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Characteristics of Fragments of Woodland and Their Influence on the Distribution of Soil Fauna in Agricultural Landscape

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Abstract: Fragments of woodland represent important natural and semi-natural elements that contribute to ecological stability and biodiversity in a landscape. In the Czech Republic, they are part of the Territorial System of Ecological Stability (TSES), which consists of bio-centers, bio-corridors, and interaction elements. The presence of fragments of woodland is of growing importance in the agricultural landscape, where they provide effective protection against soil erosion and serve as a refuge for many animals, whose presence is crucial in maintaining essential ecosystem functions. A functioning ecosystem is especially important in intensively farmed landscapes, which are exposed to frequent and heavy disturbance. Our aim was to evaluate the influence of certain habitat characteristics of fragments of woodland on the activity-density and species richness of selected groups of soil invertebrates (ground beetles, spiders, harvestmen, centipedes, millipedes, and isopods). The research was conducted in the agricultural landscape of South Moravia (Czech Republic) in the summers of 2016–2017, for which we used pitfall traps to collect soil invertebrates on preselected fragments of woodland. The results highlight a wide range of habitat preferences of individual groups of invertebrates, wherein it is not possible to clearly determine the most favorable environmental conditions for all organisms. Consequently, the priority should be to maintain the highest possible degree of heterogeneity among natural and semi-natural features, including with respect to their surrounding landscape. In addition, we found that due to their small size and width, fragments of woodland that are not included in the concept of bio-centers and bio-corridors can similarly support the activity-density and diversity of soil fauna.

Keywords: activity-density; landscape elements; soil fauna; species richness

1. Introduction

Landscape heterogeneity is usually considered an essential precondition for the promotion and conservation of biodiversity [1]. This also applies to the agricultural landscape, where production areas mostly dominate and diversity is supported mainly by the presence of green infrastructure, such as fragments of woodland, hedgerows, windbreaks, grassland, etc. [2–7]. Green infrastructure, a strategically planned network of natural and semi-natural areas with other environmental features that are designed and managed such that they deliver a wide range of ecosystem services, is discussed at the international and European levels [8,9]. In the Czech Republic, this issue is being developed within the Territorial System of Ecological Stability (TSES), which is defined as "an interconnected system of natural and modified near-natural ecosystems keeping the natural balance". The TSES is a designed system consisting of bio-centers, bio-corridors, and interaction elements and is an integral part of territorial plans [10].

The aforementioned eco services of these landscape elements include protection against water and wind erosion, the assurance of water retention in the landscape, and the

preservation of species diversity [11–15]. Pollard and Holland [16] and Valdés et al. [17] consider fragments of woodland to be among the most important non-productive elements of the agricultural landscape.

However, the owners of agricultural land often disturb the structure of fragments of woodland, which can significantly affect the organisms living in them [5,18–20]. Frequent disturbance, typical of agroecosystems [4,21], is usually the result of intensive farming and, as reported by Duelli et al. [1], also leads to a loss of biodiversity. In the Czech Republic, agriculture was considerably intensified during the 20th century. This was related to the redistribution and homogenization of land, which, in many cases, led to the decimation or complete elimination of fragments of woodland and other non-productive areas [21–24]. Sklenička et al. [25] also considers the use of the surrounding land to be a significant factor in the loss of fragments of woodland and scattered landscape greenery. As a result of this management, invertebrate communities have been disturbed and biodiversity in the landscape has decreased [26–28]. However, Skokanová et al. [24] confirm that the creation of bio-centers, bio-corridors (in the sense of fragments of woodland), and other agri-environmental programs currently being introduced can halt the loss of non-productive areas in the agricultural landscape.

In terms of landscape scale, the structure of fragments of woodland varies [5]. However, on a local scale, they are often very similar in structure and species composition [4]. Fragments of woodland may be remnants of larger forest areas; alternatively, they can be artificially created by human activity or the spontaneous spread of seeds [18]. The origins of fragments of woodland influence their vegetative composition and structure [7,11,29], which, in turn, affect other factors, such as light conditions, humidity, temperature, or leaf litter thickness. Many studies have shown that the natural conditions of fragments of woodland significantly affect the invertebrates for which they provide shelter, conditions for overwintering, and food resources [5,30–33]. Invertebrate assemblages inhabiting fragments of woodland are taxonomically very diverse, and in terms of trophic guilds, detritivores, herbivores, and predators are represented here. These organisms provide many indispensable ecosystem services, such as supporting the physical functions of soil, participating in the decomposition of organic matter, protecting against pests and weeds in crops, or constituting a source of food for other animals [16,34–38].

The more diverse the spectrum of invertebrates, the more varied and specific the environmental requirements. However, specific conditions that are ideal for one species or guild may be unfavorable for another [29,39].

In our study, we have focused on epigeic arthropods living in fragments of woodland in an agricultural landscape. Our aim was to clarify the effects of the natural characteristics of fragments of woodland (structural and vegetative character, leaf litter thickness, and soil moisture) on selected taxonomic groups. In addition, we attempted to verify whether the following general assumption, based on the theory of island biogeography [40], could be applied in the agricultural landscape: the larger the area of fragments of woodland, the greater the species richness and abundance of invertebrates. In connection with the general size of fragments of woodland, we also endeavored to answer the question of the importance of a minimum size of 3 ha for local bio-centers and a minimum width of 15 m for local bio-corridors, as stated in the guidelines for their establishment [41].

2. Materials and Methods

2.1. Description of Study Sites

The research site was located in the agricultural landscape of South Moravia around the villages of Šardice (48°58′ N, 17°2′ E), Stavěšice (49°0′ N, 17°2′ E), Čejč (48°57′ N, 16°58′ E), and Hovorany (48°57′ N, 17°0′ E). In this area, 38 fragments of woodlands were selected. These areas represent the remains of larger forests, spontaneously growing linear woodland features, or artificially planted orchards. The most common tree species in these areas are black locust (*Robinia pseudacacia*), blackthorn (*Prunus spinosa*), and elderberry (*Sambucus nigra*). Other frequently occurring tree species include birch (*Betula pendula*),

ash (*Fraxinus excelsior*), linden (*Tilia* spp.), oak (*Quercus* spp.), and maple (*Acer* spp.). The surrounding agricultural landscape mainly consists of arable land with a predominance of crops typical for this area, namely, winter wheat, corn, and rape, as well as vineyards and small areas of grassland. The fragments of woodland were often bordered by dirt roads.

2.2. Sampling Methods

Pitfall traps were used to sample invertebrates. They consisted of 300 mL plastic cups that were half-filled with a 4% formaldehyde fixative solution. The cups were buried level with the soil surface and covered with a metal sheet. On each site, five traps were placed in a line at a distance of at least 10 m from the site's edge. In the case of narrow fragments of woodland, the traps were placed in the middle of the site. The traps were exposed on the sites for three weeks during the period from June to August in 2016 and 2017. Captured invertebrates were classified into taxonomic groups and determined at species level.

2.3. Environmental Variables

Depending on the selected characteristics of the environment, the distribution of taxonomic groups on the sites was evaluated. The characteristics of the environment included the following: (1) area of fragment of woodland, ranging from 0.04 to 7 ha (measured using Google Earth software); (2) canopy coverage, which represents density of the tree canopy, determined on a scale of 1–4, where level 1 denotes canopies providing 0–25% cover, level 2 denotes canopies providing cover in the range of 26–50%, level 3 denotes 51–75% cover, and level 4 denotes 76–100% cover (the level of canopy coverage was determined as the mean of estimates carried out during simple independent observations made by three people); (3) herb layer coverage, which was estimated as the mean of three independent estimations (estimated as a percentage and rounded to tens of percent); (4) dominance of grasses in the herb layer, which was estimated using the same method as for the previous parameter; (5) tree diversity, indicating the number of tree species present on the site; (6) soil moisture, which was measured gravimetrically from a soil sample obtained during installation of traps; (7) leaf litter thickness, denoting the mean of three measurements made at different points on each site (measured in centimeters); and (8) width of fragment of woodland, denoting the mean of three measurements taken at different points on each site (measured using Google Earth software).

2.4. Data Analysis

Activity-density and species richness of individual taxonomic groups were calculated for each of the 38 samples. From these data, we also calculated the percentage of the most numerous species within their groups and the frequency of their occurrence in localities.

Subsequently, we assessed the influence of determined environmental factors (independent variables) on activity-density and species richness (dependent variables) of taxonomic groups. The analyzed environmental factors included the area of fragments of woodland, canopy coverage, herb layer coverage, dominance of grasses, tree diversity, soil moisture, and leaf litter thickness.

Generalized additive models (GAM) were selected for analyses, which consisted of one dependent variable against all environmental factors taken together. Since the dependent variable represented the count data, we chose to employ the Poisson or negative binomial distribution. Activity-density data of all taxa showed overdispersion (i.e., the variance was higher than the mean); therefore, we used a negative binomial distribution in these cases. On the other hand, the variance of species richness data was equal to, or lower than, the mean. If the variance was equal to the mean, we used the Poisson distribution. In the cases where the variance was lower than the mean (underdispersion), we used the quasi-Poisson distribution. The models were fitted with log link functions. Based on a simplification process, a minimal adequate model with the lowest Akaike's information criterion (AIC) was created by gradually removing insignificant factors.

In addition, we attempted to evaluate the effects conferred by the minimum size of the site, which is the basis for the creation of bio-centers, and the minimum width of fragments of woodland, according to which bio-corridors are created. In terms of bio-centers, we selected two datasets consisting of eleven fragments of woodland smaller than 3 ha and eleven fragments greater than, or equal to, 3 ha. For bio-corridors, we selected two datasets consisting of eight linear fragments of woodland thinner than 15 m and eight fragments wider than 15 m. Based on these distributions, we tested the equality in activity-density and species richness of all taxa together. The Shapiro–Wilk test was used to verify the distribution in the data. The nonparametric Wilcoxon rank-sum test was used to compare two datasets with different total areas of fragments of woodland. The reason for choosing this test was independence of the samples and the previous verification of the non-normal distribution of data. The parametric Welch's *t*-test was used to compare two datasets with different widths of fragments of woodland due to the normal distribution of the data [42]. The R Project for Statistical Computing software was used for analyses and graphs.

3. Results

Altogether, more than 6500 ground beetles (Carabidae) of 57 species, over 2000 spiders (Araneae) of 54 species, 800 harvestmen (Opiliones) of 9 species, more than 1000 isopods (Isopoda) of 6 species, almost 250 centipedes (Chilopoda) of 11 species, and over 300 millipedes (Diplopoda) of 7 species were caught. Among the most numerous species of ground beetles were *Pseudoophonus rufipes*, which occurred on 33 sites; *Anchomenus dorsalis* (19 sites); *Trechus quadristriatus* (31 sites); and *Calathus fuscipes* (29 sites). The proportion of these species was more than 60% of all the captured ground beetles. Regarding ground beetles capable of flight, we recorded 32 macropterous species, which together accounted for almost 4700 individuals (i.e., 56% of all the carabid species and 71% of all beetles, respectively).

The most numerous spiders were *Diplostyla concolor*, which was caught on 31 sites; *Ozyptila praticola* (29 sites); and the genus *Pardosa* (30 sites). These species accounted for more than 55% of the individual spiders. The most common harvestmen included *Astrobunus laevipes*, which was collected from 26 sites; *Nelima semproni* (17 sites); and individuals of the Phalangiidae family (17 sites). Together, these species accounted for almost 90% of all harvestmen. Among the isopods collected, the most numerous species were *Armadillidium vulgare* (27 sites), *Porcellium collicola* (31 sites), and *Trachelipus rathkii* (17 sites). In total, these species accounted for almost 100% of all isopods. Only *Lithobius forficatus* (32 sites) and *Lithobius microps* (18 sites) were among the numerous centipede species. The proportion of these individuals in the centipede group was 85%. *Polydesmus complanatus* heavily prevailed among millipedes, representing more than 95% of this group and occurring on 22 sites.

Using GAM models, we evaluated the complex influence of habitat-related environmental factors on the activity-density and species richness of the individual groups of soil fauna (Table 1).

An increase in the area of fragments of woodland was associated with a considerable decrease in the activity-density ($\chi 2 = 7.26$, $p = 0.007$) and species richness of ground beetles ($\chi 2 = 2.96$, $p = 0.0855$) and a slight decrease in spider activity-density ($\chi 2 = 6.57$, $p = 0.0104$). The size of the forest fragment also affected the species richness of centipedes ($F = 8.89$, $p = 0.0055$), which grew with increasing area (Figure 1a).
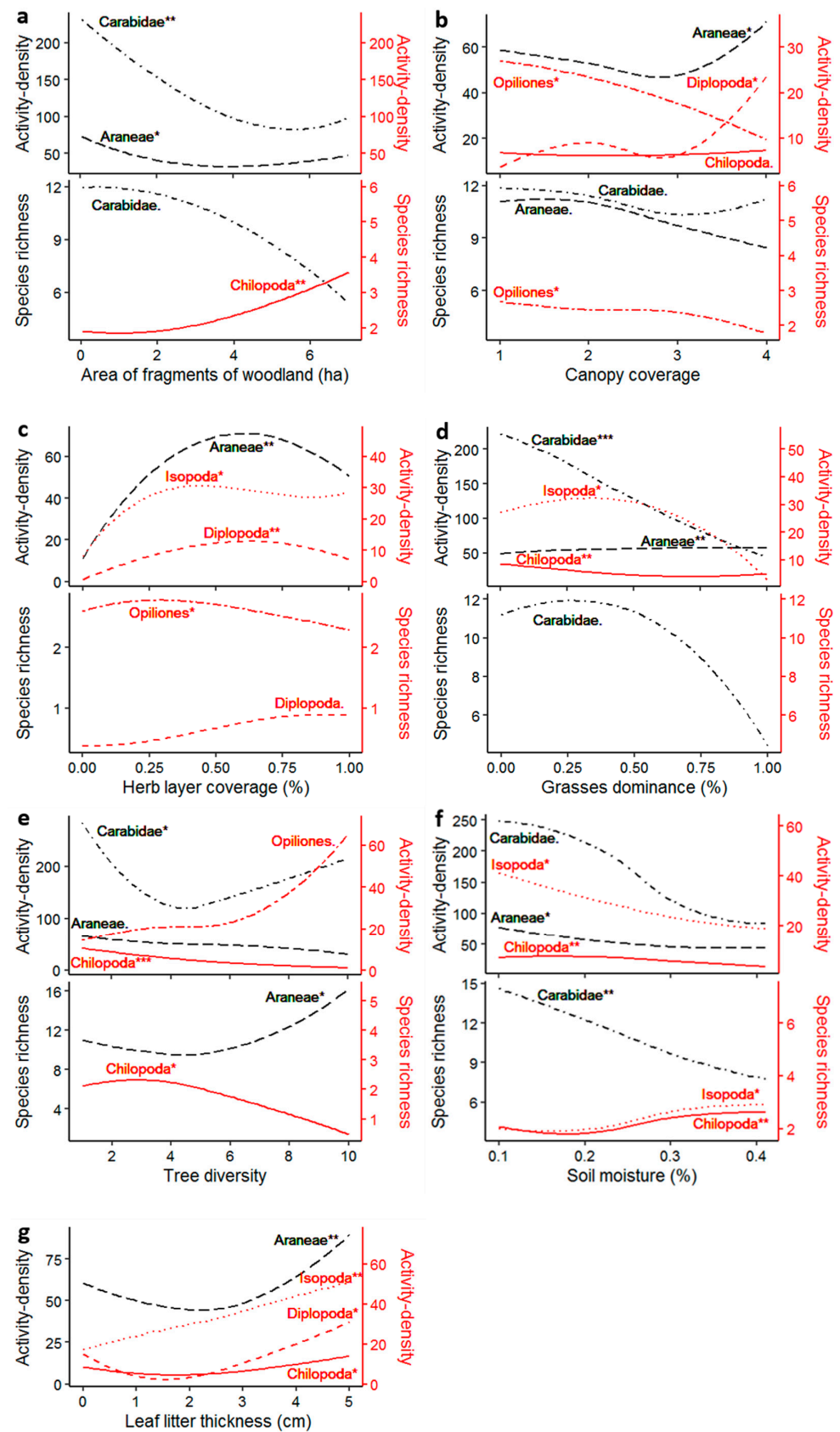
Figure 1. GAM plots visualizing significant relationships between measured environmental variables and individual taxonomic groups: (**a**) effect of the size of site on activity-density and species richness of taxa; (**b**) effect of density of tree canopy on activity-density and species richness of taxa; (**c**) effect

of herbaceous layer coverage on activity-density and species richness of taxa; (**d**) effect of dominance of grasses in the herbaceous layer on activity-density and species richness of taxa; (**e**) effect of species richness of trees on activity-density and species richness of taxa; (**f**) effect of soil moisture on activity-density and species richness of taxa; and (**g**) effect of thickness of leaf litter layer on activity-density and species richness of taxa. Codes for taxa indicate the degree of statistical significance: '***' denotes $p < 0.0001$, '**' denotes $p < 0.001$, '*' denotes $p < 0.01$, and '.' denotes $p < 0.05$. Less numerous taxa are marked in red and oriented toward the red *y*-axis on the right.

Table 1. The complex effects of measured environmental factors on activity-density (a–d) and species richness (s. r.) of invertebrate taxa. The resulting figures were obtained using GAM models. Codes for taxa indicate the degree of statistical significance: '***' denotes $p < 0.001$, '**' denotes $p < 0.01$, '*' denotes $p < 0.05$, and 'n.s.' denotes not significant.

	Carabidae				Araneae			
	a–d		s. r.		a–d		s. r.	
	χ^2	p	F	p	χ^2	p	F	p
area of wood fragment	7.26	***	2.96	*	6.57	**	1.09	n.s.
canopy coverage	0.32	n.s.	3.06	*	5.92	**	3.67	*
herb layer coverage	6.27	n.s.	1.42	n.s.	12.75	***	0.72	n.s.
dominance of grasses	11.72	***	6.53	*	8.71	***	0.47	n.s.
tree diversity	9.71	**	1.05	n.s.	3.36	*	11.95	**
soil moisture	5.70	*	8.64	***	5.26	**	0.50	n.s.
leaf litter thickness	0.27	n.s.	0.64	n.s.	20.53	***	1.17	n.s.
R2 (adj.)	0.499		0.451		0.581		0.325	
Deviation explained	64.5%		53.4%		74.6%		41%	

	Opiliones				Chilopoda			
	a–d		s. r.		a–d		s. r.	
	χ^2	p	F	p	χ^2	p	F	P
area of wood fragment	0.17	n.s.	0.13	n.s.	0.24	n.s.	8.89	***
canopy coverage	4.62	**	4.93	**	2.86	*	0.01	n.s.
herb layer coverage	1.73	n.s.	4.90	**	0.29	n.s.	0.62	n.s.
dominance of grasses	1.66	n.s.	2.16	n.s.	6.64	***	0.31	n.s.
tree diversity	2.73	*	1.97	n.s.	16.23	***	7.34	**
soil moisture	2.29	n.s.	0.26	n.s.	6.76	***	3.60	***
leaf litter thickness	0.54	n.s.	1.12	n.s.	11.26	**	0.22	n.s.
R2 (adj.)	0.096		0.197		0.519		0.445	
Deviation explained	17.3%		30.5%		63.7%		54%	

	Diplopoda				Isopoda			
	a–d		s. r.		a–d		s. r.	
	χ^2	p	F	p	χ^2	p	F	p
area of wood fragment	0.01	n.s.	1.79	n.s.	0.15	n.s.	0.28	n.s.
canopy coverage	9.65	**	1.12	n.s.	1.93	n.s.	0.03	n.s.
herb layer coverage	10.79	***	3.33	*	5.20	**	0.56	n.s.
dominance of grasses	0.22	n.s.	0.41	n.s.	7.09	**	0.25	n.s.
tree diversity	1.69	n.s.	0.25	n.s.	0.002	n.s.	0.66	n.s.
soil moisture	4.82	n.s.	0.20	n.s.	4.17	**	5.31	**
leaf litter thickness	11.08	**	0.59	n.s.	8.09	***	0.02	n.s.
R2 (adj.)	−2.14		0.27		−0.103		0.305	
Deviation explained	47.5%		31%		28%		41.1%	

We can note that the activity-density ($\chi^2 = 4.62$, $p = 0.0315$) and species richness (F = 4.93, $p = 0.0329$) of harvestmen were negatively correlated with increasing canopy coverage. The species richness of ground beetles ($\chi^2 = 3.06$, $p = 0.0804$) and spiders ($\chi^2 = 3.67$, $p = 0.0555$) was similarly affected, although their values were slightly above

the significance level. On the other hand, the activity-density of millipedes ($\chi2$ = 9.65, p = 0.0111) and centipedes ($\chi2$ = 2.86, p = 0.0907) showed an opposite trend in this respect. Spider activity-density ($\chi2$ = 5.92, p = 0.0398) was lowest at mean values of canopy coverage (Figure 1b).

Spiders ($\chi2$ = 12.75, p = 0.0056) and millipedes ($\chi2$ = 10.79, p = 0.0010) preferred about 50% coverage of herb layer, which was reflected in their increased activity-density in such areas (Figure 1c). Higher values of herb layer coverage also increased the activity-density of isopods ($\chi2$ = 5.2, p = 0.0226) and supported the species richness of millipedes, although this dependence proved slightly above the significance level (F = 3.33, p = 0.0773). However, we observed the opposite trend in species richness for harvestmen (F = 4.9, p = 0.0333).

The activity-density ($\chi2$ = 11.72, p = 0.0006) and species richness ($\chi2$ = 6.53, p = 0.0616) of ground beetles dropped significantly with an increasing proportion of grasses (Figure 1d), and the activity-density of isopods ($\chi2$ = 7.09, p = 0.0354) and centipedes ($\chi2$ = 6.64, p = 0.0099) also showed a similar dependence. On the other hand, with an increasing proportion of grasses in the herbal layer, there was a very slight increase in the activity-density of spiders ($\chi2$ = 8.71, p = 0.0032).

The influence of tree diversity proved to be very variable. Figure 1e shows that the activity-density of ground beetles reached the highest levels in species-poor sites, but high activity-density also occurred in the most species-diverse sites ($\chi2$ = 9.71, p = 0.0462). The activity-density of harvestmen ($\chi2$ = 2.73, p = 0.0985) increased considerably with the increasing number of tree species in the locality, although this dependence proved slightly above the significance level. The opposite situation was recorded for spiders, whose activity-density ($\chi2$ = 3.36, p = 0.0667) declined with an increasing number of woody plants, although their species richness ($\chi2$ = 11.95, p = 0.0498) increased. Centipedes preferred sites with lower tree diversity in terms of their activity-density ($\chi2$ = 16.23, p = 0.0001) and species richness ($\chi2$ = 7.34, p = 0.0102).

Sites with lower soil moisture were preferred by ground beetles ($\chi2$ = 5.7, p = 0.0659), isopods ($\chi2$ = 4.17, p = 0.0411), spiders ($\chi2$ = 5.26, p = 0.0219), and centipedes ($\chi2$ = 6.76, p = 0.0093), which is evident from Figure 1f. This trend was also identical with regard to the species richness of ground beetles ($\chi2$ = 8.64, p = 0.0033). In contrast, the species richness of isopods ($\chi2$ = 5.31, p = 0.0273) and centipedes ($\chi2$ = 3.6, p = 0.0089) grew very slightly with increasing moisture.

Leaf litter thickness significantly affected the activity-density of spiders ($\chi2$ = 20.53, p = 0.0013), isopods ($\chi2$ = 8.09, p = 0.0045), millipedes ($\chi2$ = 11.08, p = 0.0146), and centipedes ($\chi2$ = 11.26, p = 0.0107). In all taxa, activity-density grew with increasing leaf litter thickness, although in spiders and millipedes this was initially a declining trend (Figure 1g).

No significant difference was found in a comparison of similarity in terms of total activity-density (W = 62, p = 0.9487) and species richness (W = 68, p = 0.6432) between fragments of woodland according to a 3 ha gradient (Wilcoxon rank-sum test). Similarly, the distribution of linear fragments of woodland did not have a significant effect on either the total activity-density (t = -0.67393, df = 12.766, p = 0.5124) or species richness (t = −0.28036, df = 11.364, p = 0.7842) of invertebrates according to the 15 m gradient of their width (Welch's *t*-test).

4. Discussion

We attempted to evaluate how the natural character of fragments of woodland in an agricultural landscape can affect the activity-density and species richness of invertebrates. For this purpose, we focused on several surface-dwelling groups of macrofauna (ground beetles, spiders, harvestmen, isopods, centipedes, and millipedes), which together cover a wide range of trophic and ecological requirements. Subsequently, habitat characteristics that may have a direct or mediated effect on the distribution of these invertebrates were selected.

4.1. Area of Fragments of Woodland

With an increasing size of fragments of woodland, there was a significant decrease in the activity-density and species richness (slightly above the significance limit) of ground beetles, a group that was dominated by species that prefer open habitats [4]. This trend was also noted by Griffiths et al. [43], Knapp and Řezáč [44], and, in the context of ground beetle abundance, Niemelä et al. [45]. We also recorded a similar result with respect to the activity-density of spiders. The explanation for this finding may be that habitats with less dense and lighter vegetative cover are suitable for these generally mobile predatory species that actively hunt their prey [46]. Such conditions mostly corresponded to smaller fragments of woodland with a more open habitat. In addition, the edge effect may also play a role in this regard, as small fragments of woodland often acted as an edge habitat over their entire area [44,47]. Accordingly, Lövei et al. [48] state that generalists and edge species benefit from smaller sites as the edge/interior ratio increases. In addition, Bender et al. [49] found a positive effect of smaller sites with a larger proportion of edges on the density of edge species. However, in this case, the generalists were only negligibly affected by the size of the site; conversely, a decrease in size of the site negatively affected the interior species. In any case, many studies, e.g., [46,50,51], have identified the edges of fields and fragments of woodland as places with high numbers of species from which these species spread to the surrounding area, where their abundance and diversity tend to be lower. The spread of species between fragments of woodland and the surrounding area was also confirmed by the authors of [4], who did not notice any significant differences in the composition of ground beetle communities between the original fragments of woodland and recently created hedgerows and field crops. In contrast to previous findings, Knapp and Řezáč [44] noted an increase in the activity-density of spiders with an increasing size of the site in which they inhabited. Their explanation for this trend is the possible competition with predatory ground beetles, and the authors note that, in addition to environmental influences, interspecies interaction can also affect the distribution of invertebrates. For centipedes, we observed a positive relationship between the size of fragment of woodland and species richness. This could be due to a slightly increasing canopy density, thickness of leaf litter layer, and soil moisture in these localities, which could provide centipedes with better microclimatic conditions and more prey [52]. This is also supported by our results, which demonstrated that the species richness of centipedes grew with increasing soil moisture in the examined sites. Overall, we can state that a larger area of a fragment of woodland does not in itself support the activity-density or species richness of the studied groups of invertebrates (except centipedes) in the examined agricultural landscape.

We related these results to the Territorial System of Ecological Stability (TSES) concept, which aims to create bio-centers and bio-corridors in the Czech Republic that will constitute a system of nature-close areas, thus ensuring the maintenance of the ecological stability of the cultural landscape and supporting biodiversity. At the local level, it is recommended that bio-centers are created with an area of at least 3 ha, while bio-corridors should have a minimum width of 15 m [41,53,54]. A comparison of sites along the 3 ha gradient showed that there was no significant difference between sites in overall activity-density or species richness. This fact is also supported by a study conducted by Knapp and Řezáč [44], who indicated that the species composition of ground beetles and spiders in small sites does not differ much from that in large sites, nor did the distribution of linear sites based on their width have a statistically significant effect on the activity-density or species richness of invertebrates. Bedford and Usher [55] recorded increased species richness up to a maximum of about 5 m from the edge to the center of the examined site. Maudsley et al. [56] even found a negative relationship between the width of fragments of woodland and the abundance of ground beetles and spiders. Therefore, we can conclude that even very narrow linear fragments of woodland (<15 m) can be densely inhabited by soil fauna. However, it should be noted that these sites, with usually sparsely formed vegetation, may be exposed to higher temperature and humidity fluctuations due to the greater intensity of solar radiation threat. This may affect the species composition of the

site, as explained by Stašiov et al. [57] with respect to harvestmen. The vegetative structure, which influences the microclimatic conditions of sites, can thus be of greater importance than the size and width of fragments of woodland [44,58].

4.2. Canopy Coverage

The reason for the higher activity-density of millipedes in the sites with denser canopy coverage could be better microclimatic conditions due to greater shading [59] and the formation of a thicker leaf litter layer. In terms of activity-density, millipedes were represented almost exclusively by the species *Polydesmus complanatus*, for which these conditions are very favorable [60].

The decrease in the activity-density and species richness of harvestmen with an increasing density of the canopy could be due to a more pronounced occurrence of species that prefer lighter forests or rocks and rubble [61]. At the same time, the lighter fragments of woodland had a more developed herbaceous layer, providing more diverse microhabitat conditions. Similarly, Černecká et al. [62] recorded a higher overall abundance of harvestmen in open and lighter forest sites than in compact forest stands. However, they found only slight differences in the species composition of harvestmen between these two types of habitats, but often with a more pronounced preference of individual species for a specific degree of shade. Černecká et al. [62], therefore, emphasize the importance of intra-habitat heterogeneity. The same result was recorded by Stašiov et al. [63] when comparing sites with varying degrees of canopy coverage. A similar explanation of the decline in activity-density with increasing canopy can also be considered for some spider species preferring light forests or other open, light habitats (e.g., *Pardosa lugubris* and other individuals of this genus in sites with sparse canopy coverage). On the other hand, their subsequent higher activity-density in sites with a denser canopy coverage could be the result of the increasing occurrence of numerous shade-tolerant forest species and leaf-litter-dwelling species (e.g., *Ozyptila praticola*, *Scotina celans*) [64,65].

4.3. Herbaceous Layer Coverage and Dominance of Grasses

The herbaceous layer provides soil fauna with favorable microclimatic conditions and shelter. It is also a source of plant food for herbivores and, subsequently, dead biomass for detritivores. Due to these conditions, isopods and millipedes probably benefit from a greater coverage of the herbaceous layer. Consequently, many soil predators also benefit from the presence of these organisms [66]. A coverage of about 40–50% of the examined sites with an herbaceous layer led to the highest activity-density of spiders. Their activity-density may be supported by the increased presence of prey due to better vegetation conditions, as mentioned above, and since web-building spiders can use the surrounding vegetation as a support for their webs [67,68]. However, the activity-density of spiders gradually decreased with any further increase in herb coverage. This may relate to the declining ability of active hunting species to move and detect prey in such dense herbal or grassy undergrowth [32,46,69] as well as the preference of many species for more exposed habitats. In addition, the inhibited movement of invertebrates may reduce the efficiency of pitfall traps, as described by Sroka and Finch [70]. Similarly, we can explain the highest species richness of harvestmen at medium levels of herb coverage and the sharp decline in activity-density and species richness (although slightly above significance) of ground beetles with an increasing grass/herb ratio. Accordingly, Maudsley et al. [56] noted significantly higher abundance and diversity of ground beetles in herb-dominated habitats. Therefore, we can conclude that none of the groups of invertebrates benefitted from bare or very sparsely covered soil nor from the predominance of grasses in the herbaceous layer.

4.4. Tree Diversity

The species composition of trees can have a significant effect on the microclimatic conditions of the sites, soil pH, and leaf litter quality (C/N ratio). These conditions can be further influenced by the often dominant occurrence of invasive black locust [71]. As a

result, the distribution of invertebrates [63,72–74], which are often associated with specific species of trees, shrubs, and herbs, could be significantly affected [31]. More species-diverse tree layers were associated with a denser and more compact character of growth, and the decline in ground beetle density activity in these localities was due to numerous species, especially *Trechus quadristriatus* and *Calathus fuscipes*, which prefer non-forest and lighter habitats. On the other hand, the increase in activity-density was due to the more abundant presence of species that prefer woodlands, such as *Carabus coriaceus* or *Abax parallelepipedus* [75]. Sites with a more species-diverse tree layer are often inhabited by more diverse communities of herbivores or detritivores [31]. This may have indirectly led to an increase in the number of spider species due to their wider food supply [76]. In their review, Uetz [68] also mentions a functional relationship between the height and structural and species composition of the tree and shrub layers and the occurrence of specific spider guilds. A more diverse species spectrum of woody plants can expand the structural character of sites and thus support the presence of more species of spiders [76].

The correlation between the activity-density of harvestmen and the species richness of trees was statistically insignificant but distinctly positive. Stašiov et al. [63] noted that harvestmen can be very sensitive to microclimatic conditions, pH, conductivity, and the C/N ratio of leaf litter, which, fundamentally, are affects conferred by the vegetative structure and species composition of trees. Based on these findings, Stašiov et al. [57] also showed a positive relationship between the diversity of trees and regarding diversity of harvestmen; however, this was not reflected in our study.

Black locust dominance was frequent in sites with lower tree diversity. The presence of this species often leads to soil acidification [77]. Bååth et al. [78] noted an increase in the abundance of some species of springtails with increasing acidification. Indirectly, a higher activity-density of predators (ground beetles, spiders, etc.) could have occurred through an increase in the quantity of their prey [72]. Furthermore, due to the sparse canopy in black locust-dominated sites, many numerous species specializing in open landscapes could benefit [44,58]. In contrast, Buchholz et al. [71] did not record any differences in the abundance of ground beetles, spiders, harvestmen, millipedes, or isopods between localities with and without black locust. Only centipedes showed a higher abundance on sites without black locust, while the species composition varied in ground beetles. However, it should be mentioned that the cited study was located in an urban area. We also recorded a decrease in the activity-density and species richness of centipedes in contrast to an increase in the activity-density of ground beetles and the species richness of spiders. In this case, there may have been a partial influence conferred by interspecies competition between groups of predators, as indicated previously [36,44,79].

4.5. Soil Moisture

Due to the prevailing climate, the fragments of woodland in the agricultural landscape of South Moravia can be classified as relatively drier habitats. Therefore, these areas contain species that are mostly well adapted to these conditions. As a result, it is not surprising that rising soil moisture concentrations did not increase the activity-density of any of the invertebrate groups studied. Nevertheless, in centipedes and especially isopods, the decline in activity-density with increasing soil moisture was rather unexpected, as these are organisms that usually prefer moist and shady places [52]. However, the activity-density of these groups was mainly influenced by *Armadillidium vulgare* and *Lithobius forficatus*, and these surface-dwelling species are relatively indifferent to habitat moisture unlike most other members of these groups. Although their activity-density decreased with increasing humidity, the quantities of other hygrophilic species increased, and, as expected, moist habitats were inhabited by more diverse assemblages of isopods and centipedes. In contrast to our results, Maudsley et al. [56] found a positive correlation between soil moisture and ground beetle species richness, although these were quite different species assemblages. Consensus was reached in the case of the two most numerous species, *A. dorsalis* and

P. rufipes, which preferred drier soils, and the decline in their activity-density in moist habitats had a noticeable effect on the entire group of ground beetles.

4.6. Leaf Litter Thickness

Regarding leaf litter, we assumed that thicker layers would attract a greater number of invertebrates through better microclimatic conditions, wider shelter options, or an increased variety of food sources [66]. This was confirmed in detrital groups (millipedes and isopods) and predators (centipedes and spiders). The increase in the activity-density of spiders alongside the thickening of the leaf litter layer was due to the presence of species such as *Diplostyla concolor* and *Scotina celans*, which use deeper and more complex layers of leaf litter for hunting and hiding [64,65]. The slight initial decrease in activity-density may be related to a decrease in the abundance of the family Lycosidae, a species that actively hunts on the soil surface and prefers shallow layers of leaf litter [80–82]. Overall, our study also showed that the thickness of leaf litter did not significantly affect the species richness of ground-dwelling macrofauna.

5. Conclusions

Our results show that the selected groups of soil fauna reacted to each of our monitored habitat characteristics in a specific way. These reactions were often unexpected and difficult to explain. Therefore, we can conclude that invertebrates are likely to be affected by many other factors in their habitats and surrounding landscapes, including such areas' complementary effects. No universal characteristic of the environment was found to suit all groups of soil fauna, which indicates their high functional and ecological diversity. Therefore, it is necessary to ensure a high degree of structural heterogeneity of habitats and the surrounding landscape, covering the widest possible range of environmental conditions, and to take this into account in planned management. It should also be emphasized that in the protection, establishment, and management of these non-productive habitats (bio-centers), the effort to maximize their area may not be crucial, as even smaller habitats significantly contribute to the promotion and conservation of biodiversity in an agricultural landscape. In other words, invertebrates can benefit from any scattered landscape greenery. Likewise, very narrow fragments of woodland (bio-corridors) can be a fully-fledged habitat or an alternative to wider woodland in terms of supporting soil fauna, especially in places where the implementation of such woodlands is not possible. At the same time, this can be a positive incentive for owners of arable land to establish these natural habitats while simultaneously attempting to keep productive land area to a maximum.

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