

Article

Stand Age and Litter Shape Myriapod Communities in a Forest Mosaic (Diplopoda, Chilopoda) [†]

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Abstract

(1) Forest fragmentation and associated edge effects can strongly modify the diversity and distribution of soil invertebrates, yet their responses in temperate floodplain forests remain poorly understood. We investigated myriapod (centipede and millipede) assemblages in a fragmented forest mosaic in the protected landscape area Litovelské Pomoraví (Czech Republic), focusing on the role of stand age, ecotones and key microhabitat variables. (2) Myriapods were sampled continuously during two years using pitfall traps arranged along transects crossing four neighboring patches (clear-cut with seedlings, 10-year-old stand, 87-year-old and 127-year-old *Quercus–Ulmum* forests). Species diversity was quantified using the Shannon–Wiener index, and patterns were analyzed by t-tests, canonical correspondence analysis and generalized additive models. (3) We collected over six thousand individuals (10 centipede and 10 millipede species). Diversity peaked in old-growth stands and adjacent ecotones, and two of the three ecotones supported particularly high species abundances. Litter cover and thickness, stand age, and the structure of the herb and shrub layers were the most important predictors of species distributions. Dominant species (e.g., *Glomeris tetrasticha* Brandt, 1833, *Lithobius mutabilis* L. Koch, 1862, *L. forficatus* (Linnaeus, 1758)) showed contrasting habitat preferences, reflecting niche differentiation along microhabitat and stand-age gradients. (4) Our findings indicate that conserving a fine-grained mosaic of stand ages, together with structurally complex forest interiors and ecotones, is essential for maintaining myriapod diversity and the ecosystem functions they provide in Central European forests.

Keywords: biodiversity; centipedes; ecotone; habitat fragmentation; millipedes; Myriapoda; stand age



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1. Introduction

Forests and forest land cover 37.1% of the territory of the Czech Republic [1]. Early forest management practices, similar to those elsewhere in Central Europe, included clear-cutting and the conversion of ancient forests to agricultural land and even-aged monocultures, resulting in fragmented forests and isolated forest patches. These changes are among the most important causes of the marked decline in biodiversity in Czech forests [2].

Fragmented forests are characterized by a number of new ecological features, such as isolation of native habitats, patch size, and “ecotone” (habitat edge) length. These

often have a crucial effect on local populations, which are exposed to conditions different from those in the interior of native forest ecosystems [3,4]. Newly created patches are characterized by increased solar radiation, altered water fluxes, greater exposure to wind, and, consequently, enhanced transfer of seeds, dust, and similar particles, especially at habitat edges [5]. For this reason, ecotones are considered one of the most important emergent effects of fragmentation. Ecotones are defined as transitional zones between neighboring habitats, characterized by distinct ecological properties. They represent areas where species from adjacent habitats frequently meet and interact [6] and where specialist ecotonal species can occur [7]. Species abundance depends on the specific ecotone type and may increase, decrease, or show no difference in comparison with surrounding areas [8]. The influence of ecotones on invertebrates, which operate on comparatively small spatial scales, has not yet been fully explained [9]. Despite ecotone-specialized species, forest species are less sensitive to an edge and tend to “spill over” into grassland habitats. This effect is asymmetric as meadow species do not migrate into forests [10].

The ecological consequences of forest fragmentation and the resulting ecotone effects on myriapods (centipedes and millipedes) have been insufficiently studied. Myriapod (re)colonization capabilities are highly constrained due to their walking-based dispersal and inability to cross water barriers [11]. As a result, many species are restricted to very specific habitats and are highly vulnerable to human-induced small-scale habitat changes [4,12]. The lack of a waterproof, waxy cuticle explains their preference for habitats with high humidity, relatively stable temperatures, and low light intensity [13]. These specific microclimatic conditions are altered in fragmented forest landscapes, where edge habitats are exposed to higher temperatures and increased solar radiation, which affects millipedes [4,14]. Because of their specific habitat preferences and close contact with soil, myriapods have been used as bioindicators [15–17]. Both groups have a relatively long-life span compared with other invertebrates; some millipede species can live for more than ten years [12]. Owing to this combination of ecological and biological characteristics, myriapods represent a very important component of soil fauna and are frequently used as model organisms in ecological research.

This paper focuses on the distribution of myriapods in a fragmented habitat created by anthropogenic activities in a deciduous forest. The main objective of our study was to identify specific ecological factors and evaluate their influence on myriapod diversity and distribution within the forest mosaic. As a secondary objective, we examined the ecological preferences of selected species collected during this study. We also address issues related to the formation of secondary habitats as a consequence of modern forest management.

2. Materials and Methods

2.1. Locality

The protected landscape area Litovelské Pomoraví, where the research was conducted, covers 96 km² between the towns of Mohelnice and Olomouc (central Moravia, Czech Republic), following the alluvial plains formed by the meandering Morava River. The core of the area consists of floodplain forests and wet meadows, which are among the most important of their kind in Central Europe.

The study area was located 2 km north of the village Horka nad Moravou (49.6527681 N, 17.2051828 E; altitude 210 m). The locality consisted of four adjacent forest patches (Figure 1), whose age at end of investigation was determined using stand maps and management plans. The first patch, a three-hectare 87-year-old *Quercus-Ulmetum* stand, consisted primarily of *Quercus robur* L. and *Carpinus betulus* L., accompanied by *Acer platanoides* L., *Acer pseudoplatanus* L., *Tilia platyphyllos* Scop. and *Fraxinus excelsior* L. The shrub layer was dominated by *T. platyphyllos* and *A. platanoides*, whereas the herb layer included typical

spring flora such as *Anemone nemorosa* L., *Anemone ranunculoides* L., *Glechoma hederacea* L., *Ficaria verna* Huds., *Corydalis cava* (L.) Schweigg. & Körte, *Galanthus nivalis* L., *Pulmonaria officinalis* L., *Lathyrus vernus* (L.) Bernh., *Polygonatum verticillatum* (L.) All. and *Maianthemum bifolium* (L.) F. W. Schmidt.

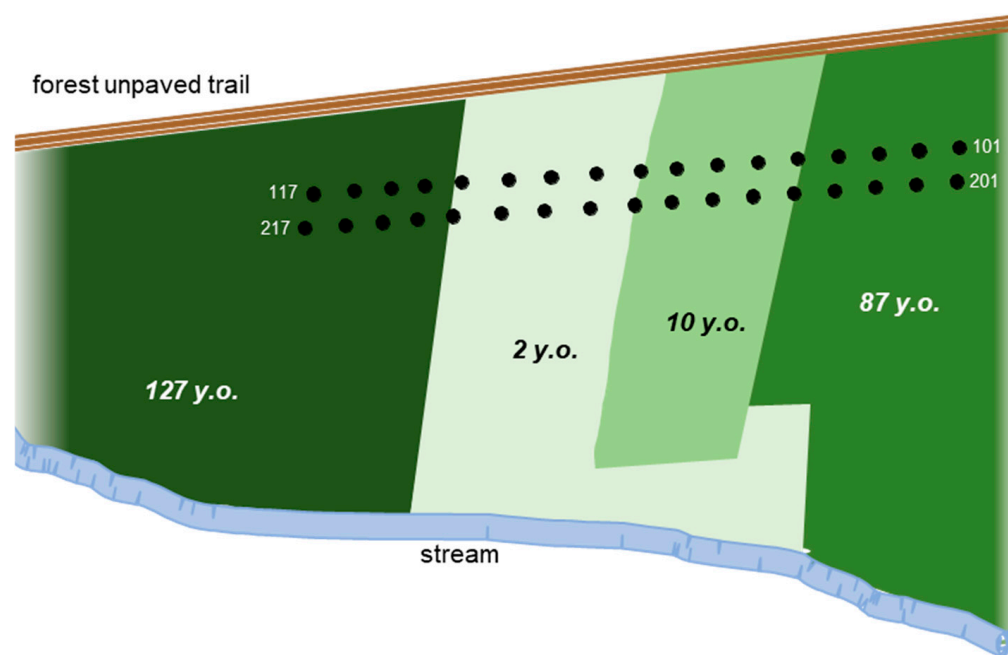


Figure 1. Sketch of the relative positions of the studied forest areas of different age (2–127 years old) with the placement of two lines of pitfall traps.

The second patch, a 10-year-old planted *Quercus* stand of area of 0.4 hectare, was dominated by *Quercus petraea* (Matt.) Liebl. in the tree layer and by *Urtica dioica* L. and *Rumex obtusifolius* L. in the herb layer. This patch represents a transitional vegetation type between the 87-year-old *Quercus-Ulmus* forest and an adjacent clear-cut.

The third patch was a 2-year-old clear-cut (0.5 ha) with seedlings of *Q. petraea* (80%), *Tilia cordata* Mill. (10%) and *Ulmus glabra* Huds. (10%). The herb layer consisted primarily of *Calamagrostis epigejos* (L.) Roth and *Impatiens glandulifera* Royle. Four older trees (*Q. robur* and *F. excelsior*) were left in the middle of the clear-cut.

The last patch, a five-hectare 127-year-old floodplain *Quercus-Ulmus* forest, was dominated by *Q. robur* and *C. betulus*, accompanied by *T. platyphyllos* and *F. excelsior* in the tree layer, and by *A. nemorosa*, *A. ranunculoides*, *C. cava*, *G. hederacea*, *F. bulbifera*, *P. officinalis*, *L. vernus*, *Isopyrum thalictroides* L. and *G. nivalis* in the herb layer.

The transitions (“ecotones”) between these stands were sharp and artificial. These were not natural ecotones with specific stand conditions; forest management on young areas included the removal of shrubs and tall herbs. These four research areas were bordered by a stream to the south and were surrounded on all sides by other extensive deciduous commercial forests, aged 30–70 years.

Regular flooding occurred in this area until the end of the last millennium, when the forests were flooded by water from melting snow in the river basin. In recent decades, however, due to insufficient winter snowfall, these floods have only occurred briefly and irregularly. The studied area was flooded for several days (in March) two years before the research period but not during the research itself (although the fortnightly/monthly inspection interval may not have recorded a specific flood, it would have been possible to detect it in pitfall traps, which would have been filled to the brim with water).

2.2. Sample Collection

Animal communities were sampled using pitfall traps, a standard method for studying surface-dwelling invertebrate fauna. Each pitfall trap consisted of a glass jar (volume 0.7 L) containing a plastic cup (diameter 65 mm, height 100 mm). Approximately one third of the plastic cup was filled with a fixative (a 4% aqueous solution of formaldehyde). At each sampling position, holes the size of the jars were excavated, and the pitfall traps were placed inside them, with the rims adjusted to ground level. Above each pitfall trap, a 30 × 30 cm metal cover was installed to prevent litter, rain, and snow from entering.

The pitfall traps were arranged in two parallel lines crossing all four of the above-mentioned patches. Each line contained 17 traps spaced 10 m apart. Traps were coded according to the line number and the position within the line, from 101 to 117 and from 201 to 217, respectively (Figure 1). Samples were collected at 14-day intervals (once a month during winter), from 1 April 2004, until 30 March 2006, altogether comprising 41 samples for each trap.

2.3. Statistical Analyses

Biodiversity in individual traps and species abundance within the forest mosaic were analyzed using Microsoft Office Excel 2007. Alpha diversity of myriapods in each trap (each trap is characterized by its surrounding environment, see below) was quantified with the Shannon–Wiener diversity index. Diversity patterns along the transect were compared for centipedes and millipedes using a paired-sample t-test. Species abundance was analyzed for each transect as the mean number of individuals per trap over the entire study period within a given transect segment.

We used CANOCO for Windows, version 5 [18] to examine the impact of environmental factors on myriapods. We analyzed the abundance of individual species in each of 34 traps during each of 41 inspections, i.e., 1394 samples. The following environmental variables were included and evaluated for each trap within a 2 m radius around it: percentage cover of herbs; percentage cover of shrubs; percentage cover of old trees, expressed as percentage canopy cover of trees higher than 5 m; percentage litter cover and litter layer thickness (mean, based on three measures in the radius); and stand age at the trap location. This semi-quantification was performed by eye by three people independently once at the beginning of this research (28 April 2004). All environmental variables except stand age were semi-quantified on a 25% scale and coded for analysis in the program (Table 1). The method used did not allow for greater accuracy in determining coverage. Stand age for traps on ecotones was calculated like mean of ages of surrounding stands. The trap ID, month of sample and year of sample were used as supplementary variables.

Table 1. Coding of selected tested environmental factors.

Coded as	10	20	30	40	
herb layer coverage	0–25	25–50	50–75	75–100	%
shrub layer coverage	0–25	25–50	50–75	75–100	%
tree-crowns coverage	0–25	25–50	50–75	75–100	%
litter coverage	0–25	25–50	50–75	75–100	%
litter thickness	0–1	1–3	3–5	5≥	cm

Based on the gradient length of the species data, environmental factors were analyzed using canonical correspondence analysis (CCA), evaluated using Monte Carlo test (4999 permutations). Generalized additive models (GAMs) were used to describe the dependence of species distributions on the strongest environmental factors independently and were graphically illustrated in CanoDraw for Windows, version 5 (part of the CANOCO

software package). We used Species Response Curves function in this software, with maximal term smoothness 2.0 df and Poisson response distribution. The numbers of individuals in the traps were logarithmized. The best model was selected using AIC.

3. Results

3.1. Diversity

During this study, a total of 6061 myriapod individuals were collected and identified (Table 2). Centipedes accounted for 3744 individuals (10 spp.), with *Lithobius mutabilis* L. Koch, 1862, being the dominant species (76% of all centipedes). Millipedes were represented by 2317 individuals (10 spp.), with pill millipede *Glomeris tetrasticha* Brandt, 1833, as the dominant species (63% of all millipedes).

Table 2. Mean number of individuals of centipede and millipede species per trap for the whole study period in a forest mosaic of four woods of different ages (2–127 years old) and their ecotones. The “ecotone” columns represent the trap at the interface between neighboring stands; the order of the columns in the table corresponds to their actual location. Maximal numbers for each species are bolded. The last column shows the total number of trapped individuals (n).

	87 y.o.	Ecotone	10 y.o.	Ecotone	2 y.o.	Ecotone	127 y.o.	n
centipedes								
<i>Lithobius agilis</i> CL Koch, 1847	0.9	–	1.4	0.5	0.5	0.5	0.5	24
<i>Lithobius erythrocephalus</i> CL Koch, 1847	0.1	–	0.2	1.0	0.2	–	0.4	8
<i>Lithobius forficatus</i> (Linnaeus, 1758)	27.9	32.5	28.2	33.0	18.0	6.5	15.6	769
<i>Lithobius mutabilis</i> L. Koch, 1862	54.8	64.0	71.5	112.0	96.4	96.0	105.6	2834
<i>Geophilus flavus</i> (de Geer, 1778)	–	–	0.2	–	–	–	–	1
<i>Geophilus impressus</i> CL Koch, 1847	0.1	–	–	0.5	–	0.5	–	3
<i>Schendyla nemorensis</i> (CL Koch, 1837)	0.1	–	–	–	0.5	–	0.8	10
<i>Strigamia acuminata</i> (Leach, 1815)	0.5	2.0	1.4	–	0.7	–	1.0	28
<i>Strigamia crassipes</i> (CL Koch, 1835)	0.1	–	–	0.5	0.4	0.5	0.3	7
<i>Strigamia transsilvanica</i> (Verhoeff, 1928)	–	–	–	–	–	1.0	–	2
millipedes								
<i>Polyzonium germanicum</i> Brandt, 1837	5.4	14.0	2.0	1.5	–	1.0	0.8	94
<i>Haplogona oculodistincta</i> (Verhoeff, 1893)	21.5	22.0	16.5	5.0	6.4	6.5	4.6	413
<i>Melogona voigtii</i> (Verhoeff, 1899)	0.8	–	–	–	1.0	–	0.6	17
<i>Leptoiulus proximus</i> (Němec, 1896)	2.9	0.5	0.7	4.5	1.0	1.0	1.3	55
<i>Unciger foetidus</i> (CL Koch, 1838)	4.4	5.0	2.5	2.5	4.4	8.5	5.3	150
<i>Unciger transsilvanicus</i> (Verhoeff, 1899)	6.9	4.5	1.7	1.5	2.0	1.5	2.3	110
<i>Brachydesmus superus</i> Latzel, 1884	–	–	–	–	0.2	–	–	1
<i>Polydesmus complanatus</i> (Linnaeus, 1761)	0.5	0.5	0.2	–	0.2	0.5	0.1	9
<i>Polydesmus denticulatus</i> CL Koch, 1847	–	0.5	–	–	0.8	–	–	6
<i>Glomeris tetrasticha</i> Brandt, 1833	48.5	80.0	67.5	111.5	30.0	14.0	9.8	1462
Sum	175.3	225.5	193.7	274.0	162.4	138.0	148.7	6061

Biodiversity in individual traps (Figure 2) was analyzed separately for millipedes and centipedes. For millipedes, diversity was highest in the 87-year-old *Quercus–Ulm* forest, whereas for centipedes it peaked in the 10-year-old stand and in the 87-year-old forest. These patterns differed significantly between the two groups ($t = 4.99$, $p < 0.001$). The lowest diversity was recorded in the ecotone between the 2-year-old clear-cut with seedlings and the 127-year-old floodplain *Quercus–Ulm* forest for centipedes and around the ecotone of the youngest stands for millipedes (Figure 2).

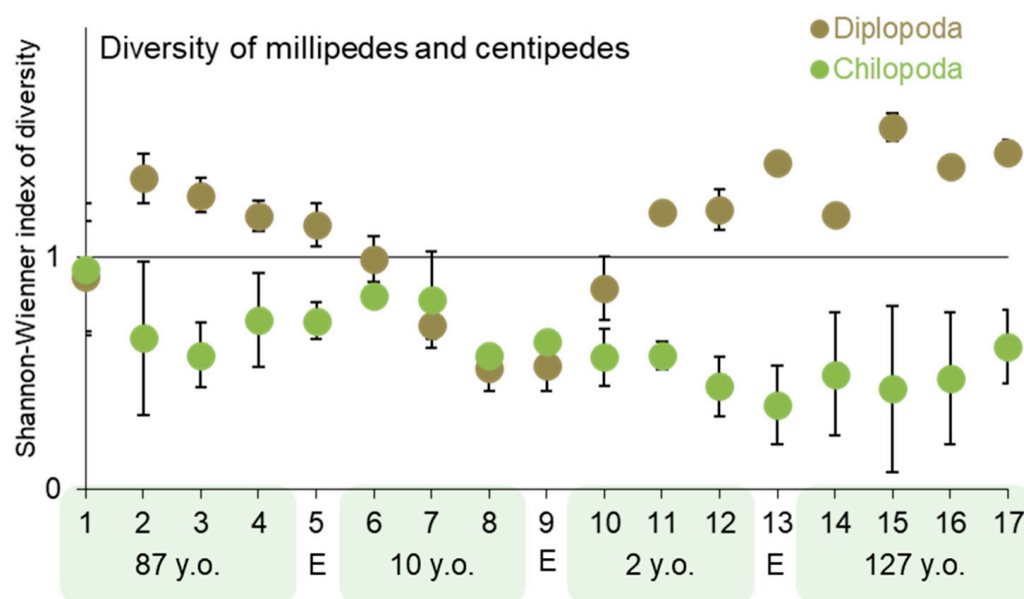


Figure 2. Biodiversity of millipedes and centipedes calculated (mean $\pm$ SD) for each individual trap position.

Species abundances in the forest mosaic reflected habitat preferences (Table 2). Among centipedes, both *L. mutabilis* and *Lithobius forficatus* (Linnaeus, 1758) were most abundant in the ecotone between the 10-year-old *Quercus* stand and the 2-year-old clear-cut with seedlings. Most millipede species also showed a positive relationship with ecotones: *Polyzonium germanicum* Brandt, 1837 and *Haplogona oculodistincta* (Verhoeff, 1893) were most abundant in the ecotone between the 87-year-old *Quercus*–*Ulm* stand and the 10-year-old *Quercus* stand; *Leptoiulus proximus* (Němec, 1896) and *G. tetrasticha*, similarly to abovementioned centipedes, reached their highest abundances in the ecotone between the 10-year-old *Quercus* stand and the 2-year-old clear-cut with seedlings, whereas *Unciger foetidus* (CL Koch, 1838) was most numerous in the ecotone between the 2-year-old clear-cut with seedlings and the 127-year-old floodplain *Quercus*–*Ulm* forest. Thus, two of the three ecotones examined in this study supported higher species abundances than the other habitat fragments.

3.2. Environmental Factors Analysis

Based on the gradient length of the species data (4.8 SD), we selected canonical correspondence analysis (CCA) with trap ID and time pattern (month, year) as covariates. The overall model was significant (pseudo- $F = 7.3$; $p = 0.002$) and explained 3.97% of the total species variability. The first two axes accounted for 93.22% of the variability described by the model. All environmental factors were evaluated as significant (Table 3), and some of them were correlated (Table 4). There was a very strong positive correlation between leaf litter coverage and litter thickness, with thickness of the litter layer considered by the model to be a more significant predictor of myriapod distribution. There was a strong negative correlation between tree canopy cover and shrub or herb presence. Shrub canopy cover correlated moderately positively with the presence of herbaceous vegetation and with litter cover. Old forests had denser tree canopy cover, low shrub layer cover, and low amounts of leaf litter.

Table 3. Significance of individual environmental factors predicting distribution of centipedes and millipedes (conditional term effects) in forest mosaic in CCA model.

Name	Explains %	pseudo-F	P	P(adj)
Litter layer thickness (cm)	2.07	22.5	0.002	0.003
Presence of herbs (%)	0.53	5.7	0.002	0.003
Presence of trees (%)	0.53	5.7	0.002	0.003
Age of growth (years)	0.39	4.3	0.002	0.003
Presence of shrubs (%)	0.24	2.6	0.006	0.0072
Litter coverage (%)	0.21	2.3	0.016	0.016

Table 4. Correlation of environmental factors used to predict the abundance of centipedes and millipedes in deciduous forest patches. The number of stars indicates the degree of significance: *** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$.

	A	B	C	D	E	F
A: Litter coverage (%)	1					
B: Litter layer thickness (cm)	0.732 ***	1				
C: Presence of herbs (%)	−0.070	−0.157	1			
D: Presence of shrubs (%)	0.395 *	0.113	0.471 **	1		
E: Presence of trees (%)	−0.003	0.199	−0.674 ***	−0.753 ***	1	
F: Age of growth (years)	−0.511 **	−0.425	−0.018	−0.561 ***	0.430 *	1

Generalized additive models were calculated separately for each factor as a predictor. The response was a log of the abundance of a specific species in the samples. Model selection compared a zero model with a linear model and quadratic model. The final model for each species was selected using AIC (see the comprehensive output from the analyses in Supplementary Materials). Only species with significant predictions are shown in the graphs (Figure 3a–f), and the species name of the curve is located near the maximum value.

Litter cover was identified as the most important factor, explaining 2% of species distribution data (Table 3), influencing the abundance of 8 species (Figure 3a). Half of these species showed a positive relationship with litter cover, reaching higher abundances in traps without bare soil ground around. The strongest response was observed in *G. tetrasticha*. *Melogona voighti* (Verhoeff, 1899), *U. foetidus*, and *Schendyla nemorensis* (CL Koch, 1837) were more abundant in traps surrounded with little or no litter cover (Figure 3a).

Herb cover was evaluated as the second most important factor (Table 3), explaining another 0.5% of variability in species data, affecting the abundance of seven species (Figure 3c). *Melogona voightii*, *H. oculodistincta* and *L. mutabilis* were associated with habitats characterized by high herb cover. In contrast, *G. tetrasticha* and *L. forficatus* preferred habitats with little or no herb cover (up to 25%). The same proportion of variability explained by the presence of shrubs was also explained by the presence of trees in the vicinity of the traps (Table 3). It influenced the distribution of six species (Figure 3e). Most species, namely, *P. germanicum*, *L. forficatus*, *Unciger transsilvanicus* (Verhoeff, 1899) and *H. oculodistincta*, occurred in highly shaded habitats, whereas *L. mutabilis* was negatively associated with high trees and was most abundant in habitats without old high trees.

Stand age was a significant environmental factor for eight species (Figure 3f). Although *G. tetrasticha* as well as *L. forficatus* occurred across the entire habitat gradient, it clearly preferred young stands, where they reached the highest abundances; in older stands its abundance rapidly declined with increasing stand age. *Lithobius mutabilis* showed an almost opposite pattern. Shrub cover was a significant predictor for distribution of seven species (Table 4). *Lithobius mutabilis*, *L. forficatus*, *G. tetrasticha* and *M. voightii* reached higher abundances in habitats with a higher proportion of shrubs (Figure 3d).

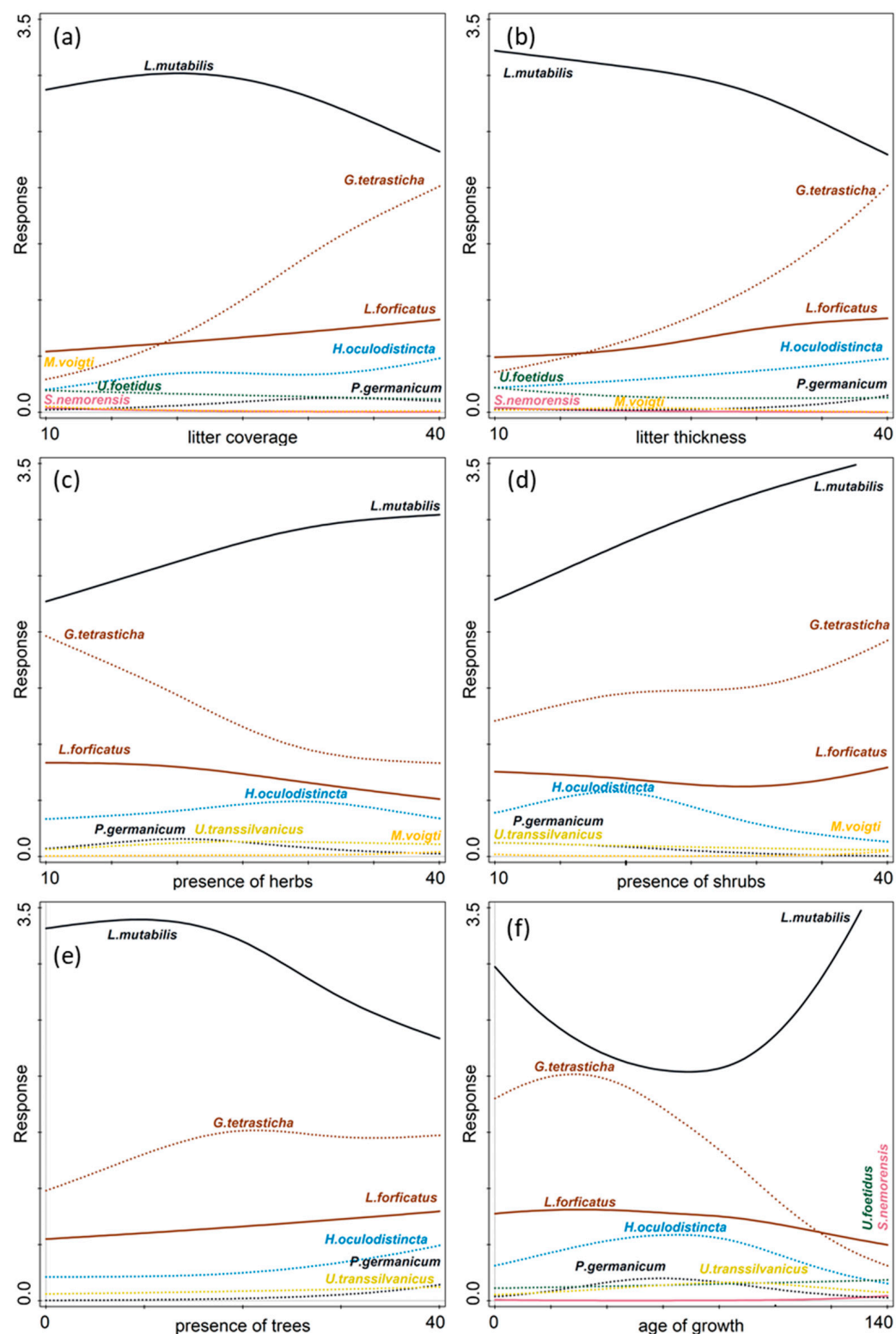


Figure 3. Predictions of distribution (fitted response values on log scale) of centipedes (solid lines) and millipedes (dotted lines) based on measured environmental factors: (a) amount of leaf litter expressed as the degree of bare soil coverage; (b) amount of leaf litter calculated as thickness of litter layer; (c) herb layer coverage; (d) shrub layer coverage; (e) tree-crowns coverage; (f) age of planted trees (for scaling explanation see Table 1). Only species with a significant response to a specific factor, which were caught in numbers of more than 10 individuals, are shown.

Litter thickness, the weakest predictor in the CCA model (Table 3), significantly affected the abundance of eight species (Figure 3b). Its strongest effect was observed in *G. tetrasticha*, which showed a clear preference for habitats where the litter layer was thickest. *Lithobius forficatus*, *P. gemanicum* and *H. oculodistincta* were also associated with habitats with a thicker litter layer. *Lithobius mutabilis* preferred habitats with a thin litter layer; in thicker layer its abundance markedly decreased. Similar preference was noticed for *S. nemorensis* and *U. foetidus* too.

Lithobius mutabilis and *L. forficatus* exhibited contrasting ecological preferences with respect to all examined factors. Their distributions within the study area indicated opposite trends ($t = 7.15$, $p < 0.001$; Figure 4). *Lithobius mutabilis* was much more abundant at sites corresponding to traps 10–16, whereas *L. forficatus* showed a marked decline in abundance at these sites.

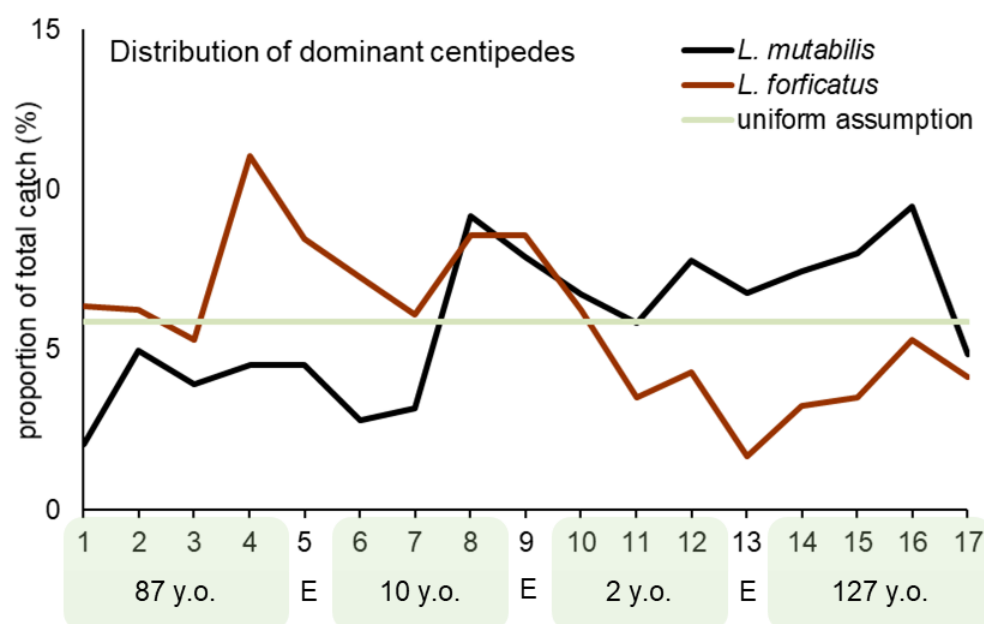


Figure 4. Preference of centipedes *Lithobius mutabilis* L. Koch, 1862 and *Lithobius forficatus* (Linnaeus, 1758) for a specific trap location in the studied patches of different ages (2–127 years old), expressed as the contribution of a specific trap to the total number of individuals of a specific species caught over two years. The expected equal contribution (one seventeenth of the catch) is also shown.

4. Discussion

4.1. Environmental Factors

The protected landscape area Litovelské Pomoraví harbors 22 millipede and 19 centipede species [19]. In the present study, we recorded 10 species of millipedes and 10 species of centipedes, which is consistent with previous findings from floodplain forests in this area [20] and typical for such types of Central European forests [21,22]. The highest biodiversity was observed in the older *Quercus-Ulmum* stands. In general, communities in old-growth forests tend to comprise more species and higher abundances [10,23–25], which may be a consequence of a more diverse supply of leaf litter [26]. Slightly higher diversity in the bordering ecotone is presumably caused by dispersal from the forest interior. We found no evidence that myriapod diversity was negatively affected in young stands (the clear-cut with seedlings and the 10-year-old stand) created by forest management. In centipedes, maintaining a certain level of heterogeneity, providing habitats of different size and developmental stages for both forest and open-habitat species, can lead to increased diversity [27,28].

Across all sites, *G. tetrasticha* was the dominant millipede species, and *L. mutabilis* the dominant centipede. Their high abundances in bordering traps suggest that these species are able to migrate between habitats. Forest ecotones are particularly important for centipedes, as they allow them to hunt in open areas while reproducing in well-protected forest habitats [16]. Ecotone theory predicts that predator species will be more common in ecotones, because predator activity often concentrates along forest edges [29]. The high occurrence of *L. forficatus* and *L. mutabilis* in ecotones is consistent with this prediction, regardless of the fundamentally opposite pattern of their preferences for specific habitats [30]. The spatial distributions of *G. tetrasticha*, *P. germanicum* and *U. foetidus* also indicate ongoing migration between habitats [31].

In species with poor dispersal ability, such as myriapods, the risk of extinction increases with habitat fragmentation [32]. Nevertheless, their migration between patches is still possible and depends on the distance between patches, their spatial arrangement, species traits, individual characteristics and intraspecific interactions [27]. A mosaic of areas of varying ages with different microclimates can provide a suitable environment for myriapods, which select the most suitable microclimate at any given time throughout the year as the weather changes [28]. Such spatial heterogeneity allows for the co-occurrence of species that otherwise show a clearer preference for a specific age stage of the forest in even-aged stands. An example of this is the preference of polydesmids for younger forests and glomerids for older forests, as documented in Normandy [33].

Among the environmental factors studied, litter cover was the most important for myriapod diversity. Our results are burdened by a minor imperfection—the leaf litter was not evaluated during this study but was recorded once, in April. This fact influenced the results. In stands dominated by *Q. robur* (Pedunculate Oak), there was relatively little amount of leaf litter because it decomposed on the ground during the winter. In contrast, *Q. petraea* (Sessile Oak) does not shed its leaves in autumn, but only when new leaves bud. For this reason, the layer of litter in April was thickest in the 10-year-old stand and also in the two-year-old stand.

In temperate forests, millipedes consume approximately 10–15% of annual leaf litter production [34,35]. All species except *L. mutabilis* and *U. foetidus* showed a positive relationship with litter cover. Leaf litter and the litter–soil interface represent the primary habitat for myriapods, providing an environment with optimal microclimatic conditions with shelters against desiccation and predators [36]; at the same time, litter contributes to the diversity of other soil invertebrates [37]. This leads to the creation of new niches and allows a higher number of species to coexist [36]. Besides creating suitable habitats, leaf litter is the main food source for millipedes, making them more vulnerable to changes in habitat structure than centipedes [38].

Forest management alters vegetation structure, which in turn affects the quality and quantity of leaf litter and, consequently, invertebrate communities. Replacement of old-growth forests by low-diversity stands or even monocultures generally has a negative impact on myriapod diversity [21,26]. However, up to a certain level, forest fragmentation increases environmental heterogeneity and leads to the creation of new habitats. Management practices that promote the formation of microhabitats within existing stands generally have a positive effect on arthropod communities [39]. David et al. [26] emphasized the irreplaceable role of habitat mosaics for millipede diversity, as their communities can vary significantly along very short spatial gradients. The same has been documented for centipedes in Slovenia [28].

The importance of ecotones resulting from forest fragmentation has already been highlighted in numerous studies. In highly fragmented landscapes, ecotone effects play a dominant role in shaping invertebrate assemblages [40]. Magura et al. [41] emphasized the

role of the combined herb and shrub layer in ecotones, which substantially contributes to landscape heterogeneity. The specific combination of environmental factors in ecotones often leads to the formation of microhabitats that do not occur in either of the adjacent habitats. A common response of invertebrates to such conditions is an increase in abundance and diversity [42]. Detailed information on ecotone effects on myriapods is still limited. It is known that the diversity of open-habitat millipede specialists has been negatively affected by the decline of coppicing and extensive grazing in Europe, and by the expansion of closed-canopy forests [26]. Therefore, habitat fragmentation and the resulting ecotones are likely to have a positive effect on these species. For centipedes and other invertebrates, one of the most important factors is the distance between habitats (i.e., edge length) and the environmental conditions in the intervening matrix [28]. Human-induced changes in plant composition and landscape mosaics can therefore be critical for their distribution [26].

Forest management should aim to create conditions that permit migration between habitats and maintain a favorable level of heterogeneity for invertebrates with limited dispersal ability [27]. A key issue, and one of the main focuses of forest management, should be the relationship between ecosystem functioning and community structure, ultimately supporting the preservation of suitable habitats [43].

4.2. Species-Specific Comments

The distribution of myriapods collected in this study indicates a strong dependence on habitat type and associated environmental factors. However, individual species responded differently to specific conditions. Below, we discuss the habitat preferences of species represented by more than 100 individuals in our samples.

Lithobius mutabilis is generally regarded as a typical woodland centipede [21,30], although in some countries (e.g., Slovenia) it is found primarily in deforested areas [28]. Our results show that its abundance decreases in habitats with higher tree cover (over 25%) and increasing litter cover. It was primarily collected in very young or very old stands, preferably with a high cover of herbs and shrubs, like in dense 10-year-old oak growth. The highest abundances were recorded in the ecotone between the 2-year-old clear-cut with seedlings and the 10-year-old oak stand. Its occurrence in ecotones, where solar radiation and temperature are higher than in the forest interior, is consistent with the findings of Grgič and Kos [44], who reported that *L. mutabilis* prefers warmer habitats; nevertheless, Fründ et al. [30] found in Germany an opposite pattern with higher abundances of this species in the forest interior, contrary to its edge. Also, Jabin [23] reported higher abundances of *L. mutabilis* in older forests.

Lithobius forficatus showed ecological preferences that were almost entirely opposite to those of *L. mutabilis*. Its abundance increased with tree cover, litter cover (and thickness), and stand age, and it was most numerous in middle-aged stands. It was also significantly associated with ecotones, reaching its highest abundances in two of the ecotones examined. This pattern agrees with previous studies reporting a close association of *L. forficatus* with anthropogenic edge habitats [10,30,45–47]. The contrasting habitat preferences of *L. mutabilis* and *L. forficatus* suggest that, although these two species co-occurred at all sites, they were distributed differently within them. Their abundance patterns may indicate the presence of interspecific competition, although not for prey, probably. No significant differences were found in food webs in forests of different ages [48].

Glomeris tetrasticha is a Central European species that typically occurs in various forest types [49] under sufficiently moist and shaded conditions [50]. Our results also indicate strong preferences for habitats with high tree, shrub and litter cover but with low herb cover. Its pronounced increase in younger stands has been documented previously by

Tufová [51] and is corroborated by our data. As a millipede species that is relatively tolerant to environmental variation [17], its occurrence in human-disturbed habitats is typical.

Haplogona oculodistincta was most abundant in middle-aged stands with dense tree cover and a thick litter layer. It thus occupies a typical millipede habitat characterized by sufficient food resources, shelter, shade and humidity [34]. The highest abundances were found in the ecotone between the 87-year-old *Quercus–Ulm* stand and the 10-year-old oak stand. However, its overall distribution suggests that this pattern is more likely due to migration between these two habitats than to a specific preference for ecotone conditions. It should be noted that *H. oculodistincta* was not recorded in the studied areas seven years earlier. It was probably introduced here when oak seedlings were planted (when the 10-year-old stand was established) and apparently took several years to form a viable population that is expanding into surrounding stands [51].

Unciger foetidus is a European species with a broad ecological amplitude [22,52]. It mostly inhabits human settlements, gardens and parks, but it is also found in forests at sufficiently humid sites [50]. In our study, it showed a positive relationship with old stands and low litter cover. Its highest abundances were recorded in one of the ecotones. A previous study [31] similarly characterized *U. foetidus* as a species that occurs in ecotones while moving between two habitats.

Unciger transsilvanicus is a central–southeastern European species. It prefers relatively dry floodplain forests but can also occur in open habitats such as meadows [52] or younger forests [22]. Our results indicate preferences for habitats with low shrub cover and intermediate herb cover (25–50%). The highest abundances were found in the 87-year-old *Quercus–Ulm* stand.

5. Conclusions

Our study shows that myriapod communities in forests are strongly structured by local habitat conditions and by forest fragmentation, particularly through the creation of ecotones. Old-growth *Quercus–Ulm* stands and the surrounding edge zones supported the highest myriapod diversity, while two of the three ecotones examined harbored notably high species abundances. Leaf litter (its cover and thickness), stand age, and the structure of the herb and shrub layers emerged as key determinants of myriapod distribution, with most species responding positively to well-developed litter layers and structurally complex vegetation. At the same time, individual species exhibited contrasting ecological preferences, as illustrated by the opposite habitat associations of *Lithobius mutabilis* and *L. forficatus*, and the broad tolerance of *Glomeris tetrasticha* to human-modified habitats.

From a management perspective, our results highlight the importance of conserving a fine-grained mosaic of stand ages and maintaining both interior forest and ecotonal habitats within managed forest landscapes. Practices that retain or restore old-growth patches, while allowing the controlled creation of younger stands and semi-open edges, are likely to enhance habitat heterogeneity and support a rich assemblage of forest-floor invertebrates. Maintaining sufficient litter accumulation and a diverse understorey (shrubs and herbs) appears crucial for sustaining myriapod diversity, and the ecosystem functions they provide, particularly litter decomposition and soil structuring. Forest management in Central Europe should therefore explicitly consider edge structure, stand age diversity and litter dynamics as key components in strategies aimed at preserving forest biodiversity.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f17010127/s1>.

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