Germany and Romania, *Anchomenus dorsalis* in Switzerland and Romania, *Nebria brevicollis* in Germany, and *Brachinus explodens* in Romania. These results are totally in contrast of the findings of Zalewski & Ulrich (2006), where the macropterous species had lower site abundances and occupied fewer sites than dimorphic and brachypterous species. Probably the reason is in the type of the habitat, since they performed their research in natural sites, whilst ours were conducted in agrocoenoses. Also in contrast to our results, Work et al. (2008) did not observe a clear association between frequency–abundance relationships and dispersal ability, probably due to the lack of quantitative evidence of dispersal ability of some species.

Macropterous, flight capable species are supposed to have higher dispersal abilities than dimorphic or brachypterous ones, they are better adapted to ecosystems with frequent disturbance and their higher abundance might be attesting to their faster dispersion and colonization of new habitats (Kryzhanovskij, 1965; Chernov & Makarova, 2008; Hendrickx et al., 2009; Venn, 2016).

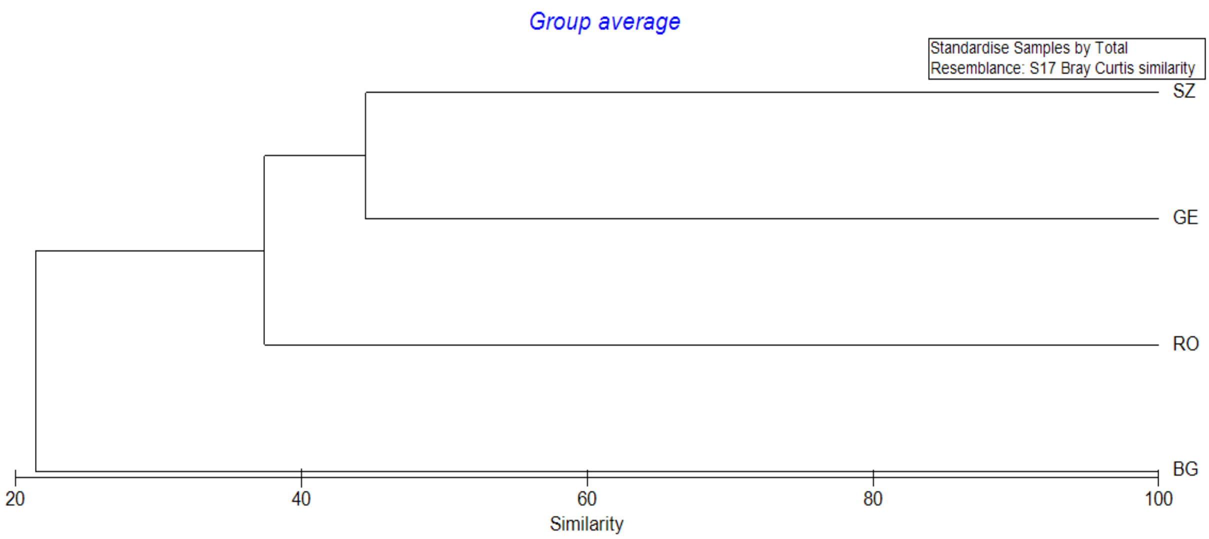
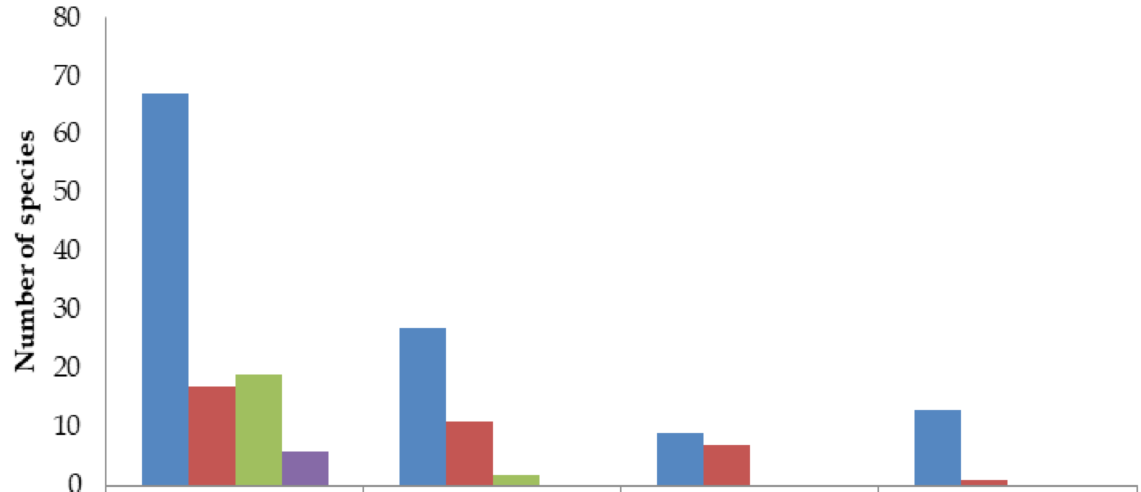
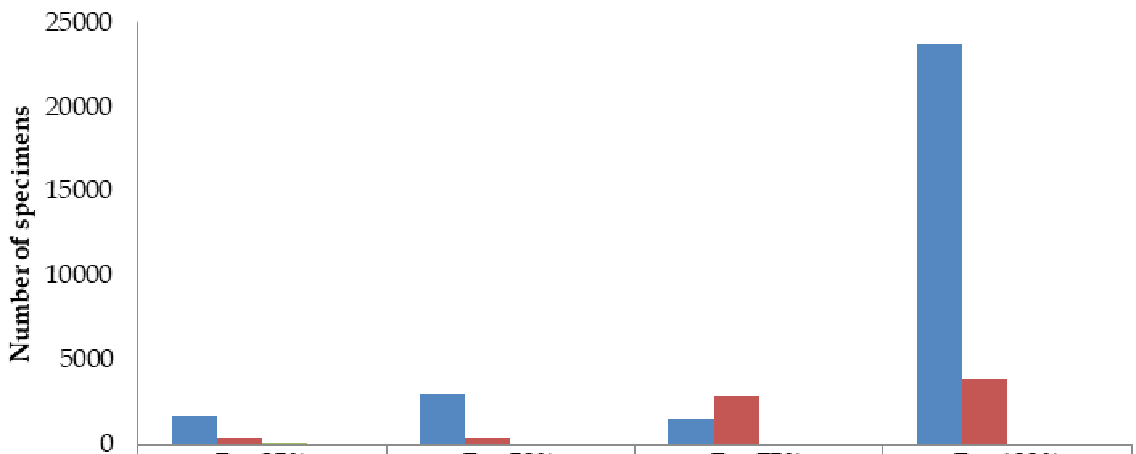


Fig. 3. Group average dendrogram of the similarity between four countries, calculated on the basis of the abundance of macropterous, dimorphic, brachypterous and not determined species. BG – Bulgaria. GE – Germany, RO – Romania, SZ – Switzerland.



	F = 25%	F = 50%	F = 75%	F = 100%
m	67	27	9	13
D	17	11	7	1
b	19	2	0	0
n.a.	6	0	0	0

Fig. 4. Number of species in the four occurrence classes (with frequency of occurrence, respectively 25%, 50%, 75% and 100%): m – macropterous, D – wing di(poly)morphic, b – brachypterous, n.a. – no data.



	F = 25%	F = 50%	F = 75%	F = 100%
m	1716	2989	1611	23765
D	377	364	2946	3913
b	150	70	0	0
n.a.	11	0	0	0

Fig. 5. Number of specimens in the four occurrence classes (with frequency of occurrence, respectively 25%, 50%, 75% and 100%): m – macropterous, D – wing di(poly)morphic, b – brachypterous, n.a. – no data.

In a study of the influence of dispersal ability of ground beetles from 15 lake islands and 2 mainland sites in northern Poland, Zalewski & Ulrich (2006) found similar share of the macropterous, dimorphic and brachypterous species as we did, respectively 66%, 22% and 11%. The presence of more beetles with fully or differently developed wings is also probably connected with their possible chance to avoid hazards in the form of agricultural treatments (Kromp, 1999). Macropterous carabids dominated and brachypterous carabid beetles were very few in assemblages in both conventional and non-inversion tillage systems in oilseed rape fields (Kosewska, 2016). Comparing forest and open areas without any land management practice, Shibuya et al. (2014) also found that macropterous carabid beetles are more common in disturbed habitats. Lower proportion of macropterous individuals was found in vineyards with lower agricultural intensification during a study of the effect of local vegetation management on carabid wing-morphology composition (Rusch et al., 2016).

Conclusions

Oilseed rape fields, being young and less stable habitats, harbor more macropterous ground beetles, while brachypterous species with lower dispersion abilities seem to be more vulnerable to anthropogenic interference in the crops.

The prevalence of the macropterous carabids reflects their higher mobility and adaptiveness, and evidences the initial stage of formation of cenoses, as well as the unstable state of carabid populations in the oilseed rape fields in all studied countries.

The combination of less species diversity and greater abundance of the established beetles in Germany and Switzerland might be a sign of some catastrophic effect in the biocoenoses there, e.g. stronger intensification of the agriculture.

Intensification of the agriculture leads to the decline of natural habitats and associated biota worldwide, and in this study the ground beetles were used as a model, as they are well studied bioindicators and have a proved role in the ecosystems as valuable pest control factor.

Since the ecosystem functions, such as pest control (and pollination), are directly dependent on the invertebrate predators (and pollinators) diversity, it is relevant to keep their habitats stable and keep them from disturbance and destruction. Environmental sustainability should be included in the agriculture standards and practices.

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Appendix 1. Species list and numbers of specimens of the ground beetles established in the oilseed rape fields: BG – Bulgaria, GE – Germany, RO – Romania, SZ – Switzerland; Wing development: m – macropterous, b – brachypterous, D – dimorphic, n.a. – no data; F – occurrence, referring to the number of countries where the species was found (in %).

Species	BG	GE	RO	SZ	Wings	F
Acinopus (s.str.) *picipes* (Olivier, 1795)	49				m	*25*
A. (Oedematicus) megacephalus (P. Rossi, 1794)	54				m	*25*
Acupalpus (s.str.) *exiguus* Dejean, 1829		2			m	*25*
Acupalpus (s.str.) *meridianus* (Linnaeus, 1760)	3	2	2	4	m	*100*
Acupalpus (Ancylostria) interstitialis Reitter, 1884	5		12		m	*50*
Agonum (s.str.) *muelleri* (Herbst, 1784)				308	m	*25*
Agonum (Europhilus) piceum (Linnaeus, 1758)		1			m	*25*
A. (Olisares) viridicupreum (J.A.E. Goeze, 1777)	1		3		m	*50*
Amara (s.str.) *aenea* (De Geer, 1774)	292	58	19	9	m	*100*
Amara (s.str.) *anthobia* Villa et Villa, 1833	2				m	*25*
Amara (s.str.) *communis* (Panzer, 1797)	3	2	19		m	*75*
Amara (s.str.) *convexior* Stephens, 1828		3			m	*25*
Amara (s.str.) *eurynota* (Panzer, 1796)	1		4	9	m	*75*
Amara (s.str.) *familiaris* (Duftschmid, 1812)	2	136	5	2	m	*100*
Amara (s.str.) *lucida* (Duftschmid, 1812)			2		m	*25*
Amara ((s.str.) *lunicollis* Schiødte, 1837		13			m	*25*
Amara (s.str.) *ovata* (Fabricius, 1792)	9	239	126	583	m	*100*
Amara (s.str.) *proxima* Putzeys, 1866				1	m	*25*
Amara (s.str.) *saphyrea* Dejean, 1828	1		1		m	*50*
Amara (s.str.) *similata* (Gyllenhal, 1810)	27	224	310	296	m	*100*
Amara (s.str.) *tibialis* (Paykull, 1798)		2			m	*25*
Amara (Bradytus) apricaria (Paykull, 1790)	1				m	*25*
Amara (Bradytus) consularis (Duftschmid, 1812)	1				m	*25*
Amara (Bradytus) fulva (O. F. Müller, 1776)	1	5			m	*50*
Amara (Curtonotus) aulica (Panzer, 1796)		1	4		m	*50*
Amara (Percosia) equestris (Duftschmid, 1812)			2		m	*25*
Amara (Zezea) chaudoiri Schaum,1858	3		1		m	*50*
Amara (Zezea) fulvipes (Audinet-Serville, 1821)	1				m	*25*
Amara (Zezea) plebeja (Gyllenhal, 1810)		4			m	*25*
Amblystomus metallescens (Dejean, 1829)	1				m	*25*
Amblystomus rectangulus Reitter, 1883	1				n.a.	*25*
Anchomenus dorsalis (Pontoppidan, 1763)	297	246	875	842	m	*100*
Anisodactylus (s.str.) *binotatus* (Fabricius, 1787)		5		34	m	*50*
A. (Pseudanisodactylus) signatus (Panzer, 1796)			17		m	*25*
Apotomus clypeonitens G. Müller, 1943	1				m	*25*
Asaphidion flavipes (Linnaeus, 1760)	6	88		4	m	*75*
Badister (s.str.) *bullatus* (Schrank, 1798)			1		m	*25*
Badister (s.str.) *unipustulatus* Bonelli, 1813		1			m	*25*
Badister (Trimorphus) sodalis (Duftschmid, 1812)			1	2	D	*50*
Bembidion (Metallina) lampros (Herbst, 1784)		111	4	52	D	*75*
Bembidion (Metallina) properans (Stephens, 1828)	20	38		42	D	*75*
B. (s.str.) *quadrimaculatum* (Linnaeus, 1760)		27		61	m	*50*
B. (Peryphanes) deletum Audinet-Serville, 1821				1	m	*25*
Bembidion (Peryphus) tetracollum Say, 1823		6			D	*25*
Bembidion (Phyla) obtusum Audinet-Serville, 1821		18		3	D	*50*
Brachinus (Brachinus) alexandri F. Battoni, 1984	2				m	*25*
Brachinus (s.str.) *crepitans* (Linnaeus, 1758)	3		398	13	m	*75*
Brachinus (s.str.) *ejaculans* Fischer-Waldheim, 1828	63				m	*25*
Brachinus (s.str.) *elegans* Chaudoir, 1842	11		1206		m	*50*

Brachinus (s.str.) *psophia* Audinet-Serville, 1821	148				D	*25*
Br. (Brachynidius) bodemeyeri Apfelbeck, 1904			1		n.a.	*25*
Br. (Brachynidius) explodens Duftschmid, 1812	189	35	1500	159	m	*100*
Br. [sp. incertae sedis] *nigricornis* Gebler, 1830	1				n.a.	*25*
Calathus (s.str.) *fuscipes* Goeze, 1777	23	3666	219	5	D	*100*
Calathus (Neocalathus) ambiguus (Paykull, 1790)	4	169	1		m	*75*
Calathus (Neocalathus) cinctus Motschulsky, 1850	6	70			D	*50*
C. (Neocalathus) melanocephalus (Linnaeus, 1758)	1	2	2		D	*75*
Calathus (Neocalathus) mollis (Marsham, 1802)		1			D	*25*
Calosoma (s.str.) *sycophanta* (Linnaeus, 1758)	2				m	*25*
Calosoma (Campatita) auropunctatum (Herbst, 1784)	692		10		m	*50*
Carabus (Archicarabus) montivagus Palliardi, 1825	2				b	*25*
Carabus (Archicarabus) nemoralis O. F. Müller, 1836		4			b	*25*
Carabus (Archicarabus) wiedemanni Ménétriés, 1836	1				b	*25*
Carabus (s.str.) *granulatus* Linnaeus, 1758	2	68		1	D	*75*
Carabus (Chrysocarabus) auronitens Fabricius, 1792				1	b	*25*
Carabus (Eucarabus) ulrichii Germar, 1824			2		b	*25*
Carabus (Megodontus) violaceus Linnaeus, 1758			36		b	*25*
Carabus (Morphocarabus) hampei Kuster, 1846			1		b	*25*
Carabus (Pachystus) glabratus Paykull, 1790			1		b	*25*
Carabus (Pachystus) hortensis Linnaeus, 1758		1			b	*25*
Carabus (Procrustes) coriaceus Linnaeus, 1758	45		20		b	*50*
Carabus (Tachypus) auratus Linnaeus, 1761		10			b	*25*
Carabus (Tachypus) cancellatus Illiger, 1798			11		b	*25*
Carabus (Tomocarabus) convexus Fabricius, 1775	1		4		b	*50*
C. (Trachycarabus) scabriusculus G.-A. Olivier, 1795			1		b	*25*
Carterus (Carterus) dama (P. Rossi, 1792)	2				n.a.	*25*
Cicindela (Cicindela) campestris Linnaeus, 1758	4		1		m	*50*
Chlaenius (Chlaeniellus) vestitus (Paykull, 1790)	1				m	*25*
*Chlaenius (Dinodes) decipiens (*L. Dufour, 1820)	70		6		m	*50*
Chl. (Trichochlaenius) aeneocephalus Dejean, 1826	498				m	*25*
Clivina (Clivina) fossor (Linnaeus, 1758)		29	6	21	D	*75*
Cychrus caraboides (Linnaeus, 1758)		1			b	*25*
Cylindera (s.str.) *germanica* (Linnaeus, 1758)			87		m	*25*
Demetrias (s.str.) *atricapillus* (Linnaeus, 1758)		5			m	*25*
Diachromus germanus (Linnaeus, 1758)	1	1		9	m	*75*
Dixus obscurus (Dejean, 1825)	5				n.a.	*25*
Dolichus halensis (Schaller, 1783)			15		m	*25*
Drypta (s.str.) *dentata* (P. Rossi, 1790)	1				m	*25*
Gynandromorphus etruscus (Quensel, 1806)	19				m	*25*
Harpalus (s.str.) *affinis* (Schrank, 1781)	4	135	18	294	m	*100*
Harpalus (s.str.) *caspius* (Steven, 1806)	1		17		m	*50*
Harpalus (s.str.) *cupreus* Dejean, 1829	25				m	*25*
Harpalus (s.str.) *dimidiatus* (P. Rossi, 1790)				16	m	*25*
Harpalus (s.str.) *distinguendus* (Duftschmid, 1812)	714	59	64		m	*75*
Harpalus (s.str.) *flavicornis* Dejean, 1829	52		1		D	*50*
Harpalus (s.str.) *fuscicornis* Ménétriés, 1832	2				m	*25*
Harpalus (s.str.) *hospes* Sturm, 1818	5		6		m	*50*
Harpalus (s.str.) *latus* (Linnaeus, 1758)		3			m	*25*
Harpalus (s.str.) *luteicornis* (Duftschmid, 1812)				1	m	*25*
Harpalus (s.str.) *pygmaeus* Dejean, 1829	14				m	*25*
Harpalus (s.str.) *rubripes* (Duftschmid, 1812)	8	24	1		m	*75*
Harpalus (s.str.) *serripes* (Quensel, 1806)	82				m	*25*
Harpalus (s.str.) *smaragdinus* (Duftschmid, 1812)	11				m	*25*
Harpalus (s.str.) *subcylindricus* Dejean, 1829	13		3		m	*50*
Harpalus (s.str.) *tardus* (Panzer, 1796)	10	4			m	*50*

H. (s.str.) *xanthopus* Gemminger et Harold, 1868	1	1			m	*50*
H. (Pseudoophonus) calceatus (Duftschmid, 1812)	1		4	1	m	*75*
Harpalus (Pseudoophonus) griseus (Panzer, 1796)	1		21		m	*50*
Harpalus (Pseudophonus) rufipes (De Geer, 1774)	39	267	640	268	m	*100*
H. (Semiophonus) signaticornis (Duftschmid, 1812)	10	187	4	1	m	*100*
Laemostenus (Pristonychus) cimmerius (Fischer-Waldheim, 1823)	1				b	*25*
Laemostenus (Pristonychus) terricola (Herbst, 1784)			1		D	*25*
Licinus (s.str.) *depressus* (Paykull, 1790)	2				D	*25*
Limodromus assimilis (Paykull, 1790)		84		1	m	*50*
Loricera (s.str.) *pilicornis* (Fabricius, 1775)		444		34	m	*50*
Microlestes apterus Holdhaus, 1904			1		b	*25*
Microlestes corticalis (L. Dufour, 1820)	26				m	*25*
Microlestes fissuralis (Reitter, 1901)	114				D	*25*
Microlestes fulvibasis (Reitter, 1901)	33				b	*25*
Microlestes maurus (Sturm, 1827)	13		2		D	*50*
Microlestes minutulus (Goeze, 1777)	215	1		1	D	*75*
Microlestes negrita (Wollaston, 1854)	9				D	*25*
Microlestes plagiatus (Duftschmid, 1812)	1				m	*25*
Microlestes schroederi Holdhaus, 1912	6				m	*25*
Nebria (s.str.) *brevicollis* (Fabricius, 1792)	8	1474	4	2	m	*100*
Notiophilus aestuans Dejean, 1826	1	38			D	*50*
Notiophilus biguttatus (Fabricius, 1779)	1	41			D	*50*
Notiophilus germinyi Fauvel, 1863			1		D	*25*
Notiophilus palustris (Duftschmid, 1812)		4			D	*25*
Ophonus (Hesperophonus) azureus (Fabricius, 1775)	14		3		D	*50*
Ophonus (Hesperophonus) cribricollis (Dejean, 1829)	38				m	*25*
O. (Metophonus) brevicollis (Audinet-Serville, 1821)			1		m	*25*
Ophonus (Metophonus) puncticollis (Paykull, 1798)			4		m	*25*
Ophonus (Metophonus) rufibarbis (Fabricius, 1792)			1		m	*25*
Ophonus (s.str.) *ardosiacus* (Lutshnik, 1922)			1	1	m	*50*
Ophonus (s.str.) *diffinis* (Dejean, 1829)	1				m	*25*
Ophonus (s.str.) *sabulicola* (Panzer, 1796)	3		8		m	*50*
Parophonus (s.str.) *laeviceps* (Ménétriés, 1832)	36				m	*25*
Parophonus (s.str.) *mendax* (P. Rossi, 1790)	26				m	*25*
Parophonus (s.str.) *maculicornis* (Duftschmid, 1812)	1			1	m	*50*
Parophonus (s.str.) *planicollis* (Dejean, 1829)	6				m	*25*
P. (Ophonomimus) hirsutulus (Dejean, 1829)	3				m	*25*
Pedius inquinatus (Sturm, 1824)	6				D	*25*
Poecilus (Ancholeus) puncticollis (Dejean, 1828)	8				m	*25*
Poecilus (s.str.) *anatolicus* (Chaudoir, 1850)	9				m	*25*
Poecilus (s.str.) *cupreus* (Linnaeus, 1758)	543	4014	1760	7126	m	*100*
Poecilus (s.str.) *cursorius* (Dejean, 1828)	193				m	*25*
Poecilus (s.str.) *koyi* Germar, 1823			3		m	*25*
Poecilus (s.str.) *kugelanni* (Panzer, 1797)		1			m	*25*
Poecilus (s.str.) *lepidus* (Leske, 1785)		33			D	*25*
Poecilus (s.str.) *punctulatus* (Shaller, 1783)		2			m	*25*
Poecilus (s.str.) *versicolor* (Sturm, 1824)		92	2		m	*50*
Polystichus connexus (Geoffroy in Fourcroy, 1785)	2				m	*25*
Pterostichus (Adelosia) macer (Marsham, 1802)	12		3		m	*50*
Pterostichus (Argutor) vernalis (Panzer, 1796)		12		7	D	*50*
Pterostichus (Bothriopterus) oblongopunctatus (Fabricius, 1787)		2			D	*25*
Pt. (Feronidius) hungaricus (Dejean, 1828)			33		b	*25*
Pterostichus (Feronidius) melas (Creutzer, 1799)			9		b	*25*
Pt. (Petrophilus) melanarius (Illiger, 1798)		1654	13	663	D	*75*
Pterostichus (Phonias) strenuus (Panzer, 1796)		9			D	*25*
Pterostichus (Platysma) niger (Schaller, 1783)		4		1	D	*50*

Pt. (Pseudomaseus) anthracinus (Illiger, 1798)	1			73	D	*50*
Pterostichus (Steropus) madidus Fabricius, 1775		35			D	*25*
Scybalicus oblongiusculus (Dejean, 1829)	1				m	*25*
Stenolophus (s.str.) *abdomialis* Gene, 1836	1				m	*25*
Stenolophus (s.str.) *teutonus* (Schrank, 1781)				1	m	*25*
Stomis (s.str.) *pumicatus* (Panzer, 1796)				2	D	*25*
Syntomus obscuroguttatus (Duftschmid, 1812)	43	1			m	*50*
Syntomus pallipes (Dejean, 1825)	2				D	*25*
Synuchus (s.str.) *vivalis* (Illiger, 1798)		2			D	*25*
Tachys (Paratachys) bistriatus (Duftschmid, 1812)	3				m	*25*
Tachys (s.str.) *scutellaris* (Stephens, 1828)				11	m	*25*
Tachyura (s.str.) *parvula* (Dejean, 1831)	1				m	*25*
Thalassophilus longicornis (Sturm, 1825)		3			m	*25*
Trechus (Epaphius) secalis Paykull G., 1790		1			b	*25*
Trechus (s.str.) *irenis* Csiki, 1912	1				n.a.	*25*
Trechus (s.str.) *quadristriatus* (Schrank, 1781)	42	360	8	66	m	*100*
Zabrus (s.str.) *tenebrioides* (Goeze, 1777)	7		3		m	*50*
Zuphium olens (Rossi, 1790)	13				m	*25*
Number of specimens = 37912	**5018**	**14285**	**7576**	**11033**		
Number of species = 179	107	68	71	45		
Number of **m** species = 116	78	41	48	31		
Number of **D** species = 36	18	22	11	13		
Number of **b** species = 21	6	5	11	1		
Number of **n.a.** species = 6	5		1			