Plant-dwelling spider communities of three developmental phases in primeval oak-lime-hornbeam forest in the Białowieża National Park, Poland

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(Received 27 October 2020; accepted 12 May 2021)

Abstract
The Białowieża Forest is the only place in Europe where the full development cycle of temperate forest can be observed on a large scale, starting from the regeneration phase until the terminal (decay) phase. At present, the terminal phase is not observed in most forests in Europe due to management practices such as logging and removal of dead trees. In this study, we analysed plant-dwelling spider communities in three developmental phases (optimal, terminal and regeneration) of a primeval oak-lime-hornbeam stand in the Białowieża National Park. Spiders were sampled from May to October in 1998 and 1999 using a sweep net. A total of 3693 spider individuals from 13 families were collected, of which 2278 were identified at the species level. In total, 63 spider species were recorded (including species identified based only on juvenile individuals): 33 in the optimal phase, 36 in the terminal phase, and 41 in the regeneration phase. The composition of plant-dwelling spider communities in three developmental phases was similar. Among adult individuals, Linyphia triangularis (Clerck, 1757) was the most numerous species on the plot in the optimal phase, whereas Bathypantes nigrimus (Westring, 1851) was the most abundant species on the plots in the terminal and regeneration phases of the stand development. Significantly higher species diversity (calculated for the whole study period) was found in the regeneration and optimal phases compared to the terminal phase. We revealed no difference in the abundance, species richness, and species diversity (calculated per sample) between the analysed plots. On the other hand, each of the developmental stages was characterised by a significant proportion of exclusive species, even though they were represented by a few individuals. This suggests that the presence of different forest stages in a given area favours higher species diversity.

Keywords: Araneae, Białowieża Forest, herb-dwelling spiders, primeval forest, forest structure

Introduction
A forest is a dynamic ecosystem and its structure changes significantly with the time and age of a tree stand (Oliver & Larson 1996; Bobiec et al. 2000; Franklin et al. 2002). Identification of different developmental stages of forest in its natural transformation cycle is useful in research on ecological processes taking place in it. Miścicki (1994) distinguished the following developmental phases in natural forests: initial, juvenile, even-aged pole, premature, optimal, terminal, decay, and regeneration. On the other hand, Bobiec et al. (2000), when studying stands in the Białowieża Forest, defined six phases: regeneration, young, pole, late pole, optimal, and terminal. However, the terminal (decay) phase no longer occurs in most European forests due to logging and the removal of dead trees. The Białowieża National Park is the only place in Europe where the full developmental cycle of deciduous forest still occurs on a large scale (Bobiec et al. 2000; Miścicki 2012). This national park was established to protect primeval stands, which are distinguished from other European temperate forests by a great diversity of tree communities, multi-storey structure of stands, high trees, and a large amount of dead wood (Tomiałojć 1991; Bobiec 2002; Wesolowski 2007). Moreover, the Białowieża National Park is a refuge for many plant and animal...
species (Gutowski & Jaroszewicz 2004; Okońow et al. 2009), including spiders (Stańska 2007).

Changes in vegetation during the forest stand development are fairly well researched (e.g. Faliński 1991; Kalacská et al. 2004; Gutiérrez & Huth 2012), but changes in animal assemblages are less investigated. Studies comparing communities of different groups of animals in different forest phases were frequently conducted in tropical forests (e.g., Avila-Cabadilla et al. 2009; Gomes et al. 2014), whereas such studies in temperate forests are relatively scarce (e.g. Hilszczanka et al. 2005; Oxbrough et al. 2005). In particular, very little is known about the differences in the composition and structure of invertebrate communities in different phases of primeval forest development.

Previous research conducted in different stages of the Białowieża Forest on 27 taxa of animals (including spiders) concerned pine stands (Trojan et al. 1994). To our knowledge, there were no studies describing spider communities in different developmental phases of primeval oak-lime-hornbeam forest.

Spiders are an excellent model group of organisms to study differences between developmental phases of stands because they are very sensitive to changes in habitat structure and microclimatic conditions (Oxbrough et al. 2005; Stańska et al. 2016; Lafage et al. 2019; Ramberg et al. 2020). Moreover, spiders are good indicators of both ecosystem disturbance resulting from forest management (Pearce & Venier 2006) and succession stages (Haase & Balkenhol 2015; Hazzi et al. 2020).

In this paper, we present the results of a two-year study conducted in the Białowieża National Park on plant-dwelling spiders (i.e., inhabiting the vegetation) in three developmental phases of primeval oak-lime-hornbeam forest: optimal, terminal and regeneration. The analysed oak-lime-hornbeam forest phases differ considerably in terms of such factors as size, height, age, species and the number of growing trees, the number of tree storeys, the amount of dead wood, as well as canopy cover, which clearly translates into the development of ground vegetation (Bobiec et al. 2000). Many of these factors significantly affect spider communities. For example, Košulić et al. (2016) found that the composition of spider communities was significantly affected by canopy openness. Gómez et al. (2016) showed that the density of spiders building aerial webs increases with increasing vegetation height and the number of vegetation layers. Zhang et al. (2018) showed that spider communities living on the European beech Fagus sylvatica are significantly affected by such parameters of trees as trunk diameter at breast height, canopy volume, and foliage cover.

The primary objective of our research was to determine the species composition of plant-dwelling spider communities in relation to stand development. Another objective was to compare the spider abundance, species richness, and species diversity (expressed by the Shannon diversity index) between these developmental phases, and to assess how these parameters change over time, i.e., in particular, sampling months during the sampling period. Given the differences in the habitat structure between the developmental phases of the oak-lime-hornbeam forest, we assumed that spider communities would differ from each other. We hypothesised that more species and individuals, as well as higher species diversity, would be found on plots with a more heterogeneous and complex habitat structure, i.e., in the terminal and regeneration phases compared to the optimal phase. Our assumption was based on the findings of many authors who show that complex and structurally diverse habitats, providing a broad spectrum of niches, promote species diversity of spiders (e.g., Malumbres-Olarte et al. 2013; St. Pierre & Kovalenko 2014; Ávila et al. 2017; Hamíř & Košulić 2021).

Material and methods

Study area

The study was carried out in the Białowieża Forest located on the border between Poland and Belarus, with a total area of 1,500 km². The best-preserved part of this area has been protected as the Białowieża National Park (BNP) since 1921. The oldest part of the BNP has never been logged, and tree stands growing there are multistorey, mixed species, and uneven-aged with a great amount of dead wood (Tomiałojć 1991; Bobiec 2002). The study was conducted in the southern part of BNP in the primeval oak-lime-hornbeam stands, Tilio-Carpinetum, which is the dominant forest type there, covering c. 45% of the total area, and the most structurally diverse with three canopy layers and many tree species. The most numerous tree species are lime Tilia cordata, hornbeam Carpinus betulus, Norway spruce Picea abies, pedunculated oak Quercus robur, ash Fraxinus excelsior and elms Ulmus spp. Bobiec et al. (2000), based on the definitions of developmental phases proposed by Leibundgut (1959) and Miścicki (1994), distinguished six developmental phases of the oak-lime-hornbeam stand in the BNP: regeneration, young, pole, late pole, optimal, and terminal. Our study was conducted in three of them: optimal, terminal and regeneration. The structure of the oak-lime-hornbeam forest in the BNP is heterogeneous, which is manifested by the occurrence of numerous patches of
stands at specific developmental stages in a relatively small area (Bobiec et al. 2000).

Stands in the optimal phase (52°43′50″N; 23° 51′40″E) are characterized by good vitality and a large diameter at the breast height of most trees. In this phase, the canopy was dense – its cover was above 90%. The higher layer of the stand consisted of pedunculate oak, Norway spruce, lime and maple *Acer platanoides*, whereas the lower layer – by hornbeam. The renewal in this phase was poor. Herbaceous vegetation was not well developed (Figure 1) and consisted of species typical of deciduous forests: *Anemone nemorosa, Aegopodium podagraria, Stellaria holostea, Galium schultesii, Dactylis polygama, Carex pilosa* and *Ranunculus cassubicus*.

The dominant trees on the terminal-phase plot (52°43′30″N; 23°51′50″E) had a large diameter at breast height, but they were usually in poor condition. The canopy of trees in this stand had some gaps due to reduced crowns of dying old trees (average canopy cover was about 80%). The higher level of the canopy was formed exclusively by pedunculate oak and the lower layer – by Norway spruce and hornbeam. The understorey consisted exclusively of hornbeams. The undergrowth was created mainly by *Anemone nemorosa, Stellaria holostea, Aegopodium podagraria, Impatiens noli-tangere, Galeobdolon luteum* and *Galium schultesii*.

The stand on the plot with the regeneration phase (52°43′10″N; 23°51′00″E) was destroyed by a strong wind 20 years before our research, falling most of the old trees. For this reason, patches without trees or with single trees were created, which resulted in a very thin canopy (average canopy cover was about 20%). The upper storey of the stand was built by pedunculate oak and lime, whereas the lower storey – by hornbeam and Norway spruce. The understorey consisted of hornbeam, lime, maple and hazel *Corylus avellana*. A large amount of dead wood was present here due to fallen, dead trees. Young trees were abundant, the undergrowth was dense and the herbaceous vegetation was the lushest, most diverse and highest of all the studied standing developmental phases (Figure 1). The main species in the undergrowth were ferns *Athyrium filix-femina* and *Dryopteris carthusiana, Stellaria holostea* and *Aegopodium podagraria*. Species such as *Rumex sanguineus, Festuca gigantea* and *Stachys sylvatica* dominated mainly in pits formed in places previously occupied by the roots of fallen trees. Moreover, the undergrowth was characterised by the presence of many sun-loving species, such as *Lysimachia vulgaris, Glechoma hederacea*, and *Ranunculus repens*.

In the course of the study, 15 measurements were made on each study plot (a given measurement was

![Figure 1. Median cover of vegetation in three height classes in relation to the developmental phase of the tree stand. Whiskers indicate 25–75% quartile ranges.](image-url)
made at the same time on all plots), during which the herbaceous vegetation cover degree was determined. The herbaceous vegetation was divided into three groups depending on its height: a) low vegetation (up to 10 cm height), b) medium vegetation (10–30 cm) and c) high vegetation (more than 30 cm).

The surveyed plots differed in the degree of vegetation cover in all analysed groups: low vegetation (ANOVA, \( F_{2,15} = 23.42, p < 0.001 \); Figure 1), medium vegetation (ANOVA, \( F_{2,15} = 17.39, p < 0.001 \); Figure 1) and high vegetation (ANOVA, \( F_{2,15} = 17.71, p < 0.001 \); Figure 1).

Spider sampling and material analysis

Spiders were sampled from May to October in 1998 and 1999 on three study plots (rectangles 20 × 40 m) located in three developmental phases of the oak-lime-hornbeam forest: optimal, terminal and regeneration. A total of 21 samples were collected every two weeks on each study plot. Spiders were collected from herbaceous vegetation growing on the study plots using a sweep net with a diameter of 35 cm. One sample consisted of 100 beats (4 × 25 sweeps). Spiders were collected only on days with no rain to ensure the collection of representative and comparable material. Spider specimens were identified to the species level, or if this was not possible, to the genus or family level. Only adult specimens identified to the species level were included in all statistical analyses, which allowed us to avoid a bias caused by the overrepresentation of species easily identifiable as juveniles. However, for information purposes, Table I shows all collected spiders identified to the species, genus or family level.

To relate the spider species composition to the stages of forest development, the redundancy analysis (RDA) was used, which is a constrained linear ordination method. Inter-species correlations were applied, species scores were divided by standard deviation and species were centred (Lepš & Šmilauer 2003). Statistical significance of the ordinations was assessed via the Monte Carlo Permutation tests (499 unrestricted permutations, reduced model).

Spider species diversity was calculated using the Shannon diversity index (\( H' \)):

\[
H' = - \sum p_i \ln p_i,
\]

where \( p_i \) is the proportion of individuals belonging to species \( i \) (Shannon & Weaver 1998). The Hutcheson test was used to compare Shannon indices between the developmental phases of the forest stand (Hutcheson 1970).

Generalized linear models (GLMs) were used to assess the relationship between the phase of stand development and the spider abundance, species richness, and species diversity. In the first model, where the response variable was the number of collected spider individuals, we used the negative binomial error distribution and the log-link function. In the second model, where a response variable was the number of species, the Poisson error distribution and the log-link function were used. In the third model, where the Shannon diversity index was treated as a response variable, the Gaussian error distribution and the identity-link function were used. The “developmental phase” (optimal, terminal, regeneration) and “sampling month” (six months from May to October) were treated as fixed categorical explanatory variables. Interactions between the above-mentioned variables were also included in all models to show potential differences between the stand development phase in particular sampling months. If the analysis showed a significant effect of a given variable, paired contrasts were calculated to find statistically significant differences between its levels. Statistical analyses were conducted using SPSS 21.0 for Windows. The redundancy analyses were performed in CANOCO for Windows 4.5 (ter Braak & Šmilauer 1998). To verify sampling sufficiency, we calculated richness estimators (Chao1, Chao2, Jackknife1, Jackknife2, and Michaelis-Maten) using 1000 randomizations in all calculations. These calculations were performed in software EstimateS version 9.1.0 (Colwell 2019).

The collected material was deposited in the Institute of Biological Sciences, Siedlce University of Natural Sciences and Humanities, Poland.

Results

A total of 3693 spider individuals representing 13 families were collected in three developmental phases (1176 ind. in the optimal phase, 1434 ind. in the terminal phase and 1083 ind. in the regeneration phase). We identified 2278 individuals to the species level: 764 from the optimal-phase plot, 862 from the terminal-phase plot, and 652 from the regeneration-phase plot. Of the spiders identified to the species level, 344 adult individuals were found in the optimal phase, 507 in the terminal phase, and 311 in the regeneration phase. A total of 63 spider species were found (eight of them were identified based solely on juveniles), but only 16 species were common to the three analysed plots. We found 33 species in the optimal phase (including nine species.
Table I. Spiders collected on herbaceous vegetation in three developmental phases of oak-lime-hornbeam stand of the Białowieża National Park (spider families and species in alphabetical order). In the percentage composition, only adult specimens identified to species level were included. Abbreviations: % - percentage composition, ad./juv.– number of adult/juvenile spider individuals, un. – individuals identified only to the family level.

| Family/Genus/Species                     | Optimal phase | Terminal phase | Regeneration phase |
|-----------------------------------------|---------------|----------------|-------------------|
|                                         | %  | ad./juv. | %  | ad./juv. | %  | ad./juv. |
| Family Anyphaenidae                     |    |         |    |          |    |          |
| *Anyphaena accentuata* (Walckenaer, 1802) | -/15 | -/1     | -/19 |          |    |          |
| Family Araneidae                        |    |         |    |          |    |          |
| Araneidae                               |    |         |    |          |    |          |
| Araneus diadematus (Clerck, 1757)       |    |         |    |          |    |          |
| Araneus marmoratus (Clerck, 1757)       |    |         |    |          |    |          |
| Araneus sp. (Clerck, 1757)              |    |         |    |          |    |          |
| Araniella sp. Chamberlin & Ivie, 1942   |    |         |    |          |    |          |
| Cyclosa conica (Pallas, 1772)           | 0.3 | 1/31    | -/28 |          |    |          |
| Cyclosa oculata (Walckenaer, 1802)      |    |         |    |          |    |          |
| Mangoara acalypha (Walckenaer, 1802)    |    |         |    |          |    |          |
| Family Clubionidae                      |    |         |    |          |    |          |
| Clubiona laetus (Westring, 1851)        |    |         |    |          |    |          |
| Clubiona reclusa Pickard-Cambridge, 1863|    |         |    |          |    |          |
| Clubiona sp. Latreille, 1804            |    |         |    |          |    |          |
| Clubiona terestris Westring, 1851       |    |         |    |          |    |          |
| Family Dictynidae                       |    |         |    |          |    |          |
| Dictyna arundinacea (Linnaeus, 1758)    | 0.6 | 2/-      |    |          |    |          |
| Dictyna pusilla (Thorell, 1856)         |    |         |    |          |    |          |
| Dictyna sp. Sundeval, 1833              |    |         |    |          |    |          |
| Family Linyphiidae                      |    |         |    |          |    |          |
| Agyneta affinis (Kulczyński, 1898)      | 0.3 | 1/-      |    |          |    |          |
| Bathyphantes nigricus (Westring, 1851)  | 21.8 | 75/-    | 37.5 | 190/18   | 27.3 | 85/4   |
| Bathyphantes sp. Menge, 1866             |    | -/21     |    | -/30     |    |          |
| Ceratiella sp. Emerton, 1882             |    |         |    |          |    |          |
| Dismodicus bifrons (Blackwall, 1841)    |    |         |    |          |    |          |
| Dismodicus elevat (C. L. Koch, 1838)    |    |         |    |          |    |          |
| Drapetica socialis (Sundeval, 1833)     |    |         |    |          |    |          |
| Enteleca acuminata (Wider, 1834)        | 0.3 | 1/-      | 0.2 | 1/-      |    |          |
| Enteleca erythrospus (Westring, 1851)   |    |         |    |          |    |          |
| Ergone atra (Blackwall, 1833)           |    |         |    |          |    |          |
| Ergone dentipalpis (Wider, 1834)        | 0.3 | 1/-      |    |          |    |          |
| Floronia bisculenta (Clerck, 1757)      | 0.3 | 1/-      | 0.4 | 2/-      | 1.0 | 3/-    |
| Gongylidium Rufipes (Linnaeus, 1758)    |    |         |    |          |    |          |
| Helophora insignis (Blackwall, 1841)    |    |         |    |          |    |          |
| Hycspoma cornucrum (Blackwall, 1833)    | 0.6 | 2/-      |    |          |    |          |
| Linyphia hortensis Sundeval, 1833       | 0.6 | 2/-      | 2.4 | 12/-     | 1.3 | 4/-    |
| Linyphia sp. Latreille, 1804            |    | -/44     |    |          |    | -/39   |
| Linyphia triangularis (Clerck, 1757)    | 35.5 | 122/-   | 16.0 | 81/55    | 5.5 | 17/-   |
| Linyphiidae un.                         |    | -/125    |    | -/145    |    | -/37   |
| Microneta viaria (Blackwall, 1841)      |    |         |    |          |    |          |
| Nerine daphneata (Sundeval, 1830)       | 0.3 | 1/-      |    |          |    |          |
| Nerine emphusa (Walckenaer, 1841)       |    |         |    |          |    |          |
| Nerine montana (Clerck, 1757)           |    |         |    |          |    |          |
| Nerine peltata (Wider, 1834)            | 2.3 | 8/-      | 0.4 | 2/47     | 0.6 | 2/5    |
| Nerine radiata (Walckenaer, 1841)       |    |         |    |          |    |          |
| Nerine sp. Blackwall, 1833              |    |         |    |          |    |          |
| Oedothorax fusis (Blackwall, 1834)      | 0.3 | 1/-      |    |          |    |          |
| Oedothorax gibbosus (Blackwall, 1841)   |    |         |    |          |    |          |
| Oedothorax retusus (Westring, 1851)     | 0.9 | 3/-      | 0.2 | 1/-      | 0.3 | 1/-    |
| Saxigna frontata Blackwall, 1833        |    |         |    |          |    |          |
| Tapinocyba pallens (Pickard-Cambridge, 1873) |    |         |    |          |    |          |
| Teniaphantus alarci (Blackwall, 1833)   | 0.6 | 2/-      |    |          |    |          |
| Teniaphantus cristatus (Menge, 1866)    | 3.8 | 13/-     | 4.3 | 22/-     | 1.3 | 4/-    |
| Teniaphantus sp. Menge, 1866             |    | -/8      |    | -/29     |    | -/11   |

(Continued)
recorded exclusively in this phase), 36 species in the terminal phase (eight exclusive species) and 41 species in the regeneration phase (15 exclusive species; Table I). When considering only adult individuals, species richness was 29 in the optimal phase, 28 in the terminal phase, and 32 in the regeneration phase. However, the estimated species richness ranged (depending on the estimator): from 42 to 51 for the optimal phase, from 40 to 49 for the terminal phase and from 46 to 73 for the regeneration phase. Sampling completeness was about 60% on each plot (Table II).

*Theridion varians* Hahn, 1833 was the most abundant species both in the optimal phase and the regeneration phase, while *Batphyphantes nigrinus* (Westring, 1851) in the terminal phase. When considering only adult individuals, *Linyphia triangularis* (Clerck, 1757) was the most numerous

| Family/Genus/Species | Optimal phase | Terminal phase | Regeneration phase |
|----------------------|---------------|----------------|-------------------|
|                      | % | ad./juv. | % | ad./juv. | % | ad./juv. |
| *Tenuiphantes tenebricola* (Wider, 1834) | 1.5 | 5/199 | 0.2 | 1/- |
| *Trematocephalus cristatus* (Wider, 1834) | 0.3 | 1/- |
| *Walckenaeria unicinctus* Pickard-Cambridge, 1873 | 1.3 | 4/188 |
| **Family Lycosidae** | **Lycosidae un.** | -/1 |
| *Pirata sp.* Sundevall, 1833 | -/52 |
| **Family Mimetidae** | **Ero furcata** (Villers, 1789) | 0.3 | 1/- |
| **Family Philodromidae** | **Philodromus sp.** Walckenaer, 1826 | -/4 |
| **Family Pisauridae** | **Pisaura mirabilis** (Clerck, 1757) | 0.2 | 1/2 |
| **Family Tetragnathidae** | **Metellina menegi** (Blackwall, 1869) | 4.7 | 16/- |
| *Metellina segmentata* (Clerck, 1757) | 2.9 | 10/- |
| *Metellina sp.* C. L. Koch, 1836 | -/66 |
| *Pachygynatha clerchi* Sundevall, 1823 | 1.7 | 6/- |
| *Pachygnatha degeeri* Sundevall, 1830 | 1.8 | 9/- |
| *Pachygnatha listeri* Sundevall, 1830 | 11.3 | 39/- |
| *Pachygnatha sp.* Sundevall, 1823 | -/16 |
| *Tetragnatha montana* Simon, 1874 | -/- |
| *Tetragnatha pinicola* L. Koch, 1870 | 0.2 | 1/- |
| *Tetragnatha sp.* Latreille, 1804 | -/82 |
| **Family Theridiidae** | **Cryptachaea sp.** Archer, 1946 | -/22 |
| *Enoplognatha ovata* (Clerck, 1757) | 4.1 | 14/106 |
| *Episius angulatus* (Blackwall, 1836) | 3.2 | 16/51 |
| *Nottaira bicamulata* (Linnaeus, 1767) | 12.9 | 40/19 |
| *Robertus neglectus* (Pickard-Cambridge, 1871) | -/5 |
| *Steatoda bipunctata* (Linnaeus, 1758) | 0.3 | 1/- |
| *Theridion sp.* Walckenaer, 1805 | -/1 |
| *Theridion varians* Hahn, 1833 | -/2 |
| **Family Theridiosomatidae** | **Theridiovoma gemmosum** (L. Koch, 1877) | -/8 |
| **Family Thomisidae** | **Diasia dorsata** (Fabricius, 1777) | 0.3 | 1/36 |
| *Misumena vatia* (Clerck, 1757) | 0.6 | 3/13 |
| *Ozyptila sp.* Simon, 1864 | 0.3 | 1/6 |
| *Xysticus audax* (Schrank, 1803) | -/2 |
| *Xysticus cristatus* (Clerck, 1757) | 0.3 | 1/- |
| *Xysticus sp.* C. L. Koch, 1835 | -/7 |
| Total no. of individuals | 344/832 | 507/927 | 311/772 |
| Total no. of species | 33 | 36 |
| Total no. of exclusive species | 9 | 8 | 15 |
species in the optimal phase, while *Bathyphantes nigrinus* (Westring, 1851) was the most abundant species in the other phases. The family Linyphiidae dominated in three developmental phases in terms of abundance and species richness (Table I).

The RDA analysis revealed that all canonical axes explained only 7.9% of the total variation of the spider species composition (Figure 2). Exclusively, the effect of terminal phase was statistically significant to variation of spider species composition (Monte Carlo Permutation Test $F = 3.007; P = 0.04$).

The highest species diversity (calculated for the whole study period) was found in the regeneration phase ($H' = 2.33$), followed by the optimal phase ($H' = 2.18$) and the terminal phase of the forest stand development ($H' = 1.99$). The Hutcheson test revealed differences between the regeneration phase and the terminal phase ($t_{645} = 3.59; p < 0.001$), as well as between the optimal phase and the terminal phase ($t_{720} = 2.01; p = 0.045$), while no differences were found between the optimal phase and the regeneration phase ($t_{650} = 1.47; p = 0.141$).

GLMs showed that the number of collected spider individuals, the number of spider species, and the Shannon diversity index were not associated with the developmental phase of the forest stand,
but instead depended on the sampling month (Table III). The largest number of spiders per sample was caught in September, above four times more than in July, when spiders were the least numerous (Figure 3). The largest number of spider species was collected in May and September and the least in July (Figure 4). The highest species diversity (expressed by the Shannon diversity index) was found in May and it was statistically different from species diversity revealed in the rest of months (Figure 5).

**Discussion**

Our hypothesis that higher spider abundance, species richness, and species diversity would be found on plots with a more diverse and complex habitat structure, i.e., in the terminal and regeneration phases compared to the optimal phase, was not confirmed. The composition of spider communities was similar on all analysed study plots and the most abundant species like *Linyphia triangularis*, *Bathyphantes nigrinus*, *Pachygnatha listeri* were common to the three developmental stages. This may result from the mosaic character of the oak-lime-hornbeam forest in the BNP, which is manifested by the fact that the individual developmental stages form small patches located close to each other (Bobiec et al. 2000). As a result, spiders can easily move between adjacent oak-like-hornbeam patches covered with forest stands at different developmental stages. However, the total number of species, the number of exclusive species and species diversity...
Figure 4. Number of spider species (mean with 95% confidence limits) collected in particular sampling months. The means are estimated from the statistical model presented in Table III. Different letters indicate significant differences between sampling months (p < 0.040).

Figure 5. Shannon diversity index (mean with 95% confidence limits) in particular sampling months. The means are estimated from the statistical model presented in Table III. Different letters indicate significant differences between sampling months (p < 0.015).
(calculated for the whole study period) reached the highest values on the plot in the regeneration phase of the tree stand. This phenomenon can probably be explained by a more complex and disordered habitat structure of the forest stand in the regeneration phase due to a large number of dead, fallen trees and snags, and lush, complex vegetation in particular. It is well documented that both habitat structure and associated microclimatic conditions, such as humidity and temperature, affect spider assemblages (Ziesche & Roth 2008; Růžička & Zacharda 2010; Staňka et al. 2016). Vegetation, in particular, is responsible for shaping spider communities as it provides sufficient humidity, shelter, abundant prey, and crucially, important for plant-dwelling species, structures for web construction (Hatley & MacMahon 1980; Scheidler 1990; Halaj et al. 2000; McDonald 2007; Diehl et al. 2013; Gómez et al. 2016). For example, the species richness of web-building spiders may increase with plant diversity and vegetation coverage (Diehl et al. 2013). Platen and Berger (2013) showed that vegetation height was most crucial for increasing both the number of species and individuals of specific species from the Araneidae family (comprising mainly plant-dwelling species). They also found that the vegetation cover affects the abundance of particular araneid and linyphiid species, despite having no significant effect on the total number of species. Hatley and MacMahon (1980), in the experiment involving manipulation of the Artemisia tridentata architecture, revealed that both the number of spider species and species diversity were positively correlated with shrub height, cover, volume mass, percentage of dense foliage, and the index of foliage diversity.

Some studies have shown that the tree canopy cover also has a significant effect on spider communities. For example, Košulič et al. (2016) found that canopy openness affects species richness, functional diversity, abundance and community composition of epigean spiders. They revealed the highest species richness in the middle of the canopy openness, whereas the abundance of rare and threatened species was shifted towards the more open canopy. Oxbridge et al. (2006) showed that open space in the forest supports the spider fauna, typically absent there, and on a large scale it was positively correlated with species richness and abundance. In the case of our study, the large canopy openness on the regeneration-phase plot contributed significantly to the fact that the vegetation growing there covered a larger area and was more complex than in the two other study plots.

Despite the considerable similarity in species composition in the analysed plots, all the developmental phases (especially the regeneration phase) were characterised by a high proportion of exclusive species even though they were represented by a few individuals. Therefore, the occurrence of forest stands in a given forest at different developmental stages has a significant positive effect on biodiversity. However, a high proportion of exclusive species may result from undersampling (Coddington et al. 2009). The sampling completeness reached about 60% for all our plots, which shows that many species were not detected.

We showed that the number of spider species and individuals varied between the months of our study. This phenomenon had two main causes: the phenology of individual spider species and changes in herbaceous vegetation and other habitat parameters (e.g. humidity, temperature) during the sampling period, which also affected spider assemblages.

To our knowledge, there are no studies on spiders or even other groups of invertebrates in different developmental phases of the oak-lime-hornbeam forest, so it is difficult to relate our results to other surveys. Such a study, analysing many groups of animals (including spiders) in different secondary succession stages, was conducted in pine stands of the Białowieża Forest (Trojan et al. 1994). The authors showed that the dominant trend was a restorative succession, where a large number of species was present in the culture stage, a smaller number in the pole wood stage, and again a large number in the mature forest (in the case of spiders this was 51, 31 and 39 species, respectively). Furthermore, only 20% of spider species were common for all three analysed developmental phases of the pine forest. The differences in the number of spider individuals were not significant, similar to our study.

We conclude that plant-dwelling spider communities in three developmental phases (optimal, terminal and regeneration) were similar in terms of abundance, species richness, species diversity, and species composition. On the other hand, each of the developmental stages was characterised by a significant proportion of exclusive species even though they were represented by a few individuals. This suggests that the presence of different forest stages in a given area may favour higher species diversity.

Acknowledgements

We would like to thank the authorities of the Białowieża National Park for their kind help while conducting our research. We also would like to thank the anonymous reviewers for their suggestions and comments that were very helpful in improving
the manuscript. The study was supported by Siedlce University of Natural Sciences and Humanities (grant 222/05/S) and by the State Committee for Scientific Research (grant 6P04G01417).

**Funding**

This work was supported by the Komitet Badań Naukowych [6P04G01417]; Siedlce University of Natural Sciences and Humanities [222/05/S].

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Geolocation information**

Poland, Białowieża National Park, coordinates 52°43’N; 23°50’E.

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