

Article

Spider Assemblages of Tree Branches in Managed and Primeval Deciduous Stands of the Białowieża Forest

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Abstract: The Białowieża Forest is an important biodiversity hotspot on a European scale, and therefore its preservation should have a high priority. However, forest management conducted over a large area of the forest, intensive logging, and elimination of dead trees pose serious threats to many species in the forest. The main aim of this study was to determine the species composition of spider assemblages inhabiting tree branches of the Białowieża Forest and to compare their species richness and the abundance of individuals (adults and juveniles) between managed and primeval stands. Between April and November 2000, we sampled three forest types (oak–lime–hornbeam forest, ash–alder riparian forest, and alder carr) in protected primeval stands within the Białowieża National Park and in managed stands. We collected 1761 specimens from 14 families and identified 41 species. Tree branches were inhabited mainly by juveniles. Species richness was smaller in managed stands compared to primeval stands. The highest number of species was found in primeval alder carr. Our study shows a negative effect of forest management on spider assemblages in terms of species richness. We emphasize the important role of alder carr forests as potential biodiversity hotspots.

Keywords: arboreal spiders; Araneae; diversity; species richness; primeval forest; managed forest; the Białowieża Forest



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1. Introduction

Spider assemblages inhabiting branches and foliage or more broadly, tree canopies, are rare objects of research. Papers dealing with this subject are often focused on orchards [1,2] and tropical or subtropical regions, e.g., [3–5]. Only a few studies concern spiders dwelling in tree branches in the natural ecosystems of the temperate zone, e.g., [6–8]. A method often used in this type of research is insecticide fogging, which is a non-selective method of spider collection. Therefore, the collected material derives not only from the foliage growing out of thin branches but also from tree trunks. As a result, spiders from these two microhabitats have previously been analyzed as one group [9–11], which might have led to incorrect conclusions as these two habitats are markedly different in terms of microhabitat structure and microclimatic conditions, and thus spider assemblages inhabiting them are likely to be different [12,13].

The present study was carried out in the Białowieża Forest, which is a remnant of the vast forests that once covered most of Europe. However, only a small part of this valuable forest complex is strictly protected as the Białowieża National Park. This national park encompasses one of the best-preserved natural European lowland forests. They are uneven-aged, multistorey, and mixed-species, and they possess a large amount of dead wood. The forest in Białowieża National Park has never been logged and therefore it may be regarded as a primeval forest [14,15]. However, a large part of the Białowieża Forest is covered by managed stands, where intensive changes in habitats take place due to

logging and removal of dead trees [16]. Therefore, it is extremely important to discover whether, and to what extent, the managed stands in the Białowieża Forest differ from those in similar habitats in the primeval forest in respect of the abundance, species richness, and species diversity of particular groups of organisms. Studies conducted in this respect have concerned, e.g., birds such as woodpeckers [17–20], carabid beetles [21], collembola [22], and also spiders, but the latter have been limited to only rare and threatened species [23]. Generally, the majority of these studies showed that the abundance, species richness, and species diversity were higher in primeval forests compared to managed stands. Moreover, it is well documented that forest management, mainly logging and removal of dead trees, has a negative impact on some species or even on whole animal assemblages [18,20,22].

Spiders are an excellent group of organisms to use for studying the impact of human management due to their sensitivity to changes in habitat structure and microclimatic conditions [24–27]. Among the most important factors shaping the assemblages of forest spiders are the type of stand [13,28], the tree species diversity [29], tree canopy openness [30], the presence of woody debris [31], and humidity [25]. Studies concerning arboreal spiders in the Białowieża Forest have already been conducted; however, they focused exclusively on the fauna of tree trunks [13] or tree canopies and they were carried out using the insecticidal knockdown method [9,10]. In contrast to the studies mentioned above, the present paper focuses exclusively on spider assemblages inhabiting branches and foliage in the low strata of trees. Such an approach was possible due to the selectivity of branch shaking, which was the method used in this study.

The primary objectives of the present study were: (1) to determine the species composition of spider assemblages on tree branches in oak–lime–hornbeam forest, ash–alder riparian forest, and alder carr located in both managed and primeval stands of the Białowieża Forest; (2) to compare spider assemblages between managed and primeval stands in respect of the abundance of spider individuals (adults and juveniles separately) and species richness; (3) to assess how the numbers of spider individuals and spider species changed with time during the sampling period. We hypothesized that more spider species and spider individuals would be found in primeval stands compared to managed stands. Our assumption was based on the findings of other authors who showed that in the Białowieża Forest both particular species and whole animal assemblages suffer from the effects of forest management [18,20,22].

2. Materials and Methods

2.1. Study Area

The study was conducted in the Białowieża Forest, which is a large forest complex (1500 km²) located on the border between Poland and Belarus. The Polish part of the Białowieża Forest (ca. 630 km²) consists of two main parts: the Białowieża National Park (BNP) and managed forests. The area of the BNP, after its enlargement in 1996, is 105 km², of which an area of 47.5 km² has been strictly protected since 1921 and has never been logged. Stands in this zone possess many typical features of primeval forests, such as a diverse tree community, significant tree heights, a large amount of dead wood, and a multi-layered and uneven-aged stand structure [14,32]. Much larger than the BNP is the part of the Białowieża Forest managed by Polish National Forest Holding “State Forests” (525 km²). In the managed part, timber harvesting, removal of dead trees, planting, and control of forest pests (usually by cutting down infected trees) are normal practices that cause considerable disruption of the forest structure. The forests managed by “State Forests”, in comparison to primeval forests located in the BNP, are younger, less diverse in terms of structure, and much less abundant in dead wood in the form of standing snags and fallen trees [17,18,20].

Our study was conducted in three deciduous forest stands: oak–lime–hornbeam forest (*Tilio-Carpinetum*), ash–alder riparian forest (*Circaeo-Alnetum*) and alder carr (*Carici elongatae-Alnetum*). In each of the three forest types two plots were located: one in primeval stands in the Białowieża National Park and one in managed forests (Figure 1). The oak–lime–hornbeam forests are very diversified and occupy many habitat types in the

Białowieża Forest. The most numerous tree species in this forest type are small-leaved lime (*Tilia cordata* Mill.), European hornbeam (*Carpinus betulus* L.), Norway spruce (*Picea abies* (L.) H. Karst), Norway maple (*Acer platanoides* L.), pedunculate oak (*Quercus robur* L.), and elm (*Ulmus* spp.). In ash–alder riparian forests growing along the watercourses the main tree species are black alder (*Alnus glutinosa* Gaertn.) and European ash (*Fraxinus excelsior* L.), with some admixture of Norway spruce. The last studied forest type—the alder carr—occupies marshy and fertile habitats and its existence depends on permanently high water levels without outflow. The characteristic feature of this type of forest is a well-developed hummock–hollow structure in the forest floor. Hummocks are created by the roots of trees, which grow in clumps, while the hollows, where stagnant water is present for a long period of the year, are dominated by marshland plant species. The most common tree species in alder carr are black alder, European ash, and Norway spruce.

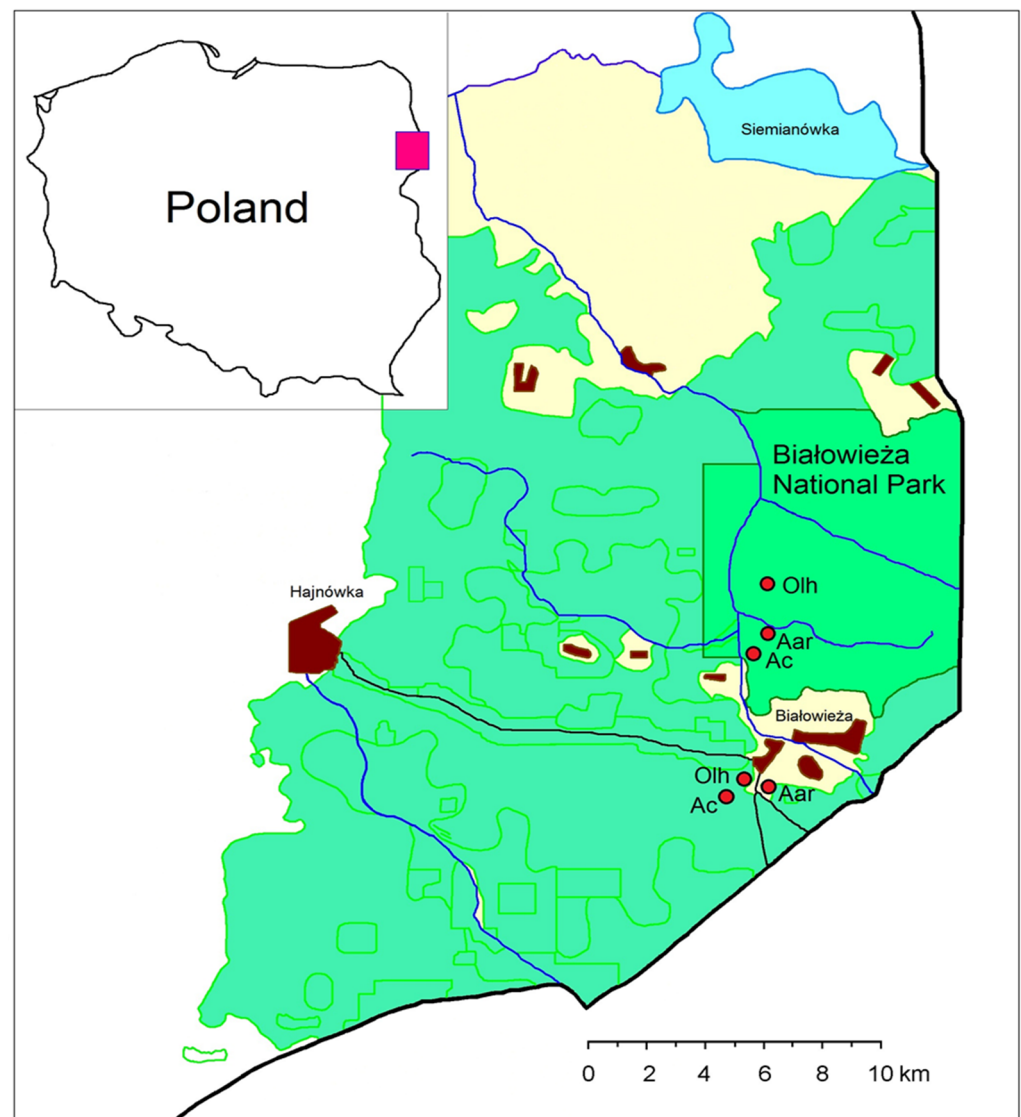


Figure 1. Location of the study plots in the Białowieża Forest. Abbreviations: Olh—oak–lime–hornbeam forest; Aar—ash–alder riparian forest; Ac—alder carr. Light green indicates the area of Białowieża National Park; dark green indicates the area of remaining Białowieża Forest.

2.2. Spider Sampling

Spiders were sampled from April to November 2000 in six study plots (rectangles of about 20 × 40 m). A total of 10 samples were collected from each study plot on the

following dates: 27 April, 12 May, 25 May, 11 June, 22 June, 8 July, 27 July, 12 October, 27 October, and 11 November. In each plot for each sampling date, ten similar-sized branches (1×0.5 m), at heights of 1–2 m were sampled. Branches were chosen from the most common tree species for a given plot. In the case of the oak–lime–hornbeam forest, these were European hornbeam, small-leaved lime, pedunculate oak, and Norway spruce, whereas in the case of both ash–alder riparian forest and alder carr they were European ash, black alder, and Norway spruce. The material samples from each sampling date in each plot were combined and considered as one sample, irrespective of the sampled tree species. Spiders were sampled by shaking the tree branches into a sweep net. To collect the spiders, the branches were put into the sweep net and then shaken. In addition, the sampling branches were carefully visually examined to collect spiders that did not fall into the sweep net during shaking. All samples were collected by the same person to reduce possible variation due to different techniques of branch shaking and choice of sampling branches.

2.3. Statistical Analysis

The collected spiders were identified at species level or, in the case of many juvenile specimens, to higher taxa (i.e., genus and family) based on available identification keys [33–36] and were deposited at the Institute of Biological Sciences, Siedlce University of Natural Sciences and Humanities, Poland.

To assess the associations of the numbers of collected spider individuals and spider species with forest type, forest management regime, and sampling period, generalized linear mixed models (GLMMs) were used. In the model where the response variable was the number of collected adult spider individuals, the Gaussian error distribution and the identity-link function were used. In the model where the response variable was the number of collected juvenile spider individuals, the Poisson error distribution and the log-link function were used. In the last model where the response variable was the number of spider species, the Gaussian error distribution and the log-link function were used. The number of species in each sample was determined on the basis of individuals identified at species level (both adult and juvenile spider individuals). The forest type (oak–lime–hornbeam stand, ash–alder riparian forest, or alder carr), forest management (managed stands vs. primeval stands), and the sampling period (ten dates from April to November, when the spiders were collected) were treated as fixed categorical explanatory variables. Spiders were sampled many times on the same plots, therefore plot identity was included in the models as a random effect. If the GLMM showed a significant effect of a given variable, paired contrasts were calculated to find significant differences between the levels.

To check if a managed stand and a primeval stand in a particular forest type differed in terms of species richness (total number of species recorded during the whole study period), the rarefaction curves for the observed species richness were computed with 95% confidence limits [37]. The confidence limits were based on a bootstrap method with 100 replications. The species richness of managed stands and primeval stands in particular forest types was considered significantly different when the confidence intervals did not overlap [38,39].

To verify sampling sufficiency, richness estimators (Chao1, Chao2, jackknife1, and jackknife2) were calculated using 100 randomizations in all calculations. Sampling completeness was calculated as the percentage of the observed species richness compared to the Chao1 richness estimate [40]. GLMM analyses were performed in SPSS 21.0 for Windows, whereas rarefaction curves (with their confidence limits) and richness estimators were calculated using the software EstimateS version 9.1.0 [41].

3. Results

A total of 1761 spider individuals from 14 families were sampled during the study period. Juvenile spiders dominated in the collected material (1454 individuals, ca. 83%) and their contribution ranged, in different plots, from 58% in the managed alder carr to 96% in the managed oak–lime–hornbeam forest. The Linyphiidae was the most numerous

family in each study plot. In the group of 1127 individuals identified at the species level, a total of 41 spider species were found (Table 1). The most abundant spider species in oak–lime–hornbeam forest were *Trematocephalus cristatus* for the plot located in the managed stand and *Diaea dorsata* for the plot in the primeval stand. In the case of ash–alder riparian forest, *Anyphaena accentuata* was the most numerous in the managed stand and *Neriere peltata* was the most numerous in the primeval stand. *Porrhomma pygmaeum* was the most abundant spider species in both alder carr plots (Table 1).

Table 1. Spiders collected on tree branches in managed and primeval stands in the Białowieża Forest. Spider species contribution (percent) is shown in brackets, given only for species that achieved 5 percent or more. All individuals identified at the species level were included in the percentage composition. Abbreviations: Man.—managed stand; BNP—primeval stand; Olh—oak–lime–hornbeam forest; Aar—ash–alder riparian forest; Ac—alder carr; ad./juv.— number of adult/juvenile spider individuals; un.—individuals identified only at the family level; dash indicates the lack of an age group.

Family/Genus/Species	Man. Olh ad./juv.	BNP Olh ad./juv.	Man. Aar ad./juv.	BNP Aar ad./juv.	Man. Ac ad./juv.	BNP Ac ad./juv.
Family Amaurobiidae						
<i>Amaurobius fenestralis</i> (Ström, 1768)		-/1				
Family Anyphaeniidae						
<i>Anyphaena accentuata</i> (Walckenaer, 1802)	(31) 3/107	(10) 3/12	(46) -/34	(17) 1/21	(8) 2/20	(15) 1/23
Family Araneidae						
Araneidae un. Clerck, 1757	-/1		-/2			
<i>Araneus diadematus</i> Clerck, 1757	-/2					-/1
<i>Araneus marmoreus</i> Clerck, 1757			-/2			
<i>Araneus quadratus</i> Clerck, 1757			-/1			
<i>Araneus</i> sp. Clerck, 1757			-/5			
<i>Araniella cucurbitina</i> (Clerck, 1757)			1/-		1/-	
<i>Araniella proxima</i> (Kulczyński, 1885)			2/-			
<i>Araniella</i> sp. Chamberlin & Ivie, 1942	-/6	-/4	-/4	-/2	-3	-/11
<i>Cyclosa conica</i> (Pallas, 1772)	-/4	(6) 3/6			-/1	-/1
<i>Gibbaranea bituberculata</i> (Walckenaer, 1802)		-/1				
Family Clubionidae						
<i>Clubiona lutescens</i> Westring, 1851					3/-	
<i>Clubiona</i> sp. Latreille, 1804	-/3	-/1	-/5	-/5	-/2	-/1
Family Dictynidae						
<i>Dictyna arundinacea</i> (Linnaeus, 1758)	1/-					
<i>Dictyna</i> sp. Sundevall, 1833	-/4				-/4	-/5
Family Linyphiidae						
<i>Bathypantes</i> sp. Menge, 1866		-/2				
<i>Ceratinella brevis</i> (Wider, 1834)			1/-			
<i>Drapetisca socialis</i> (Sundevall, 1833)		-/3				1/-
<i>Entelecara acuminata</i> (Wider, 1834)				1/-		
<i>Gongylidium rufipes</i> (Linnaeus, 1758)				6/-	2/-	1/-
<i>Helophora insignis</i> (Blackwall, 1841)	1/-			(13) -/16	-/8	-/5
<i>Hypomma cornutum</i> (Blackwall, 1833)						1/-
<i>Tenuiphantes</i> sp. Saaristo & Tanasevitch, 1996			-/5	-/18	-/5	-/2
<i>Linyphia</i> sp. Latreille, 1804						-/1
<i>Linyphia triangularis</i> (Clerck, 1757)		1/2				2/2
Linyphiidae un. Blackwall, 1859	-/19		-/18	-/18	-/17	-/17
<i>Neriere emphana</i> (Walckenaer, 1841)		1/3		2/1		2/1
<i>Neriere montana</i> (Clerck, 1757)			-/1	-/5	-/6	(6) -/10
<i>Neriere peltata</i> (Wider, 1834)	1/-	(6) 7/3		(22) 2/26	1/4	(9) 1/13
<i>Neriere</i> sp. Blackwall, 1833	-/51	-/25	-/2		-/32	-/50
<i>Pityohyphantes phrygianus</i> (C. L. Koch, 1836)						-/2
<i>Porrhomma oblitum</i> (O. Pickard-Cambridge, 1871)					6/-	
<i>Porrhomma pygmaeum</i> (Blackwall, 1834)	1/-				(50) 131/-	(28) 44/-
<i>Trematocephalus cristatus</i> (Wider, 1834)	(50) -/178	(19) -/29	(32) -/24	(6) -/8	(23) -/61	1/5
Family Lycosidae						
<i>Pardosa</i> sp. C. L. Koch, 1847			-/12			

Table 1. Cont.

Family/Genus/Species	Man. Olh ad./juv.	BNP Olh ad./juv.	Man. Aar ad./juv.	BNP Aar ad./juv.	Man. Ac ad./juv.	BNP Ac ad./juv.
Family Mimetidae						
<i>Ero</i> sp. C. L. Koch, 1836						-/1
Family Philodromidae						
<i>Philodromus rufus</i> Walckenaer, 1826						1/-
<i>Philodromus</i> sp. Walckenaer, 1826	-/7	-/10	-/4	-/2		-/11
Family Pisauridae						
<i>Pisaura mirabilis</i> (Clerck, 1757)			-/2			
Family Salticidae						
Salticidae un. Blackwall, 1841				-/1		
Family Tetragnathidae						
<i>Metellina menzei</i> (Blackwall, 1869)		5/-				
<i>Metellina segmentata</i> (Clerck, 1757)		2/-				4/-
<i>Metellina</i> sp. Chamberlin & Ivie, 1941	-/1	-/9		-/4	-/4	
<i>Pachygnatha listeri</i> Sundevall, 1830				1/-		
<i>Pachygnatha</i> sp. Sundevall, 1823						-/1
<i>Tetragnatha montana</i> Simon, 1874						2/-
<i>Tetragnatha</i> sp. Menge, 1866	-/16		-/39	-/27	-/28	-/32
Family Theridiidae						
<i>Parasteatoda</i> sp. Archer, 1946	-/1		-/1			
<i>Enoplognatha ovata</i> (Clerck, 1757)	(7) 9/17	(23) 6/30		(17) 12/10	2/3	1/2
<i>Robertus arundineti</i>						1/-
(O. Pickard-Cambridge, 1871)						
<i>Rugathodes instabilis</i>						3/-
(O. Pickard-Cambridge, 1871)						
<i>Paidiscura pallens</i> (Blackwall, 1834)						1/-
Theridiidae un. Sundevall, 1833	-/26	-/9	-/6	-/2	-/3	-/18
<i>Platnickina tinctoria</i> (Walckenaer, 1802)		1/-		1/-		
<i>Theridion varians</i> Hahn, 1833	2/-		1/1	1/0	2/1	1/0
Family Thomisidae						
<i>Diaea dorsata</i> (Fabricius, 1777)	(8) 3/24	(24) -/37	1/1	(11) 1/13	-/5	(15) 2/21
<i>Misumena vatia</i> (Clerck, 1757)			1/-			
<i>Ozyptila</i> sp. Simon, 1864	-/2	-/2	-/1	-/1	-/1	
<i>Xysticus cristatus</i> (Clerck, 1757)					1/-	
<i>Xysticus</i> sp. C. L. Koch, 1835	-2					
<i>Xysticus ulmi</i> (Hahn, 1831)			1/-			
Total no. of individuals	21/471	29/189	8/170	28/180	151/208	70/236
Total no. of species	11	14	13	13	15	23
No. of common species		6		5		11

The lowest number of species was found in the managed oak–lime–hornbeam forest (11) and the highest in primeval alder carr (23 species). However, the calculated estimators indicated higher species richness (varying depending on the estimator), especially for primeval alder carr, for which the sampling completeness was the lowest, at 53%, whereas in the other plots sampling completeness was about 70–80% (Table 2).

Table 2. Observed species richness and species richness estimates for the spider communities of tree branches in managed and primeval stands in the Białowieża Forest. Sampling completeness was calculated using Chao1 estimator. Abbreviations: Man.—managed stand; BNP—primeval stand; Olh—oak–lime–hornbeam forest; Aar—ash–alder riparian forest; Ac—alder carr; SD—standard deviation.

	Man Olh	BNP Olh	Man Aar	BNP Aar	Man Ac	BNP Ac
Observed richness	11	14	13	13	15	23
Estimates						
Chao 1 ± SD	15 ± 5	18 ± 7	17 ± 4	19 ± 7	19 ± 7	43 ± 20
Chao 2 ± SD	17 ± 7	20 ± 7	31 ± 18	14 ± 2	19 ± 4	48 ± 21
Jackknife 1 ± SD	16 ± 3	19 ± 3	21 ± 2	17 ± 2	20 ± 2	35 ± 3
Jackknife 2	18	21	27	16	21	43
Sampling completeness	73%	78%	76%	68%	79%	53%

Comparisons based on the rarefaction curves revealed that species richness did not differ between managed stands and primeval stands for either oak–lime–hornbeam forest or ash–alder riparian forest (Figures 2 and 3). However, rarefaction curves revealed that for the same number of collected spider individuals, species richness in primeval alder carr was twice as high as in managed alder carr, and that this result was statistically significant (Figure 4).

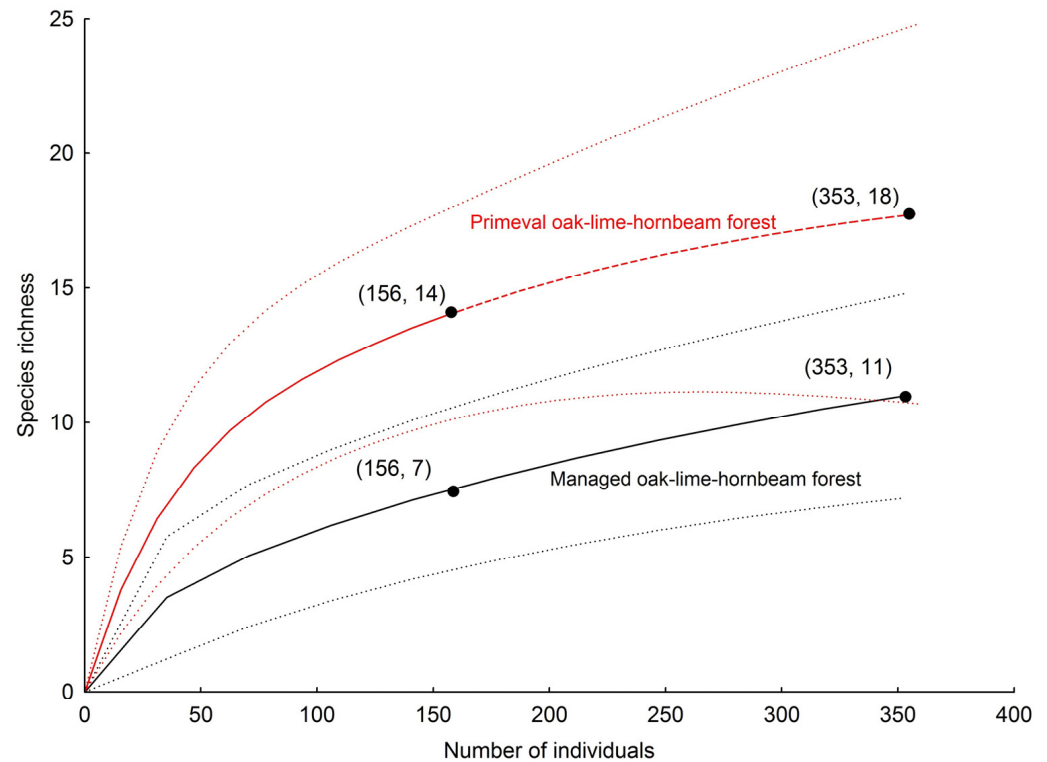


Figure 2. Individuals-based rarefaction (solid) and extrapolated (dashed) curves with 95% confidence limits (thin, dotted curves) comparing species richness in primeval oak–lime–hornbeam forest (red) and managed oak–lime–hornbeam forest (black). Solid black dots indicate reference samples. The number of individuals and the number of species in reference samples are shown in brackets.

The GLMMs showed that the number of collected spider species (on particular sampling dates) was associated with both the presence of forest management and the forest type (Table 3). More spider species were collected in primeval forest compared to managed stands, and more species were collected in alder carr compared to ash–alder riparian forest (Figure 5).

Table 3. Results of GLMM assessing the association of number of spider species with forest type, forest management, and sampling date. Significant results are shown in bold.

Variable	df1, df2	F	p
Forest type	2, 47	5.839	0.005
Managed/Primeval	1, 47	9.487	0.003
Sampling date	9, 47	1.931	0.070
Random effect	Estimate ± SE	Z	p
Plot	0.001 ± 0.014	0.077	0.939

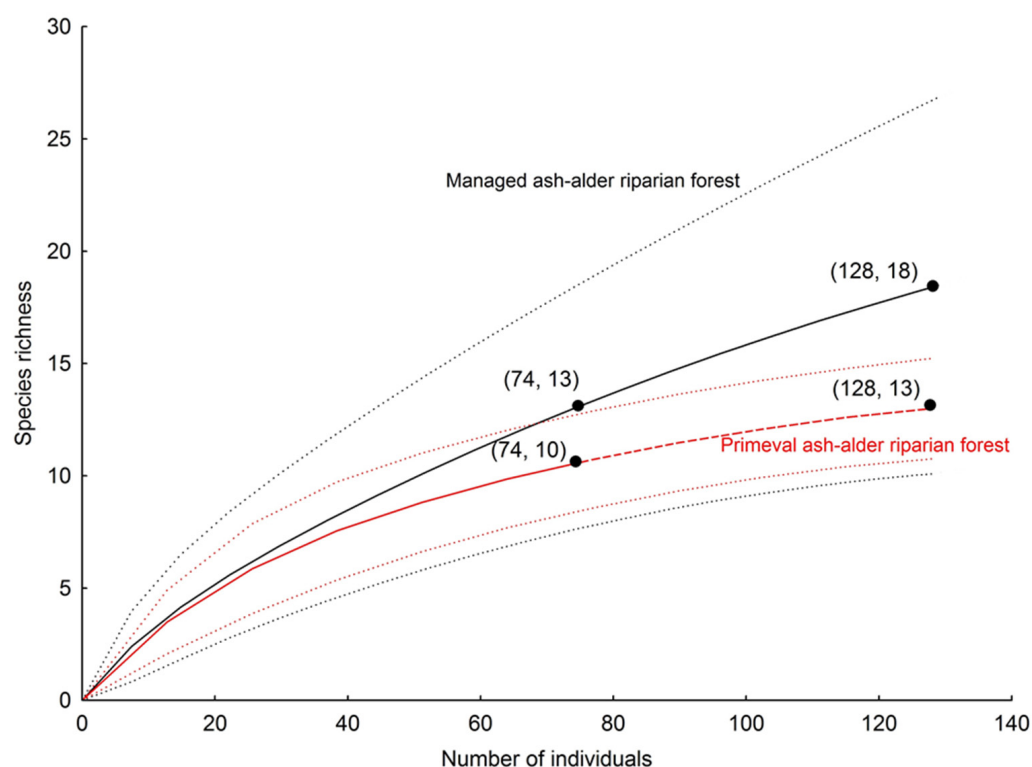


Figure 3. Individuals-based rarefaction (solid) and extrapolated (dashed) curves with 95% confidence limits (thin, dotted curves) comparing species richness in ash-alder riparian forest (red) and managed ash-alder riparian forest (black). Solid black dots indicate reference samples. The number of individuals and the number of species in reference samples are shown in brackets.

Table 4. Results of GLMM assessing the association of number of adult spider individuals with forest type, forest management, and sampling date. Significant results are shown in bold.

Variable	df1, df2	F	p
Forest type	2, 47	3.485	0.039
Managed/Primeval	1, 47	0.308	0.582
Sampling date	9, 47	1.802	0.093
Random effect	Estimate $\pm$ SE	Z	p
Plot	2.027 $\pm$ 15.474	0.131	0.896

Table 5. Results of GLMM assessing the association of number of juvenile spider individuals with forest type, forest management, and sampling date. Significant results are shown in bold.

Variable	df1, df2	F	p
Forest type	2, 47	0.852	0.433
Managed/Primeval	1, 47	0.530	0.470
Sampling date	9, 47	77.632	<0.001
Random effect	Estimate $\pm$ SE	Z	p
Plot	0.165 $\pm$ 0.169	0.976	0.329

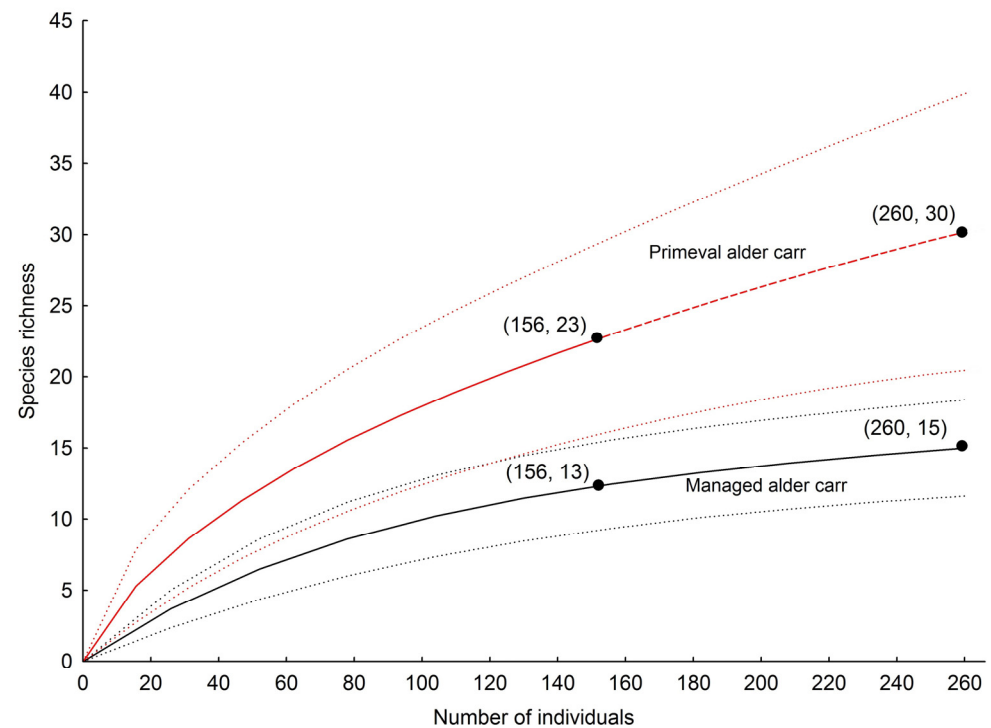


Figure 4. Individuals-based rarefaction (solid) and extrapolated (dashed) curves with 95% confidence limits (thin, dotted curves) comparing species richness in primeval alder carr (red) and managed alder carr (black). Solid black dots indicate reference samples. The number of individuals and the number of species in reference samples are shown in brackets.

The numbers of both adult and juvenile individuals collected were not associated with forest management (Tables 4 and 5). However, the abundance of adult spiders was associated with forest type, and more individuals were captured in alder carr compared to the other types of forests (Table 4, Figure 6). The numbers of juvenile spiders were influenced by sampling date; the samples from October and November contained up to a few times more individuals than the samples from the other dates (Table 5, Figure 7a). In contrast, the sampling date had no effect on the number of adult individuals. Adult individuals were very few in number for all sampling dates except the first two (Table 4, Figure 7b).

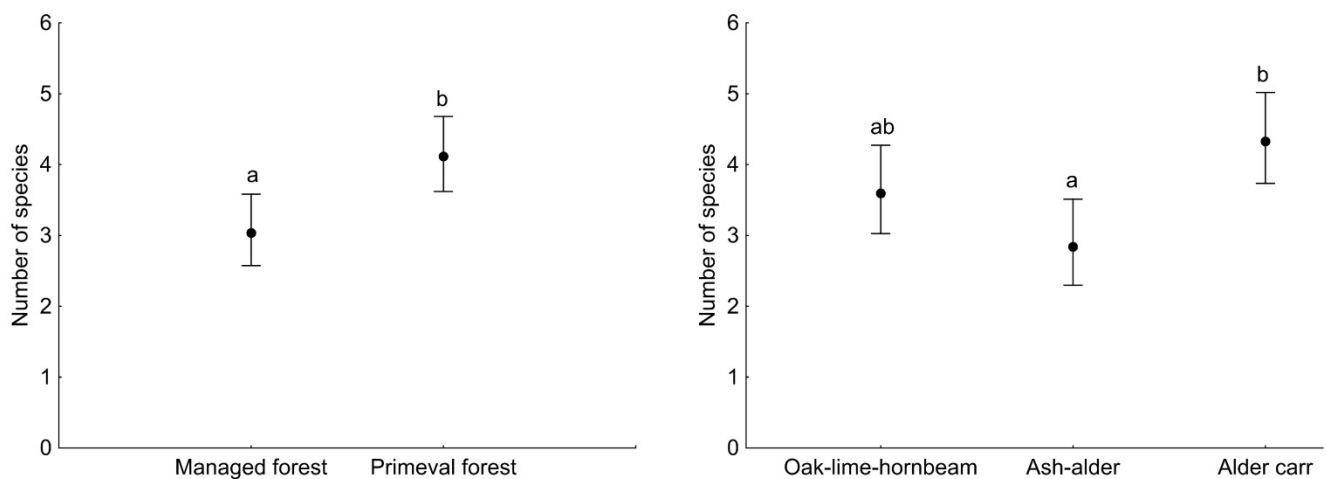


Figure 5. The number of spider species (means with 95% confidence limits) recorded in a single sample in different types of forest. Different letters indicate significant differences between forests.

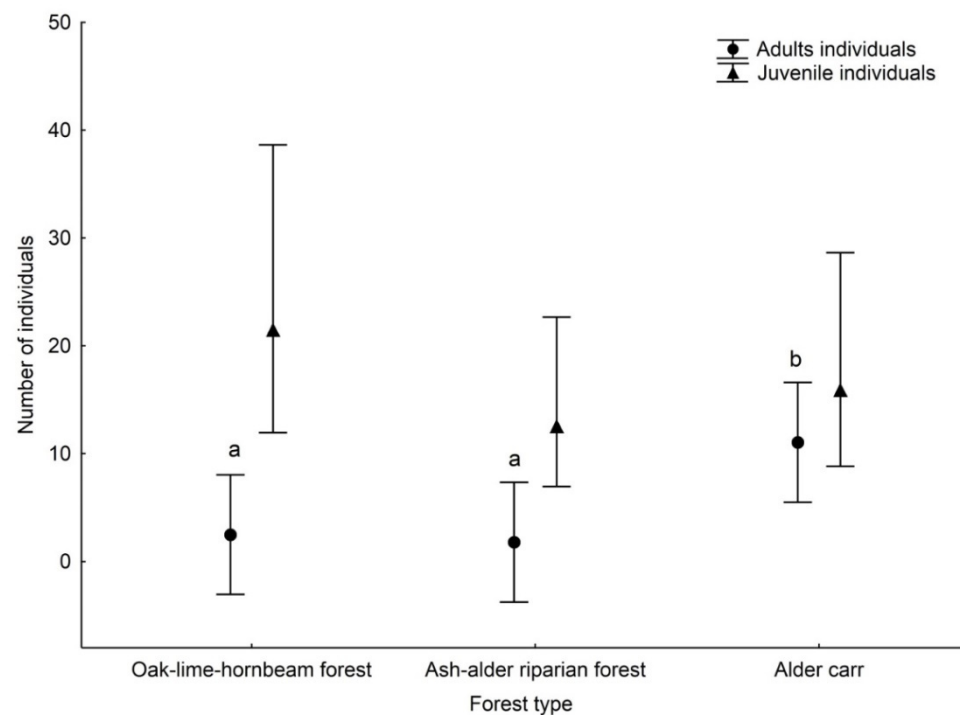


Figure 6. The number of adult and juvenile spider individuals (means with 95% confidence limits) recorded in a single sample in three analyzed forest types. Different letters indicate significant differences between forest types.

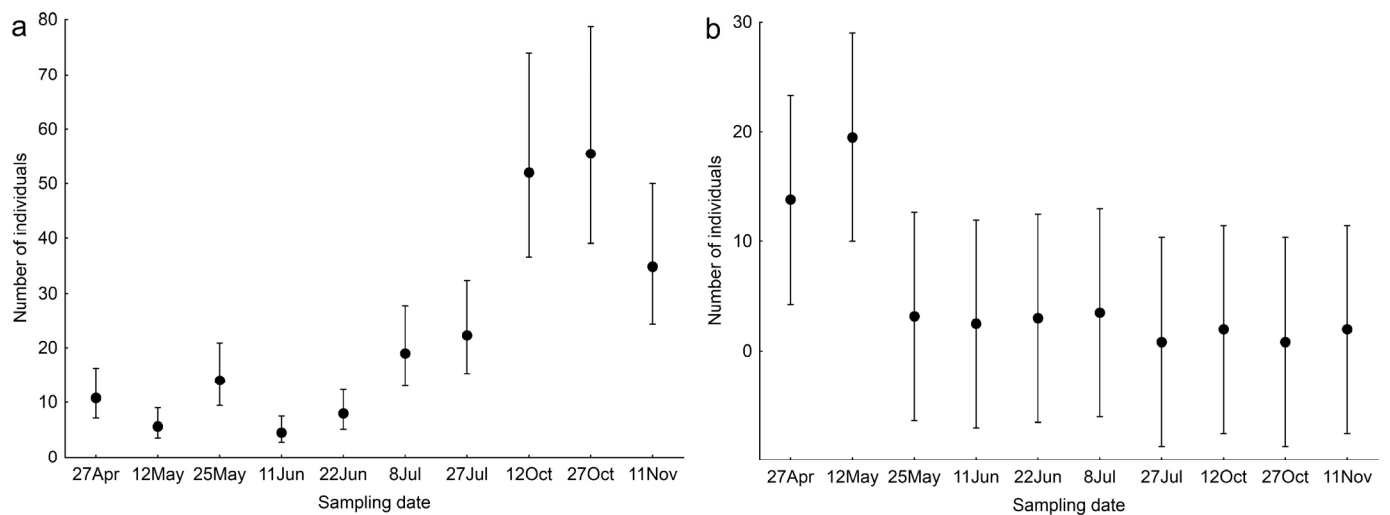


Figure 7. The number of juvenile (a) and adult (b) spider individuals (means with 95% confidence limits) recorded in a single sample in a particular sampling period.

4. Discussion

The Białowieża Forest is a unique biodiversity hotspot on a European scale. In addition, it plays an important role as a refuge for many rare and threatened species [42,43]. Therefore, its preservation in a good condition should be a high priority. However, forest management conducted over a large area of the Białowieża Forest, especially intensive logging and the elimination of dead trees, is a serious threat to many species, causing their abundance to decrease. For example, the lower abundance of the three-toed woodpecker in managed stands compared to primeval stands located in the BNP is a result of the removal of dying and dead spruces from the forest [44]. Moreover, human influence in the Białowieża Forest

ecosystems may be a reason for disappearing relic species, as Skłodowski [45] showed in carabid beetles. Negative changes caused by forest management in the Białowieża Forest have also affected spiders, as revealed by Stańska [23], who found that the numbers of rare and threatened spider species and the numbers of individuals from these groups were higher in primeval alder carr and primeval ash–alder riparian forest compared to similar managed forests.

The results of the present study confirmed the negative influence of forest management on spider assemblages. We found that the number of species revealed in particular samples was lower in managed forest compared to primeval forest. Moreover, we showed the species richness in primeval alder carr was twice as high as in the managed alder carr. The explanation for this phenomenon may be the less diverse and less complex structure of managed stands compared to primeval stands, due to forest management, which is usually responsible for the simplification of the structure of stands. This difference was particularly visible in the hummock–hollow structure of alder carr, where trees growing in primeval stands of this type of forest were older and larger, and thus the hummocks created by their roots provided more space and shelter for spiders. Many authors have shown that structurally diverse and complex habitats favor higher species diversity of spiders as a result of providing a broad spectrum of niches [46–49].

It might seem that spider fauna inhabiting the foliage in low strata of trees should consist largely of plant-dwelling spider species and species occurring on tree trunks. Small leafy branches apparently resemble herbaceous plants and sometimes they are located at similar heights from the ground. Furthermore, spiders living on tree trunks can reach the leaves relatively easily. Our research, however, only partially confirmed this assumption. Indeed, a species such as *T. cristatus*, which was numerous in our studied plots, was also found to be abundant on plants in the oak–lime–hornbeam forest [50]. Another foliage-dwelling species, *A. accentuata*, which was also numerous in our study, was also a common spider found on tree trunks [13]. On the other hand, species such as *Batyphantus nigrinus* or *Linyphia triangularis*, found in great numbers on plants in the oak–lime–hornbeam forest, were not found on foliage at all or only in low numbers [50]. Moreover, some species such as *Amaurobius fenestralis* or *Segestria senoculata* were not found at all on tree foliage, whereas they were recorded regularly and in great numbers on tree trunks in the BNP [13]. Epigeic spiders from the Lycosidae family were sporadically collected on tree branches. These spiders were probably, like many other species, only accidental visitors on leaves. This group may include, for example, some linyphiids, which could be located on branches by accident due to ballooning. However, many recorded spider species are typical web hunters (e.g., Araneidae, Tetragnathidae, and Theridiidae families), and tree branches may be excellent structures for web construction [24].

The number of collected spider species and the species compositions may depend on the species of trees sampled during the study. Mupepele et al. [10], in their study from the Białowieża Forest, showed that the fauna of the canopy is tree-species-specific. They revealed the richest fauna on oaks; however, a clear tree-species-specific pattern was observed for hornbeams, Norway spruces, alders, and Scots pines. The same regularity may apply to branches located in the lower strata of trees, but unfortunately, material collected from different tree species was not analyzed separately in our research. On the other hand, in spite of the fact that the same tree species were sampled in ash–alder riparian forest and alder carr, we found a significant difference between these two stand types in terms of the abundance of adult spiders and the number of species. It seems that the differences may result mainly from the hummock–hollow structure of alder carr and the presence of stagnant water in this type of forest. The higher numbers of adult individuals in alder carr resulted mainly from the fact that *P. pygmaeum* occurred there in great numbers, while this species was completely absent in ash–alder riparian forest.

Our study showed that tree leaves were inhabited mainly by juvenile spider individuals. The exception was in alder carr, where the contribution of adult spiders to the whole quota of collected individuals was quite high, and their numbers significantly differed

from those in the other two types of forests. This phenomenon may be explained by the hummock–hollow structure of alder carr. Hummocks, together with the trees growing on them, are refuges where spiders can shelter, escaping from the water appearing seasonally in hollows [25].

5. Conclusions

In conclusion, our study showed the negative effect of forest management on spider assemblages manifested in the smaller number of collected species in particular samples from managed stands compared to primeval stands. However, a difference in the total number of spider species recorded in the study plots was found only in the case of alder carr. Primeval alder carr was characterized by a higher species richness, and the number of species found there was twice as high as in managed alder carr. This emphasizes the important role of alder carr stands as potential biodiversity hotspots and highlights the need for their protection.

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