

Article

Landscape Heterogeneity Determines the Diversity and Life History Traits of Ground Beetles (Coleoptera: Carabidae)

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Abstract: Functional diversity is crucial to ecosystem functioning in agricultural landscapes. Intensive agriculture has led to habitat homogeneity and thus a decrease in biodiversity and the disappearance of useful epigeic fauna. This study investigated how local habitat types in an agricultural landscape affect the assemblage parameters (abundance, species richness and Shannon–Wiener diversity index) and life history traits of ground beetles (Coleoptera: Carabidae). The study was conducted in four habitat types: Orchard, meadow, shrubs, and forest. In each type, 12 sampling transects were selected, in which individuals were caught in pitfall traps. Non-metric multidimensional scaling revealed significant differences in ground beetle (Coleoptera: Carabidae) assemblage composition between habitats. The generalized linear model showed that the habitat type influenced the beetles' assemblage parameters and life history traits. Abundance, number of species, and species diversity were highest in the orchard. The occurrence of large brachypterous predators was also strongly dependent on habitat heterogeneity. Their presence in the orchard depended on their distance from semi-natural habitats (shrubs or forest). The results underscore the importance of habitat heterogeneity for populations of predatory Carabidae in intensively used agricultural landscapes and demonstrate the role of functional parameters, providing detailed information on agroecosystem condition and functioning.

Keywords: landscape heterogeneity; semi-natural habitats; carabids; functional traits; predators; body size; dispersal ability



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1. Introduction

The landscapes most severely transformed by human activity include agricultural landscapes [1–3]. Changes in land use, intensive agriculture, and habitat fragmentation or homogeneity result in changes in the abiotic parameters of the agroecosystem (e.g., soil and hydrological parameters) as well as in biotic parameters, such as species number or species diversity. According to many authors, it is this type of activity that has been the greatest cause of the decline in overall biodiversity in the agricultural landscape [4–11]. For this reason, many programs and strategies are implemented with the aim of restoring the lost natural value of these areas, thereby also increasing their species and functional diversity [12–14].

Particular focus is placed on the number and diversity of habitats that can potentially be colonized by animals and plants [15–17]. A number of studies have shown that spatiotemporal landscape heterogeneity has a positive effect on biodiversity [18–21]. This applies to various groups of organisms, including plants, vertebrates, and invertebrates [15,22–24], and therefore, it is an important factor that should be taken into account in biodiversity conservation [17]. The creation of greater habitat diversity and accessibility is crucial not only to the biodiversity of these areas per se but also in terms of important

ecological functions, such as pest management, in which specific species are used to control crop pests [25,26]. Increasing the area of semi-natural habitats (meadows, shrubs, or woodland remnants) and their distribution in a mosaic pattern within a landscape used intensively for agriculture maintains refuges and increases the chances of colonization, including by predators that are useful in agroecosystems [27].

One useful group with an important role in agroecosystems is ground beetles (Coleoptera: Carabidae), a highly diverse family whose taxonomy and ecology are well known [28–30]. These invertebrates are common inhabitants of agricultural landscapes and regulate populations of numerous pests, such as Collembola, Diptera, or Hemiptera (e.g., aphids). Herbivorous species that eat the seeds of weeds are also allies of farmers [31]. In addition, ground beetles (especially habitat specialists) are sensitive to changes in the natural environment and, therefore, often serve as bioindicators in ecological studies, warning not only of disturbances in the environment but also of the rate and efficiency of its restoration [32–35]. While analyses very often compare the general parameters of assemblages, such as abundance, species richness, or species diversity, the distribution of life history traits can be a useful indicator as well [36,37]. According to [17], the species filtered by landscape heterogeneity represent the pool of species suitably adapted to the habitat conditions on both a local and regional scale (specialist species). A disturbance of these conditions results in an increased proportion of habitat generalists in assemblages [23,36].

The aim of the study was to determine the abundance of ground beetles (Coleoptera: Carabidae) and the distribution of their life history traits in a mosaic of orchard and semi-natural habitats in an agricultural landscape. This knowledge is extremely important, as species with specific life history traits perform crucial functions in ecosystems, particularly as predators regulating populations of pests in intensively managed agroecosystems. There have been few studies on the influence of landscape diversity and semi-natural habitats close neighborhood on the life history traits of ground beetles, i.e., body size, wing development, and feeding preferences, in a food orchard.

2. Material and Methods

2.1. Study Site

The study was carried out at the experimental Station of the Agricultural University in Krakow, located in southern Poland, about 10 km from Krakow, in the village of Garlica Murowana (50°8'25" N 19°55'39" E, Figure 1). The area has a typical intensive agricultural landscape as well as fragments of semi-natural habitats (shrubs, forest fragments, and meadows).

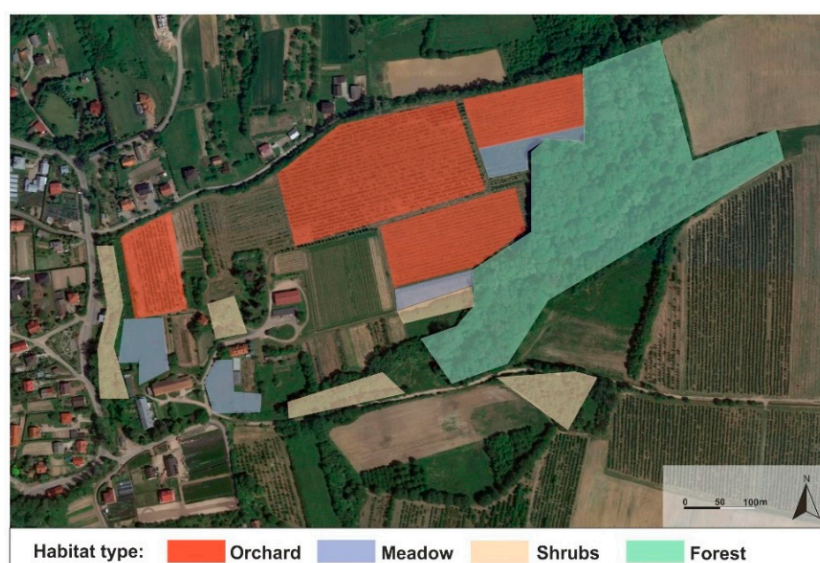


Figure 1. The map of the study area.

The area of the station is about 10 ha and is covered mainly by fruit orchards (primarily apple trees, but also pear, sour cherry, and peach) and a vineyard, interspersed with semi-natural habitats of varying area and shape, such as shrubs and meadows. The soil at the station is brown soil consisting of clayey silt in the humus layer, with average organic carbon content of 6.92 ± 0.29 g/kg, average pH_{KCL} 5.4 ± 0.21 , and $\text{pH}_{\text{H}_2\text{O}}$ 6.2 ± 0.23 . In the immediate vicinity of the station, there is a woodland area of about 6 ha.

Sampling transects were set up in the study area for the purpose of collecting ground beetles. Four habitat types were selected: Orchard (Or), meadow (Me), shrubs (Sh), and forest (Fo). Within each habitat type 12 sampling plots were designated, arranged in a mosaic, and at different distances from the forest. The orchard habitat (or, mean size of about 0.26 ha) is an intensive apple orchard situated in an area with heterogeneous habitats. Fruit trees (mainly apple) were planted in even rows about 4 m apart. Perennial meadow grasses grow between the rows. The tree crowns are cut regularly, and plant protection products are applied in compliance with the principles of Integrated Pest Management. The meadow habitat (Me, mean size about 0.71 ha) consisted of irregular patches (mowed twice during the growing season) of numerous species typical for *Arrhenatheretalia* group and *Molinio-Arrhenatheretea* class. Among them, the most common in all patches were, for example, *Dactylis glomerata*, *Phleum pratense*, *Carum carvi*, *Taraxacum officinale*, *Lotus corniculatus*, *Alopecurus pratensis*, and *Centaurea jacea*. The shrub habitat (Sh, mean size about 0.27 ha) consisted of irregular patches overgrown with shrubs and isolated trees. Among them, the most dominant were *Crataegus* sp., *Prunus spinosa*, *Rosa canina*, *Cornus sanguinea*, *Sambucus nigra* as well as *Quercus robur*, *Carpinus betulus* and *Ulmus* sp. The forest habitat (Fo) was selected within a mixed forest adjacent to the experimental station. The species composition of this community consists of native species of trees and shrubs of the multi-species *Querco-Carpinetum* medioeuropaeum association, in which mainly *Carpinus betulus*, *Quercus robur*, and *Acer pseudoplatanus* are dominant.

2.2. Ground Beetles Sampling

Ground beetles (Coleoptera: Carabidae) were caught from April to September 2020. Samples were collected four times: In May, June, September, and October. The traps were closed in the summer (July and August) due to the decreased activity of ground beetles [28] and re-opened at the beginning of September to collect autumn samples. Beetles were collected using Barber traps, consisting of plastic cups (7 cm in diameter and 10 cm high) filled up to one-third with ethylene glycol as a preservative. There were 12 sampling transects for each habitat type. Three traps were placed within each transect (parallel to the trees in the orchard and in the other habitats depending on their shape). The distance between traps was about 5–10 m (depending on the shape and size of the habitat patch). Where possible, traps were placed at least 15 m from the edge of the plots. However, due to the shape of some of the plots, this was not always possible.

The individuals were identified at the species level using taxonomic keys [38,39]. Data from the three traps in each sampling transect and four collection periods were pooled. Then the basic parameters of the assemblages were calculated: Abundance (the total number of beetles per transect), species richness (the total number of species found in the transect), and Shannon–Wiener species diversity for each sampling transect [40]. Body size, wing development, and food preferences were analyzed in order to determine whether the life history traits of ground beetles were associated with the habitat type [41,42]. In the case of body size, two size classes were used: Small (<10 mm; abbr. Sm) and large (>10 mm, abbr. La). With respect to wing development, ground beetles (Coleoptera: Carabidae) species were classified as brachypterous (with no or reduced wings, abbr. Br) and macropterous (abbr. Ma). In the case of feeding strategy, they were classified as predators (abbr. Pr) or hemizoophages (abbr. He). Basically, the morphological and life history traits were taken from Hürka [39], additionally, body size and wing development were measured during the species identification.

2.3. Data Analysis

Spatial autocorrelation was tested using Moran's I index for species richness of Carabidae (Past 4.03 software) [43]. Spatial correlograms were constructed using Moran's I at 10 distance classes. The Shapiro–Wilk test was used to test the data for normality of distribution using Statistica 13.0 software [44]. As the variables did not have a normal distribution, nonparametric tests were used. Non-metric multidimensional scaling (NMDS) was used to analyze the differences between the compositions of ground beetle assemblages inhabiting the four habitats: Meadow, shrubs, orchard, and forest. ANOSIM with the Bray–Curtis dissimilarity matrix was performed with 499 permutations of the data to show the significance of dissimilarity differences between habitat types. Similarity percentage analyses (SIMPER) were performed to determine the relative contribution of the various species and to reveal an indicator species in each habitat type (Past 4.03 software) [43]. The differences between ground beetle parameters (abundance, species richness, and Shannon–Wiener diversity index) as well as life history traits (body size, wing development, and food preferences) in relation to habitat types were tested using a generalized linear mixed effect model (GLMM) for Poisson distribution (Wald statistics), where sampling transects were random factors and the fixed effects included habitat type [44]. The Kruskal–Wallis nonparametric analysis of variance was used to assess differences in species abundance of the most dominant orchard ground beetles (Coleoptera: Carabidae) among habitats. The NMDS, GLMM analyses, and Kruskal–Wallis test were performed in the Statistica 13.0 software [44].

3. Results

A total of 3547 ground beetle individuals belonging to 37 species were collected. There were 15 species caught on the forest plots, 29 in the orchard, 22 in the meadow, and 21 in the shrubs. The species *Pseudoophonus rufipes*, *Harpalus affinis*, *Pterostichus melanarius*, and *Poecilus versicolor* were the most abundant in the total sample (respectively 9%, 7%, 6%, and 6%). The species composition of Carabidae from different habitat types revealed significant differences in species dominance. In the orchard, the dominant were *Harpalus affinis* (15%), *Pseudoophonus rufipes* (13%), and *Amara familiaris* (8%). In the meadow habitats, *Poecilus versicolor* (11%), *Harpalus affinis* (10%), *Pterostichus melanarius* (11%), *Amara aenea* (10%), and *Amara familiaris* (8%) were the most abundant. The highest dominance in the shrubs was *Pseudoophonus rufipes* (17%), *Pterostichus niger* (14%), *Pterostichus strenuus* (11%), as well as *Poecilus versicolor* (10%) and *Harpalus atratus* (9%). In the forest stands, the most abundant were *Leistus piceus* (21%), *Pterostichus niger* (16%), *Pseudoophonus rufipes* (11%), and *Leistus rufomarginatus* (11%).

Non-metric multidimensional scaling (NMDS) revealed differences between the assemblages collected in each habitat type (Figure 2a). The ANOSIM analysis indicated significant differences between the assemblages collected in habitat types: Or-Me ($R = 0.60$, $p < 0.001$), Or-Sh ($R = 0.85$, $p < 0.001$), Or-Fo ($R = 0.99$, $p < 0.001$), Me-Sh ($R = 0.89$, $p < 0.001$) and Sh-Fo ($R = 0.48$, $p < 0.001$). The NMDS analysis also showed that the habitat type influenced the ground beetle species distribution (Figure 2b).

Species that mainly prefer typical forest habitats (e.g., *Carabus* sp., *Pterostichus* sp., *Leistus* sp.) and are highly sensitive to disturbances, were associated with forest (Fo), but in some cases, were also components of orchard assemblages (Or) (*Carabus granulatus*). Furthermore, in the orchard areas, mainly species with broader ecological plasticity were found like, e.g., *Harpalus affinis*, *Pseudoophonus rufipes*, or *Poecilus versicolor*. In shrub (Sh) and meadow (Me) areas, we found mainly open area species, characteristic for agroecosystems (e.g., *Amara similata*, *Amara communis*, *Bembidion lampros*).

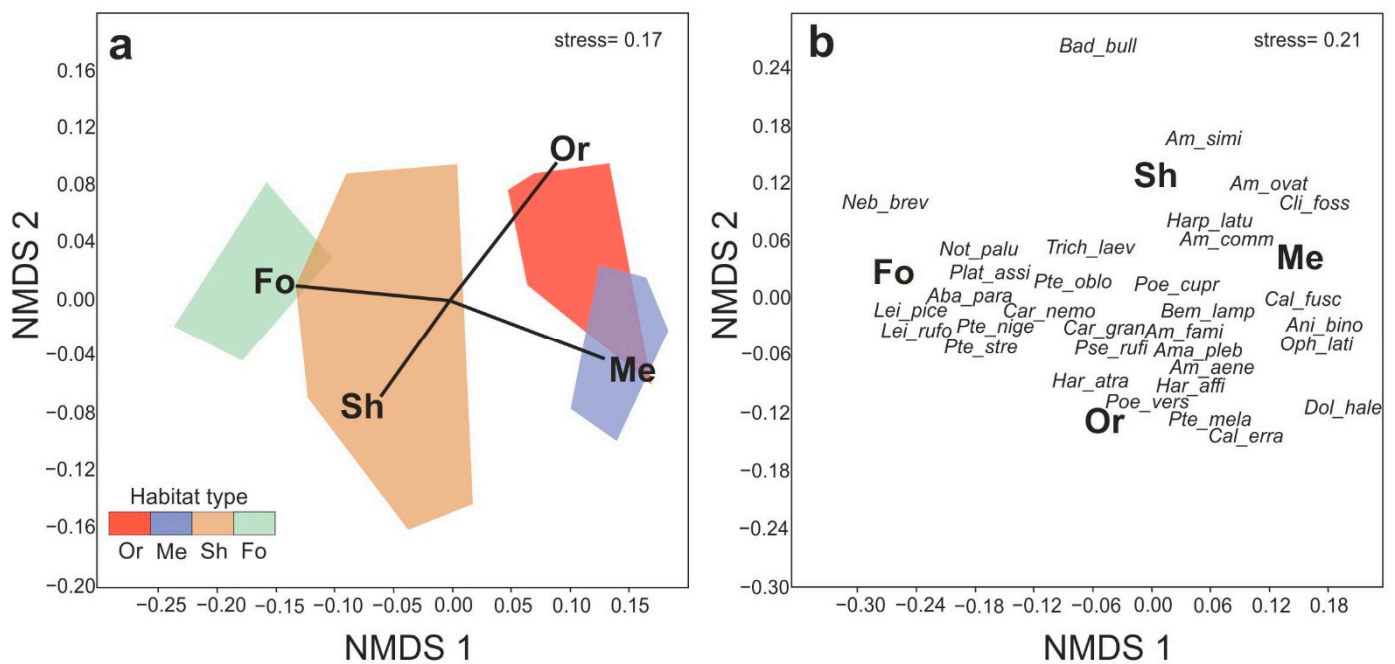


Figure 2. Non-metric multidimensional scaling ordination of ground beetle (Coleoptera: Carabidae) assemblages (a) and species distribution (b). Assemblages from individual habitat types are designated as follows: Or-orchard, Me-meadow, Sh-shrubs, and Fo-forest.

A difference in the composition of ground beetles according to habitat type was also shown by the SIMPER analysis (Table 1). Species characteristic (indicator species) for orchard habitat (Or) were *Harpalus affinis*, *Pseudoophonus rufipes*, *Carabus granulatus*, *Harpalus atratus*, and *Bembidion lampros*. In the case of meadow habitat (Me), the indicators species were *Harpalus affinis*, *Pterostichus melanarius*, *Poecilus versicolor*, *Amara aenea*, *Amara familiaris*, *Bembidion properans*, *Amara plebeja*, as well as *Carabus cancellatus*, *Calathus erratus*, and *Poecilus cupreus* (Table 1). Only three species: *Pterostichus strenuus*, *Pterostichus oblongopunctatus*, and *Pseudoophonus rufipes* were characteristics ground beetles in shrubs (Sh). Forest habitat (Fo) was described mainly by *Leistus piceus*, *Pterostichus niger*, *Carabus nemoralis*, *Leistus rufomarginatus*, *Abax parallelepipedus*, *Nothioplus palustris*, and *Platynus assimilis* (Table 1).

Table 1. Simper analysis for the ground beetles species contributing more than 1% to the dissimilarity between orchard (Or), meadow (Me), shrubs (Sh), and forest (Fo) assemblages.

Taxon	Mean Abundance				Average Dissimilarity	Contribution (%)
	Or	Me	Sh	Fo		
<i>Harpalus affinis</i> (Schrank von Paula, 1781)	10.8	10.8	0.0	0.0	5.77	7.35
<i>Pseudoophonus rufipes</i> (Ch. De Geer, 1774)	9.3	7.7	8.6	8.4	5.71	7.27
<i>Leistus piceus</i> (Frölich, 1799)	0.0	0.0	1.8	16.2	5.29	6.73
<i>Pterostichus niger</i> (Schaller, 1783)	0.3	0.0	6.8	12.1	5.23	6.66
<i>Pterostichus melanarius</i> (J.K.W. Illiger, 1798)	3.2	10.5	3.3	0.0	4.69	5.97
<i>Poecilus versicolor</i> (J. Sturm, 1824)	0.3	10.9	5.2	0.0	4.56	5.80
<i>Amara familiaris</i> (C. Duftschmid, 1812)	5.8	8.3	0.0	0.0	3.73	4.75
<i>Amara aenea</i> (Ch. De Geer, 1774)	2.8	9.7	0.4	0.0	3.71	4.72
<i>Carabus nemoralis</i> (O.F. Müller, 1764)	4.4	0.0	2.5	5.9	3.31	4.22
<i>Leistus rufomarginatus</i> (C. Duftschmid, 1812)	0.0	0.0	2.8	8.4	3.26	4.15
<i>Carabus granulatus</i> (E.G. Kraatz)	5.6	2.8	0.0	4.8	3.13	3.99
<i>Bembidion properans</i> (J.F. Stephens, 1828)	5.0	6.8	0.0	0.0	3.10	3.95

Table 1. Cont.

Taxon	Mean Abundance				Average Dissimilarity	Contribution (%)
	Or	Me	Sh	Fo		
<i>Amara plebeja</i> (L. Gyllenhal, 1810)	5.2	6.6	0.0	0.0	3.10	3.95
<i>Harpalus atratus</i> (Latreille, 1804)	5.4	0.0	4.3	0.4	3.00	3.83
<i>Carabus cancellatus</i> (J.K.W. Illiger, 1798)	4.4	5.3	0.8	0.0	2.73	3.48
<i>Pterostichus strenuus</i> (Panzer, 1796)	0.0	0.0	5.3	3.1	2.51	3.20
<i>Abax parallelepipedus ater</i> (C. Villers)	0.2	0.0	1.6	4.5	1.97	2.51
<i>Calathus erratus</i> (C.R. Sahlberg, 1827)	0.0	5.9	0.2	0.0	1.96	2.50
<i>Notiophilus palustris</i> (C. Duftschmid, 1812)	0.2	0.0	0.5	4.8	1.78	2.27
<i>Bembidion lampros</i> (J.F.W. Herbst, 1784)	2.7	2.5	0.0	0.0	1.49	1.89
<i>Platynus assimilis</i> (G. Paykull, 1790)	0.7	0.0	1.3	3.0	1.45	1.84
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	1.4	0.0	2.8	1.7	1.39	1.77
<i>Poecilus cupreus</i> (Linnaeus, 1758)	0.8	2.5	0.9	0.3	1.15	1.47

The habitat type was shown to have a statistically significant influence on all analyzed parameters of the structure of ground beetle assemblages, i.e., total abundance, species richness, and species diversity, as well as the abundance of ground beetles with specific life history traits (Table 2). Spatial autocorrelation of ground beetle parameters and life history traits between transects were not significant (Table 2).

Table 2. GLMM results showing the effect of habitat type with sampling transects as a random factor and ground beetle (Coleoptera: Carabidae) assemblage parameters and abundance of ground beetle life history traits and spatial autocorrelation (Moran's I).

		Variable	df	Wald Stat.	<i>p</i>	Spatial Autocorrelation	
Assemblage parameter						Moran's I	<i>p</i>
Abundance		Habitat type (sampling transects)	3	176.8	<0.0001	0.16	0.269
Species richness		Habitat type (sampling transects)	3	18.1	0.0004	0.19	0.274
Shannon Diversity index		Habitat type (sampling transects)	3	32.4	<0.0001	0.12	0.265
Life-history trait							
Body size	Small (<10 mm)	Habitat type (sampling transects)	3	386.9	<0.0001	0.44	0.275
	Large (>10 mm)	Habitat type (sampling transects)	3	231.3	<0.0001	0.23	0.257
Wing development	Brachypterous	Habitat type (sampling transects)	3	192.2	<0.0001	0.36	0.245
	Macropterous	Habitat type (sampling transects)	3	208.6	<0.0001	0.37	0.273
Food preferences	Hemizoophages	Habitat type (sampling transects)	3	417.1	<0.0001	0.47	0.275
	Predators	Habitat type (sampling transects)	3	205.5	<0.0001	0.15	0.259

The highest abundance, species richness, and Shannon diversity were noted in meadow habitats (Figure 3a–c). Moreover, orchard habitats had high values of abundance, species richness, and Shannon diversity index. The orchard is situated in the center of a farm, and the sampling plots located in this habitat type were mainly adjacent to semi-natural habitats (shrubs, forest, and meadow).

In addition, the orchard is characterized by varied environmental conditions, and therefore diverse species can be found here (open-area or forest species). In the case of shrub and forest, the number of species and diversity were lower than in other habitat types (Figure 3b,c).

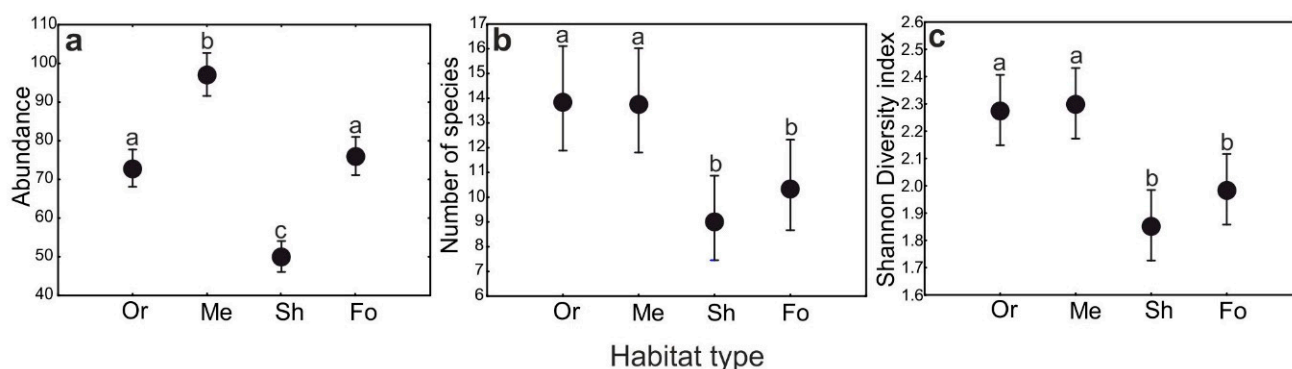


Figure 3. Mean \pm SE abundance (a), species richness (b), and Shannon diversity (c) of the ground beetle (Coleoptera: Carabidae) assemblages in the four habitat types (Or-orchard, Me-meadow, Sh-shrub, Fo-forest). Different letters indicate significant differences between habitats. Multiple comparisons of means were performed using the Bonferroni test at 0.05 significance.

The habitat type was shown to have a statistically significant influence on the life history traits of ground beetles, i.e., body size, wing development, and food preferences (Table 2). The highest number of ground beetles in the large body size class was observed in the forest environment (Figure 4a).

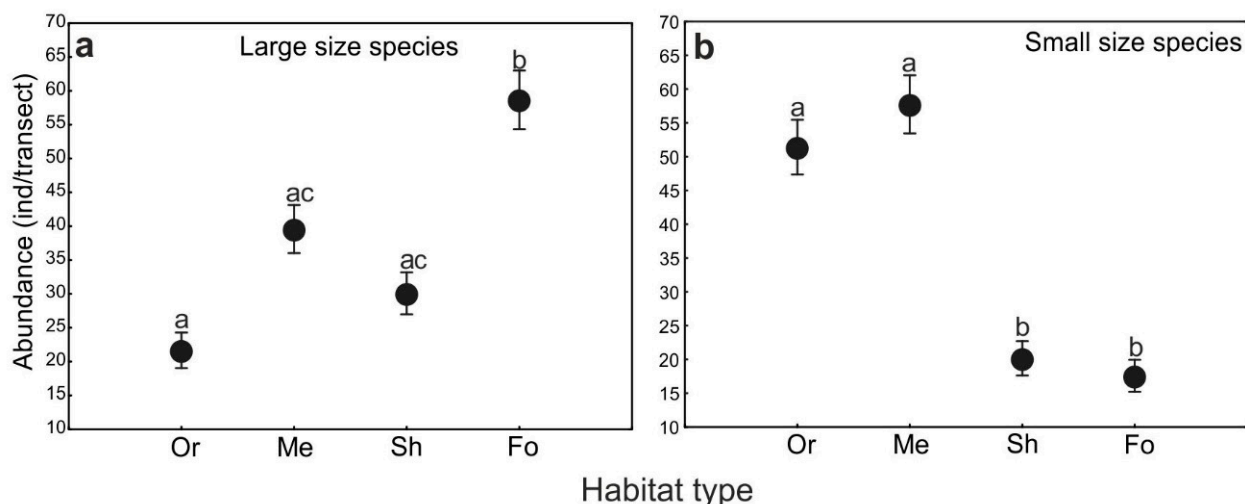


Figure 4. Mean \pm SE abundance of ground beetles (Coleoptera: Carabidae) according to body size class: (a) Large size species, (b) small size in four habitat types (Or-orchard, Me-meadow, Sh-shrub, Fo-forest). Different letters indicate significant differences between habitats. Multiple comparisons of means were performed using the Bonferroni test at 0.05 significance.

The fewest large ground beetle species were found in the orchards and shrubs. Species in the small body size class were most abundant in the meadows as well as in orchards (Figure 4b). In the case of wing development, there were also statistically significant differences depending on the habitat type (Table 2). Brachypterous species were most abundant in the forest (forest specialists), whereas species with high dispersal power were abundant in the meadow and also in the orchard (Figure 5a,b).

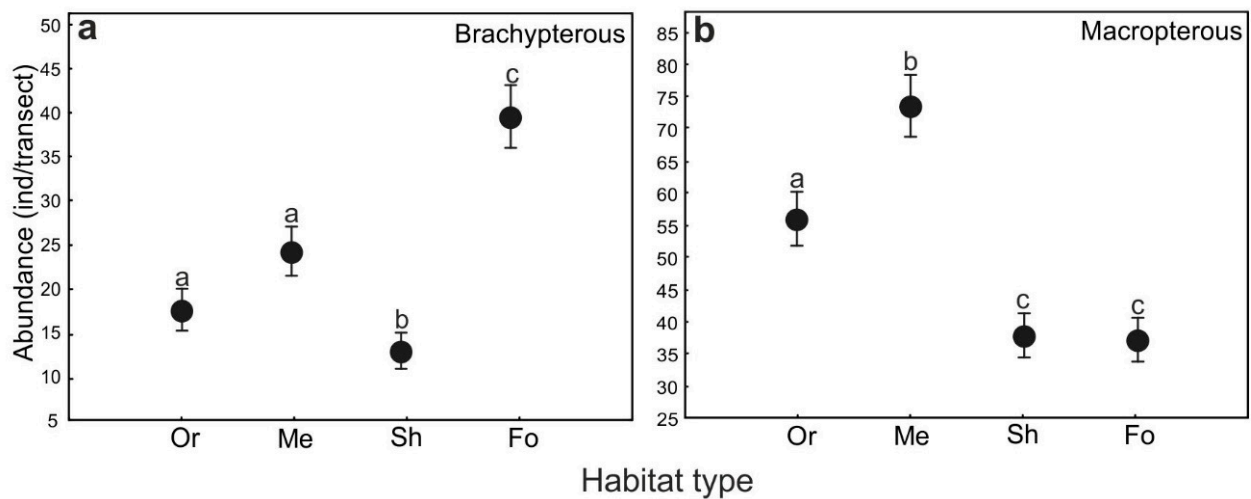


Figure 5. Mean \pm SE abundance of ground beetles (Coleoptera: Carabidae) according to wing morphology: (a) Brachypterous, (b) macropterous in four habitat types (Or-orchard, Me-meadow, Sh-shrub, Fo-forest). Different letters indicate significant differences between habitats. Multiple comparisons of means were performed using the Bonferroni test at 0.05 significance.

The distribution of ground beetle species with specific food preferences (predators and hemizoophages) is a very important functional trait in agroecosystems (i.e., for regulation of pest populations). The most hemizoophages were noted in the meadows and orchards, and the most predators were found in the forest (Figure 6a,b). In the assemblages in the orchard plots, the abundance of predators was the lowest compared to other habitats (Figure 6a).

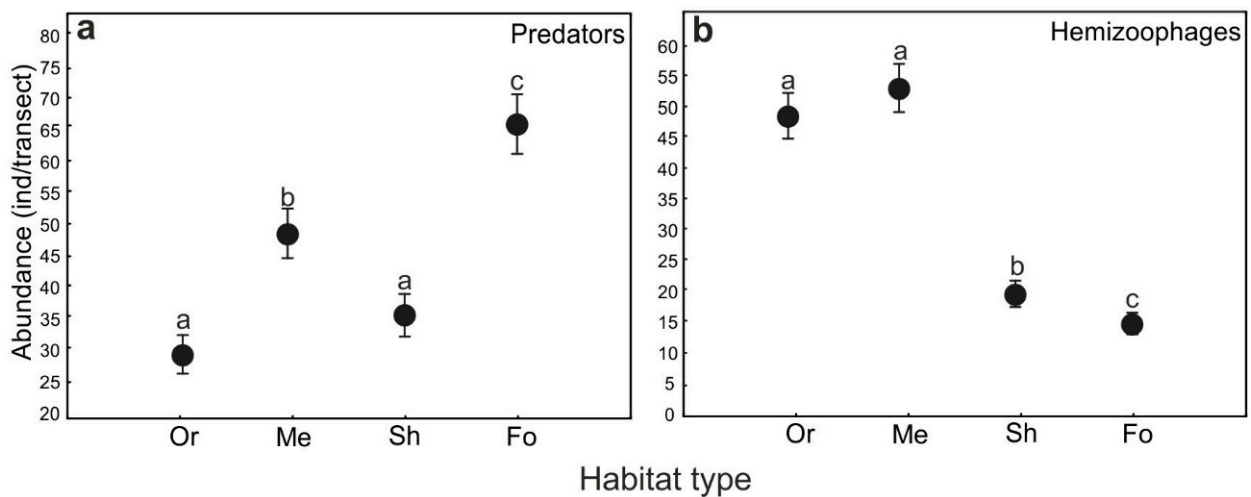


Figure 6. Mean \pm SE abundance of ground beetles (Coleoptera: Carabidae) according to food preferences: (a) Predators, (b) hemizoophages in four habitat types (Or-orchard, Me-meadow, Sh-shrub, Fo-forest). Different letters indicate significant differences between habitats. Multiple comparisons of means were performed using the Bonferroni test at 0.05 significance.

Significant differences were observed in the distribution of the most dominant species in orchards compared to other types of habitats (Me, Sh, or Fo) (Figure 7). Only the mean abundance of *Pseudoophonus rufipes* did not differ significantly and was similar in all habitat types (Figure 7f). In the case of open area species, the most dominant in orchards were *Amara familiaris*, *Amara plebeja*, *Harpalus affinis*, *Bembidion properans*, and *Carabus cancellatus*, species which were also abundant in adjacent meadow habitats (Figure 7a–e). In the case of forest specialists, the most dominant in the orchard were *Carabus nemoralis* and

Carabus granulatus (Figure 7i,j). These species were also abundant in the forest situated near orchards sampling transects.

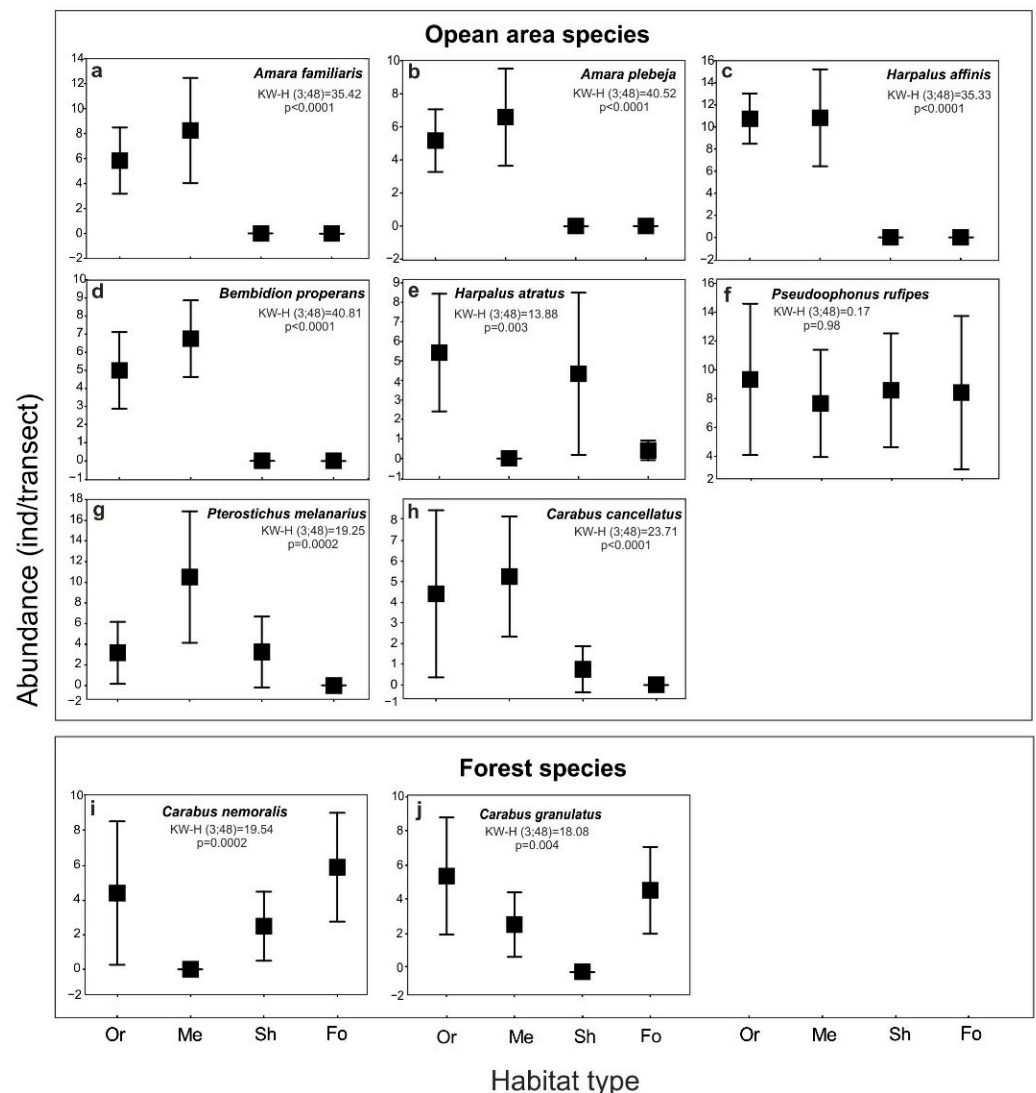


Figure 7. Mean \pm SE abundance of the most dominant orchards (Or) ground beetle (Coleoptera: Carabidae) populations (Open area species: (a) *Amara familiaris*, (b) *Amara plebeja*, (c) *Harpalus affinis*, (d) *Bembidion properans*, (e) *Harpalus atratus*, (f) *Pseudoophonus rufipes*, (g) *Pterostichus melanarius*, (h) *Carabus cancellatus* and Forest species: (i) *Carabus nemoralis*, (j) *Carabus granulatus*) in relation to adjacent habitats (Me-meadow, Sh-shrub, Fo-forest) with Kruskal–Wallis test results.

4. Discussion

High biodiversity is known to be very important in every type of ecosystem, especially in agroecosystems, which, for many years, have been subjected to continuous and intensive disturbances [1,37]. Biological diversity is responsible for ensuring ecosystem balance, and thus a loss of biodiversity disturbs the functioning of the entire ecosystem and the functions of ecosystem services and reduces the resistance of these systems to disturbances. The maintenance of high biodiversity is influenced by numerous factors. Our study focused on the role of habitat diversity in an agricultural landscape, especially with regard to epigenic fauna, which many studies have emphasized can be used to control crop pests [45,46]. This group includes beetles of the family Carabidae [17,36].

A special example of an agricultural landscape is land covered by orchards, in which various species of fruit trees are grown [47,48]. These are often large areas, with regular

rows of trees and herbaceous vegetation growing between the rows. In many cases, these areas are isolated from semi-natural habitats, which can function as refuges for useful epigeic fauna [49]. This influences the diversity of ground beetles. For example, [7] showed significant differences in ground beetle species composition between different habitats located in an intensively cultivated agricultural landscape, while [50] highlighted that landscape fragmentation results in habitat destruction and loss of organisms occurring within the biotope.

It is extremely important to focus not only on diversity or species richness itself, but also on the distribution of species with different life history traits [36]. Analysis of results based only on parameters such as diversity, abundance, or species richness shows that the orchard habitat has high values of these parameters (Figure 3). Could this mean that the ecosystem is functioning normally? In this situation, a detailed analysis of life history traits is necessary. According to [17], functional traits control species response to landscape heterogeneity gradients. Our study placed a special focus on life history traits of importance in agroecosystems, i.e., body size, wing development, and food preferences. Many studies have used the life history parameters of ground beetles to assess the functioning and condition of ecosystems [35,51]. The results of the GLMM analysis indicate that large predatory ground beetles appear in much smaller numbers in the orchard than in the shrubs and forest plots. The dominant species in the orchard were mainly habitat generalists, species with high ecological plasticity and high dispersal power (Figure 7). In addition, the adjacent forest may play an important role in maintaining forest specialists of Carabidae (especially predators).

Does this mean that interweaving a variety of patches of semi-natural habitats (even of small size) into such a landscape can facilitate colonization by predatory ground beetles? The present study was conducted in a single area of orchards (to avoid differences resulting from exposure, soil type, and other factors that might affect the results), within which a mosaic of habitats was interspersed between the areas with orchard cultivation. In addition, immediately adjacent to the study area, there was a fragment of forest that was not transformed by human activity. Forest species of ground beetles were more abundant in the orchard plots that were closer to the shrubs or forest (Figure 7i,j). A short distance from stable forest habitats allows non-flying predatory ground beetles of large body size to migrate [52,53]. The NMDS analysis showed a short distance between the ground beetle assemblages from the habitats with shrubs and the forest assemblages. In addition, some forest specialists were observed in the shrubs, such as *Pterostichus oblongopunctatus*, *P. niger*, and *Carabus cancellatus*. On the orchard and meadow plots, the results showed the highest diversity, species richness, and abundance of ground beetles. These habitats have highly variable environmental conditions, and therefore, mainly smaller, macropterous species characteristic of open areas were observed in the assemblage.

5. Conclusions

We have presented a case study carried out in an agricultural landscape with high habitat heterogeneity (orchards, meadows, shrubs, and forests). With regard to biodiversity conservation measures in the agricultural landscape, our study demonstrates the importance of habitat heterogeneity for maintaining a high functional diversity of ground beetles. The habitats formed in the orchard may create conditions for species with specific life traits, including large predators, but neighboring semi-natural habitats, which are a local reservoir for these species, also play an extremely important role. Another significant factor is the distance from semi-natural areas out of the reach of agricultural activity. To maintain the highest possible functional diversity of ground beetles in the agricultural landscape, it is important to ensure the presence of a large number of semi-natural habitats with varied vegetation structure. Of course, there is a need for further research analyzing the functional diversity of ground beetles in the agricultural landscape, taking into account many other factors affecting agroecosystems.

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