

Comparisons of the composition of spider assemblages in three vegetation habitats in Bogor, West Java, Indonesia

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Abstract. Lia M, Rauf A, Hindayana D. 2021. Comparisons of the composition of spider assemblages in three vegetation habitats in Bogor, West Java, Indonesia. *Biodiversitas* 23: 244-255. Vegetation structures are known to influence the microclimate and consequently the invertebrate assemblages. This study, therefore, aims to compare the species composition of assemblages of ground- and foliage-dwelling spiders in three vegetation habitats: undisturbed urban forest, oil palm plantation, and cornfield, in Bogor, West Java. To ensure a thorough representation of all spider guilds, spiders were collected using pitfall traps, sweep net, and through a direct search on ground and vegetation from January to July 2016. A total of 2299 individual spiders, representing 28 families and 207 species/morphospecies were collected. The spider species richness, abundance, and diversity were higher in the forest and oil palm plantation, compared to the cornfield. Furthermore, the dominant guild in the forest habitat was orb weavers, while the oil palm and corn habitats were dominated by ground runners. The non-metric multidimensional scaling exhibited that the composition of spider assemblages varied among the three vegetation habitats, with spider assemblages in forest habitat associated with higher RH, while the corn habitat was correlated with high light intensity and air temperature. The indicator species analysis revealed that Tetragnathidae has high potential as indicators of the dense, complex vegetation structure of the forest, while Lycosidae is indicators of the more open vegetation of oil palm plantation and cornfield habitats.

Keywords: Biodiversity, cornfield, forest, indicator species, oil palm, spider assemblages

INTRODUCTION

Among terrestrial invertebrates, spiders (order Araneae) are one of the most significant in terms of abundance, diversity, biomass, and functional roles (Foelix 2011; Mammola et al. 2017), with over 49000 species reported worldwide (World Spider Catalog 2021), and 2526 of these species are found in Indonesia (Gutierrez 2020). Spiders are very common in most habitat types and are crucially important in biodiversity conservation (Kaltsas et al. 2019; Michalko et al. 2019; Milano et al. 2021). These invertebrates are predators in most terrestrial ecosystems and serve as a significant source of food for higher trophic levels like reptiles, birds, and mammals (Nyffeler and Birkhofer 2017), hence providing vital ecosystem services to humans regarding the control of arthropod pests in the agroecosystems (Michalko et al. 2019). The silk, venom and hemolymph obtained from spiders are sources of inspiration for biological engineering (Ko and Wan 2018), pharmacology, and medicine (Ricuca et al. 2012; Pineda et al. 2018). Additionally, these invertebrates also serve as an indicator of environmental quality due to their sensitivity to environmental changes (Buchholz and Schroder 2013; Rubio 2016; Hadad and Butler 2018).

Spiders have proven to be a suitable model group within a wide variety of ecological studies due to their high abundance and species diversity, ease of sampling, and distinct spatial habitat preferences (Buchholz and Schroder

2013). Numerous factors influence the species composition of spider assemblages, including variations in plant community structure, ecosystem dynamics, like disturbances, and abiotic factors, for instance, soil, ambient humidity, and temperature (Foelix 2011; Galle and Schweger 2014; Rodrigues et al. 2016). A meta-analysis by Prieto-Benitez and Mendez (2011) highlighted the negative effects of land management, particularly mechanical disturbances (ploughing, cutting, harvesting) on spider species richness, abundance, and diversity at agroecosystems due to the detrimental impacts on habitat heterogeneity or prey populations. However, these effects are less prominent in forest habitats, where the main negative effect is fragmentation.

According to Rodrigues et al. (2016), understanding the composition and distribution of spider species within different habitats is the first step to increasing scientific knowledge on the dynamics of spider assemblages. However, the existing studies on the ecology of spider communities in Indonesia are very few and restricted to one vegetation habitat type (Suana et al. 2009; Koneri and Nangoy 2017; Potapov et al. 2020). Therefore, this study aims to describe and compare the richness and species composition of ground- and foliage-dwelling spiders in forest, oil palm plantation, and cornfield habitats and determine possible habitat associations of spider species and indicators species for each vegetation habitat.

MATERIALS AND METHODS

Study areas

The study areas are located within the city of Bogor ($6^{\circ} 35' 42.1368''$ S and $106^{\circ} 48' 59.8860''$ E), which is about 50 km south of Jakarta (Figure 1), with an average, maximum and minimum elevation of 265 m, 330 m, and 190 m above sea level, respectively. Furthermore, the soils are dominated by volcanic sedimentary rocks, while the terrain is rather uneven, with a relatively flat northern region and a hilly southern region. Based on the Köppen climate classification, Bogor has a tropical rainforest climate (Af) that is more humid and rainy than many other West Java areas. The most rainfalls in the city occur between December and February, with an average annual precipitation of about 1700 mm. However, over 3500 mm has been recorded in certain areas.

An experimental forest (Dramaga Research Forest) located in Situ Gede village, West Bogor district was selected to represent the forest habitat (Figure 2A). The Dramaga Research Forest, owned by the Indonesian Forest Research and Development Center, was established in 1956

and had a land area of 60 ha, of which 10 ha is used for offices of the Center for International Forestry Research (CIFOR) and the International Center for Agroforestry Research (ICRAF). This forest is home to 88 genera and 43 families of trees reaching 45–50 m in height, with a dense canopy, and the dominant species are *Hymenaea courbaril*, *Agathis loranthifolia*, *Hopea bancana*, *Maranthes corymbosa*, *Hopea odorata*, *Calophyllum tomentosum*, and *Hopea mengarawan* (Haryadi 2016). The forest floor is covered with thick leaf litter, as well as various understory vegetation. Meanwhile, the oil palm plantation (Figure 2 B) in the villages of Cimulang and Bantarsari, Subdistrict of Rancabungur (owned and managed by PTPN VIII), was selected to represent perennial plants. This plantation has a land area of 1000 ha and was established in 2005. Likewise, the farmer's cornfields (Figure 2 C) located in the Subdistricts of South Bogor and Bojong Gede were selected to represent annual plants. The distance between the three vegetation habitats was at least 5 km. Table 1 presents the average abiotic parameters measured for each vegetation habitat.

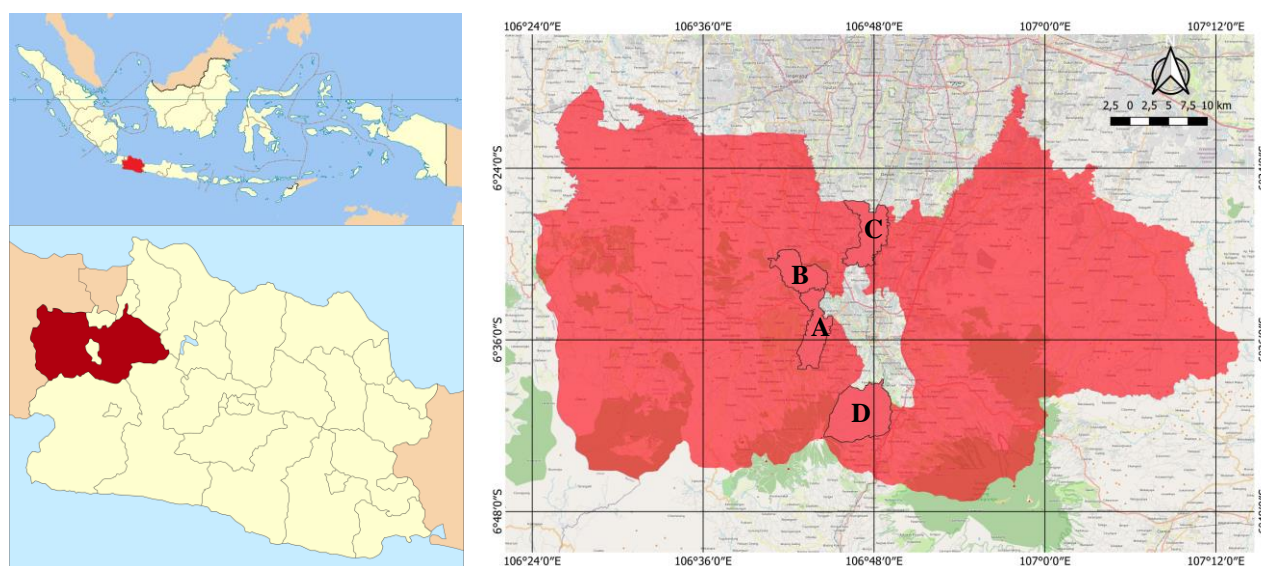


Figure 1. A map of the study area showing the exact locations of the forest in Dramaga (A), oil palm plantation in Rancabungur (B), and cornfield in Bojonggede (C) and Cijeruk (D) of Bogor District, West Java, Indonesia



Figure 2. The three vegetation habitats where the study was conducted: Darmaga Research Forest (A), oil palm plantation (B), and farmer's cornfield (C)

Table 1. Environmental characteristics of the three vegetation habitats where spiders were sampled

	Forest	Oil palm	Corn
Light intensity (lux)	533.24	2650.28	6768.60
Temperature (°C)	28.09	29.06	34.16
RH (%)	86.40	80.46	65.58
Soil pH	5.91	6.01	6.11
Soil moisture (%)	78.90	79.14	81.90

Spider sampling and identification

A total of eight sites were surveyed in each vegetation habitat. In each site, five plots measuring 20 x 10 m were placed randomly, with a distance of at least 200 m maintained between each plot to avoid pseudoreplication. Subsequently, the spiders in each plot were collected using pitfall traps and semi-quantitative sampling. This sampling design was selected to produce a relatively complete species list and associated abundance data for each vegetation habitat. The pitfall traps comprised 9 cm deep-plastic cups with an opening diameter of 7 cm. A total of four pitfall traps were laid along a diagonal line of each plot, with a 10 m spacing between each cup. The cups were completely buried in the ground with the rims at ground surface level and filled with 2% formalin to preserve the specimen, and 1% detergent to reduce water surface tension. Subsequently, the traps were protected from the rain using a 20 x 20 cm can plate, then left in the field for 3 x 24 hours. Meanwhile, the semi-quantitative sampling comprised aerial collection, ground collection, and sweeping methods. Aerial sampling (for upper layer spiders up to 1.5 m) involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to a maximum overhead arm's reach, while ground collection (for ground layer spiders) involved searching on hands and knees, exploring the leaf litter, logs, rocks, and plants below knee level. Sweep netting (for middle layer spiders up to 1 m) was carried out to access foliage dwelling spiders. Each sampling method comprised 1-hour active sampling and was conducted from February to May 2016. Observations were made every two weeks, and each plot was observed eight times in four months (February to May), resulting in a total of 40 samples for each vegetation habitat.

In the laboratory, the samples were sorted into families and morphospecies, then identified to lower taxonomic levels using the available identification keys (Barrion and Litsinger 1995; Deeleman-Reinhold 2001), and the scientific names were checked in the World Spider Catalogue version 22.5 (World Spider Catalogue 2021). Subsequently, the spiders were grouped into five major guilds: ground runners, foliage runners, ground weavers, space weavers, and orb-web weavers, based on hunting strategy, as well as web-building types (Hore and Uniyal 2008; Cardoso et al. 2011; Dzulhelmi et al. 2019).

Data analysis

After identification, the data were compiled into a spreadsheet (Microsoft Excel) for analysis. The total

number of individuals, families, species/morphospecies, and relative abundance for each vegetation habitat, were calculated and species accumulation curves were built using the Mao Tau method to analyze the total spider species richness in each habitat. The total spider species richness was significantly different between vegetation habitats in cases where the 95% confidence interval did not overlap (Colwell 2013). Also, the true species richness was estimated using the Jackknife 1 estimator because this estimator is able to produce a reasonable estimate with a small number of samples (Bizuet-Flores et al. 2015).

The rank-abundance curves were elaborated to visually compare the abundance patterns of species between the different vegetation habitats. Subsequently, the relative abundance of each species on a logarithmic scale (\log_{10}), was plotted based on the species rank order, from most to least abundant. The two-sample Kolmogorov-Smirnov test was performed to test whether any two samples come from the same distribution, while the chi-square test (χ^2) was carried out to compare the frequency of spider per guild between habitats. Also, the mean spider abundance, species density, Shannon-Wiener diversity index (H), were compared among the vegetation habitats using one-way ANOVA, followed by a posthoc Tukey test.

A non-metric multidimensional scaling (NMDS) was applied to understand the existence of distinct assemblages. The analysis was performed following the steps outlined by Peck (2016), and the "autopilot" function was executed in PC-ORD 7 (McCune and Mefford 2016) with the "medium" option selected for "speed vs thoroughness", while the Sorensen (Bray-Curtis) option was selected for the distance measure. This autopilot function was chosen to enable the automated execution of multiple runs and tests for significance. Subsequently, the NMDS analyses were repeated specifying two dimensions, while the configuration was judged superior by the autopilot results, and the relationship between environmental data and species abundance ordination was graphically represented in a joint plot by a series of vectors. The joint-plot overlay displays the habitat variables most strongly related to the ordination axes and portrays the relative association of the variables with each axis, as well as the relative magnitude of the association (Peck 2016).

Multi-response permutation procedures (MRPP) were used to test community species composition differences among different vegetation habitats. MRPP is distribution-free and non-parametric statistics that test the difference among two or more data matrixes and are a good complement to NMDS ordinations. The analysis does not require homogeneity of variance and is, consequently, widely applied in ecological research. Furthermore, the MRPP output comprises a test statistic (T), a measure to describe the separation between the groups, a P-value, and the chance-corrected within-group agreement (A), a descriptor of within-group homogeneity, as well as a measure of effect size. In cases where all the items within groups are identical, the observed $\delta = 0$ and $A=1$, the highest value for A. However, $A=0$ for cases where the within-group heterogeneity equals expectation by chance, and for cases where the within-group agreement is less than

expected by chance, then $A < 0$. In community ecology research, the values for A are often below 0.1 (McCune and Grace 2002).

An indicator species analysis (ISA) was then performed to identify the taxa strongly associated with each vegetation habitat. The indicator values were obtained by multiplying a relative species abundance in a particular habitat, expressed as a percentage of the total abundance, with the relative frequency of occurrence in that habitat, meaning the proportion of samples in which a species was collected. Therefore, a species' specificity (narrow association with a particular habitat) and fidelity (frequency of occurrence in that habitat) is expressed as a percentage compared with other species in sampled habitats (Legendre 2013). The indicator values range from zero (no indication) to 100 (perfect indication). A high indicator value illustrates a species' high affiliation to a particular habitat, with a suitable benchmark of 70% being suggested (for instance, Haddad and Butler 2018). Taxa were considered significant indicators in cases where the indicator values (% of perfect indication) were $> 70\%$ with $P < 0.001$, as adopted by Hadad and Butler (2018).

The species accumulation curve and Jackknife 1 richness estimation were carried out using the software EstimateS 9 (Colwell 2013). The Chi-square test and ANOVA were then performed using PAST 2.17 (Hammer et al. 2001), while NMDS, MRPP, and ISA were performed in PC-ORD 7 (McCune and Mefford 2016). The species that occurred on less than 5% of the plots were excluded from the analysis, thus, the analysis was completed on only 135 species/morphospecies. Also, the abundance data were $\log_{10}(x + 1)$ transformed before the analysis, to reduce the effect of extremely abundant taxa (McCune and Grace 2002).

RESULTS AND DISCUSSION

Assemblage composition

A total of 2299 spiders representing 28 families and 207 species/ morphospecies, were collected for all the sites. However, of the recognized species, only 89 (33%) were identified to species level, highlighting the poor taxonomic knowledge of the Indonesian spiders. Table 2 summarizes the abundance and number of species for each family distinguished during the study. In terms of the number of species, the most prevalent families were Salticidae (43 species), followed by Araneidae (30 species), Linyphiidae (23 species), and Lycosidae (20 species) (a full species list is available on request). Meanwhile, regarding the number of individuals, the most predominant families in forest habitat were Tetragnathidae (37.1%), followed by Salticidae (14.7%), Araneidae (11.8%), Nephilidae (8.7%), and Sparassidae (6.3%). The oil palm plantation was generally occupied by Lycosidae (30.7%), followed by Oxyopidae (18.3%), Araneidae (16.1%), Tetragnathidae (10.9%), and Salticidae (6.2%). Additionally, the most numerous spiders in the cornfield were Lycosidae (43.2%), followed by Oxyopidae (18.6%), Linyphiidae (13.8%), and Oonopidae (8.1%). Three families were represented by

only one specimen (Agelenidae, Gnaphosidae, and Phyllodromidae) and four were represented by two specimens each (Hahniidae, Hersiliidae, Mimetidae, and Theraphosidae).

Table 1 displays a summary of the data on the actual number of species observed and estimated species richness. The total number of species was discovered to be 67, 96, and 98, for the cornfield, oil palm plantation, and forest habitat, respectively. Meanwhile, the total percentage of singleton species was discovered to be 38.8%, 29.2%, and 28.6%, for the cornfield, oil palm plantation, and forest habitat, respectively. The expected richness, calculated through the Jackknife 1 estimator, was 99 for the cornfield habitat and 128 for the oil palm and forest habitats. Based on the visual inspection of the Mao Tau accumulation curves, the forest and oil palm habitats have a higher rate of species accumulation and species density, than the cornfield habitat (Figure 3). However, the curves have not reached an asymptote, indicating a considerable portion of each habitat's spider fauna was unsampled. Also, the higher completeness values were recorded for the forest and oil palm plantation (76% and 75%, respectively), while the least value (67%) was recorded for the cornfield.

Following the rank abundance analyses, the species-abundance distribution was similar at the forest and oil palm plantation (Kolmogorov-Smirnov two samples test: $D=0.142$; $P=0.121$), forest and cornfield ($D=0.125$; $P=0.423$), oil palm and cornfield ($D=0.118$; $P=0.465$). The uniformity in the distribution of species abundance of spiders is depicted by the slope of the rank-abundance curve (Figure 4). This was confirmed by the Pielou evenness indices (J) having nearly equal values (0.74, 0.75, and 0.79 respectively for forest, oil palm, and corn). Further examination proved the species rank-order varied among the habitat types and illustrated a highly uneven species abundance. A total of five dominant species (relative abundance $> 5\%$): *Tylorida ventralis*, *Opademata fastigata*, *Nephila pilipes*, *Epeus falvobilineatus*, and *Leucauge vibrabunda* were discovered in the forest and this composed 50 % of all individuals. Meanwhile, six species: *Oxyopes lineatipes*, *Pardosa nigriceps*, *Neoscona nautica*, *Tetragnatha anguila*, *Lysania* sp., as well as *Pardosa* sp., were dominant in oil palm and composed 57% of all individuals. Also, four dominant species: *Oxyopes javanus*, *Draposa tenasserimensis*, *Arctosa* sp., *Pardosa sumatrana*, were discovered in the cornfield, and these made up 48% of all individuals.

The spiders were grouped into five main functional groups (guild): ground runners, foliage runners, ground weavers, space weavers, and orb weavers. According to the test of independence, there was a significant association ($\chi^2=812.8$; $P<0.0001$) between the guilds and vegetation habitats. Figure 5 exposes the frequency of guilds in each habitat. In the forest, orb weavers were the most abundant spiders (57.6%), followed by foliage runners (28.6%), space weavers (9.1%), ground weavers (2.9%), and ground runners (1.8%). Meanwhile, in the oil palm plantation, ground runners were the most prevalent (34.6%), followed by foliage runners (32.1%), orb weavers (28.3%), space weavers (2.8%), then ground weavers (2.1%). Furthermore,

the cornfield was dominated by ground runners (53.2%), followed by foliage runners (24.7%), ground weavers (14.7%), space weavers (4.3%), and orb weavers (3.2%). The major orb-weaver families were Tetragnathidae, Nephilidae, Araneidae, and Theridiidae; while the foliage runner were Salticidae, Oxyopidae, and Sparassidae. Also, the major ground runner family was Lycosidae, while the ground weaver were Lynphiidae and space weaver were Theridiidae, Pholcidae, as well as Pissauridae.

Table 3. Summary of actual and estimated species richness of spiders in three vegetation habitats

Items	Forest	Oil palm	Corn
Number of individuals	971	886	442
Sobs	98	96	67
Singleton	28	28	26
Doubleton	26	18	8
Jackknife 1 (\pm SD)	128.23 \pm 6.62	128.20 \pm 5.26	99.23 \pm 5.32
Sample completeness (%)	76.4	74.9	67.5

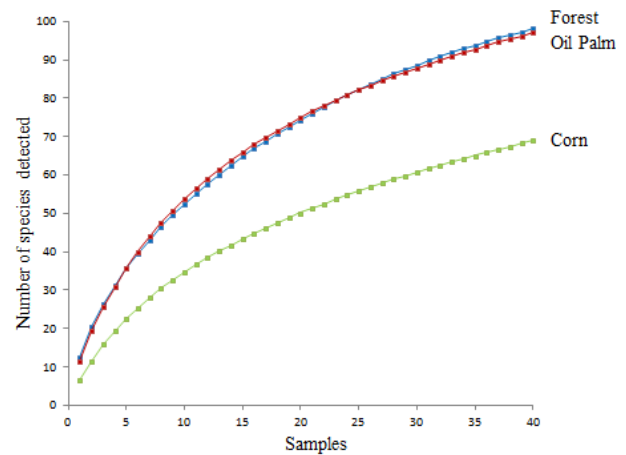


Figure 3. The species accumulation curves (Mao Tau) for spider fauna were sampled from the three vegetation habitats. For clarity, the confidence interval (95%) was omitted in the figure

Table 2. The number of individuals (N), relative abundance (RA), and number of species (S) based on family for the three vegetation habitats

Family	Guild*	Forest			Oil palm			Corn		
		N	RA (%)	S	N	RA (%)	S	N	RA (%)	S
Agelenidae	SW	1	0.1	1	0	0	0	0	0	0
Araneidae	OW	115	11.8	22	143	16.1	13	4	0.9	3
Clubionidae	FR	0	0	0	3	0.3	1	7	1.6	2
Corinnidae	FR	2	0.2	1	3	0.3	2	7	1.6	3
Ctenidae	FR	45	4.6	1	4	0.5	2	0	0	0
Desidae	SW	0	0	0	0	0	0	9	2.0	1
Gnaphosidae	GR	0	0	0	0	0	0	1	0.2	1
Hahniidae	GW	2	0.2	1	0	0	0	0	0	0
Hersiliidae	FR	2	0.2	1	0	0	0	0	0	0
Linyphiidae	GW	18	1.9	9	12	1.4	6	61	13.8	10
Liocranidae	GR	0	0	0	1	0.1	1	5	1.1	2
Lycosidae	GR	3	0.3	1	272	30.7	10	191	43.2	15
Mimetidae	FR	0	0	0	2	0.2	2	0	0	0
Mysmenidae	GW	8	0.8	1	2	0.2	1	0	0	0
Nephilidae	OW	84	8.7	1	11	1.2	1	0	0	0
Ochyroceratidae	GW	0	0	0	5	0.6	1	4	0.9	1
Oonopidae	GR	0	0	0	8	0.9	4	36	8.1	3
Oxyopidae	FR	18	1.9	5	162	18.3	2	82	18.6	3
Phyllodromidae	FR	1	0.1	1	0	0	0	0	0	0
Pholcidae	SW	22	2.3	2	0	0	0	0	0	0
Pissauridae	SW	21	2.2	1	3	0.3	1	0	0	0
Salticidae	FR	143	14.7	27	55	6.2	18	7	1.6	5
Sparassidae	FR	61	6.3	5	12	1.4	3	0	0	0
Tetragnathidae	OW	360	37.1	5	97	10.9	7	10	2.3	6
Therapsidae	GR	1	0.1	1	0	0	0	1	0.2	1
Theridiidae	SW	44	4.5	5	22	2.5	9	10	2.3	6
Thomisidae	FR	6	0.6	3	43	4.9	8	6	1.4	4
Zodariidae	GR	14	1.4	4	26	2.9	4	1	0.2	1

Note: *FR: foliage runner; GR: ground runner; GW: ground weaver; OW: orb weaver; SW: space weaver

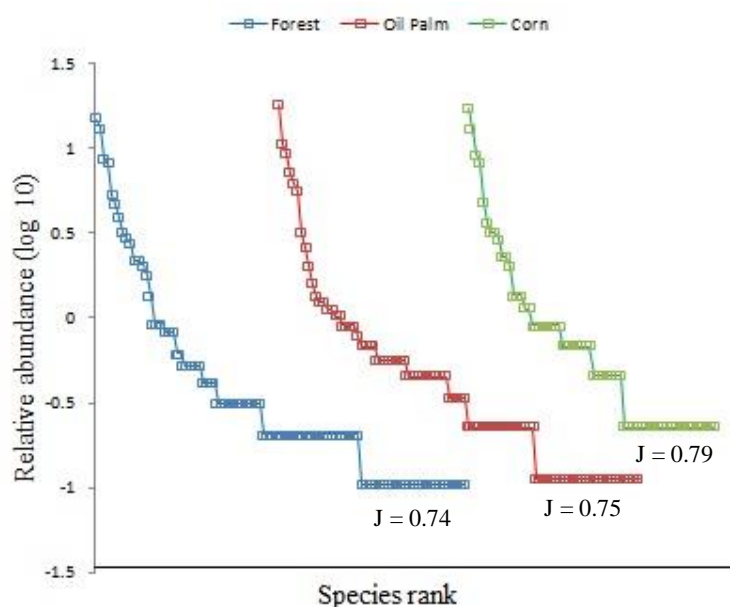


Figure 4. The rank-abundance curve of spider assemblages in the three vegetation habitats. Note: The curves were staggered for improved visibility

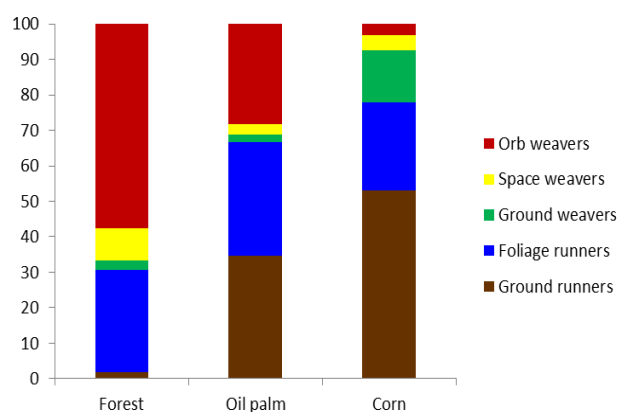


Figure 5. The proportion of spider guilds in three vegetation habitats

Density and diversity

The spider activity density was significantly different among the different vegetation habitats ($F_{2, 21}=9.11$; $P=0.001$), with the mean spider activity density in the forest (121.4 individuals) and oil palm (110.9) being almost twice as high as the corn habitat (55.4) (Figure 6A). In agreement with the rarefaction curve, the species density also differed significantly among the vegetation habitats ($F_{2, 21}=12.56$; $P<0.001$). The mean number of species per plot in the forest (34.1 species) and oil palm (30.9) was almost twice as high as the value for the cornfield (18.1) (Figure 6B). The Shannon-Wiener diversity index revealed a similar pattern ($F_{2, 21}=9.31$; $P=0.001$), where the forest and oil palm plantation habitats had significantly greater diversity indices (2.89 and 2.81, respectively), compared to the cornfield habitat (2.39) (Figure 6C).

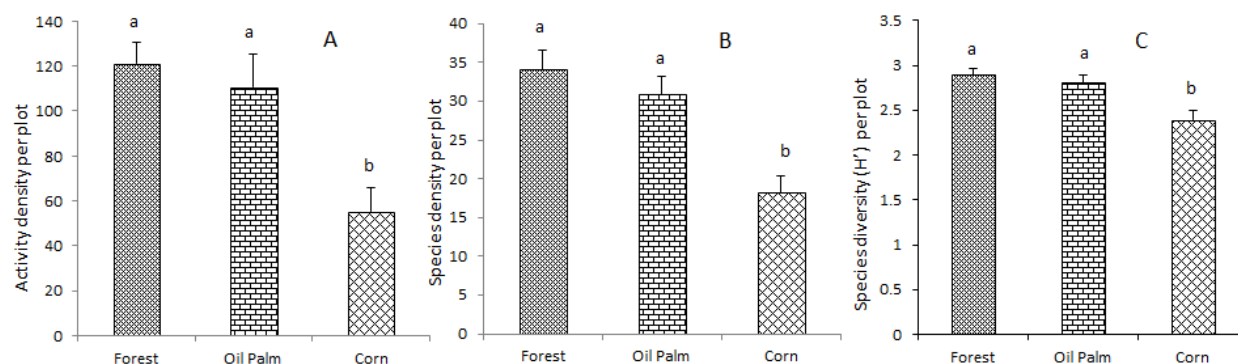


Figure 6. A comparison of the mean \pm SE of activity density (A), species density (B), and species diversity (C) of spiders in the three vegetation habitats

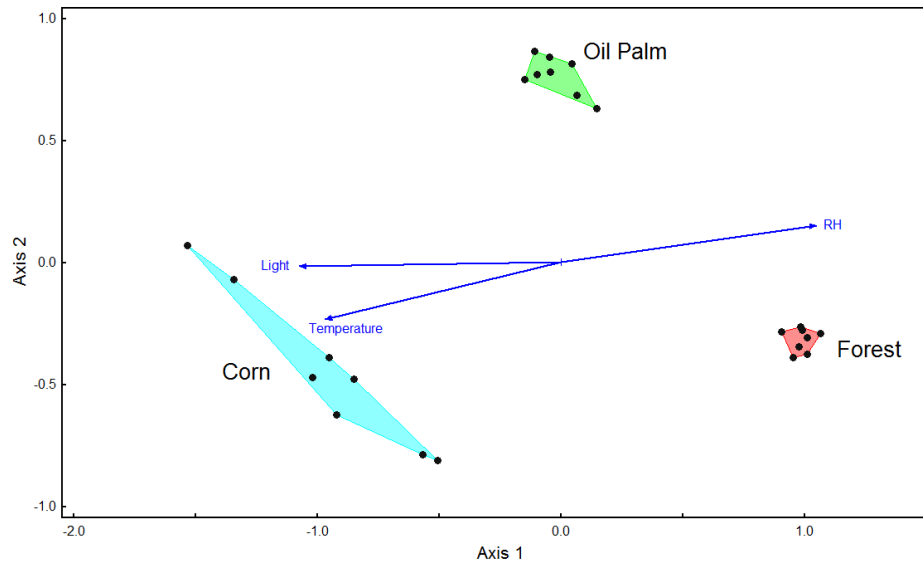


Figure 7. The NMDS ordination of spider assemblages among the three vegetation habitats (final stress: 0.06). Highly correlated environmental variables ($r^2 \geq 0.3$) are included and represented by arrows, while their relative effect on the assemblage differentiation is indicated by the length and direction of the arrows

Community structure

The ordination analysis resulted in a two-dimensional solution on a matrix of 24 plots by five environmental variables. The results of the NMDS were projected in ordination “plot-data space” as a joint plot highlighting environmental variables as overlay vectors (Figure 7), and the final NMDS solution produced a stress value of 0.06 with an instability value of 0.00. Stress value represents the degree of distortion in constructing the NMDS plot using the similarity rankings. A stress value of < 0.2 means the plot provides a potentially useful two-dimensional picture (McCune and Grace 2002). Furthermore, a Monte Carlo test of 250 random data runs versus the real data set verified a significant NMDS outcome ($P=0.004$). Subsequently, two ordination axes were recommended to best explain the trends in the spider assemblages among vegetation habitats, which accounted for 90% of the variation. Axis 1, which accounted for 66% of the variation, distinguished forest habitat from cornfield habitat, while axis 2, which accounted for 24% of the variation separated oil palm habitat from forest and cornfield habitats. The length and direction of vectors correspond to environmental variable strength and relationship to the two-dimensional plot-data space. Only environmental variables making the strongest contribution to data ordinations were shown (i.e. $r^2 > 0.3$) in the joint plot (Figure 6). Strong positive and negative responses to axis 1 represent the factors working in opposition in terms of influence on the totality of plot variable values at forest and cornfield habitats. Also, higher air temperature and light intensity are mainly related to spider fauna composition in the cornfield habitat, while higher air relative humidity is mainly related to the spider community of the forest habitat.

These results were supported by the MRPP analysis, which discovered significant differences globally between the spider assemblages in the studied habitats ($A=0.617$;

$T=-13.362$; $P<0.001$). In the comparison of the three vegetation habitats, the difference of assemblages was in the order of forest vs cornfield, followed by forest vs oil palm, then oil palm vs cornfield (Table 4). Larger negative T scores indicate greater separation (dissimilarity) between habitats. The A scores signify a chance-corrected within-group agreement, with a score of 1.0 indicating perfect agreement, a score of 0 indicating a result no better than expected by chance, while an A value of >0.3 is considered a strong indicator of within-group species homogeneity (McCune and Grace 2002).

An indicator species analysis was used to examine whether species signified an affinity for different vegetation habitats and only species with statistically significant values ($P<0.001$) were considered in the main result (Table 5). Of the 135 species analyzed, 24 species signified a solid affinity for particular vegetation habitats. The forest habitat had the most indicator spider taxa (14 species), including Araneidae, Ctenezidae, Nephilidae, Pholcidae, Pissauridae, Sparassidae, Salticidae, Tetragnathidae, Theridiidae. Meanwhile, the oil palm had seven indicator taxa, including Araneidae, Lycosidae, Oxyopidae, and Thomisidae. Also, the corn habitat's indicator taxa comprised two species of Lycosidae and one species of Oxyopidae. The forest habitat was subjugated mainly by web-building spiders (85.7%), while 71.4 % of the indicator species in oil palm habitat and 100% of the species in cornfield habitat were either plant or ground runners (Table 5). This result supports the notion claiming the general spider functional groups for the species characteristics to oil palm and cornfield vegetation are more similar, compared to those of the oil palm and forest vegetation. In this study, *Opadometa fastigata* and *Tylorida ventralis* were perfect indicators ($IV=100\%$) for forest habitat, while *Lysania* sp was a perfect indicator for oil palm habitat.

Table 4. The pairwise comparison of spider communities among three vegetation habitats using the multi-response permutation procedure (MRPP)

Habitat	T	A	P
Forest vs corn	-0.9613	0.461	< 0.001
Forest vs oil palm	-0.9303	0.471	< 0.001
Oil palm vs corn	-0.8983	0.444	< 0.001

Discussion

This study provides the first comprehensive data set on ground and canopy-dwelling spiders in three separate vegetation habitats. Overall, 207 species were observed, indicating approximately 8.2 % of the total 2526 population in Indonesia (Gutierrez 2020). In terms of quantity, Tetragnathidae appeared the largest in the forest, while oil palm and cornfields widely contained Lycosidae. Koneri and Nangoy (2016) also recorded the maximum occurrence of Tetragnathidae in a tropical rain forest of Mount Tumpa Forest Park (North Sulawesi), while Solin et al. (2021) reported a high abundance of Lycosidae in oil palm plantations in Aceh Tamiang, Sumatera. Relevant literature on spider fauna of the cornfields in Indonesia is very limited; however, Khan and Rather (2012) reported that Lycosidae was as the most common taxa in cornfields in Kashmir, India. Therefore, a high abundance of spider species in cultivated fields, such as oil palm and cornfield,

might contribute significantly to insect pest population suppression (Michalko et al. 2018).

In a previous study, the number of taxa represented by a single individual (singletons) served as a measure for the sample's thoroughness (Coddington et al. 1996). Meanwhile, the present study obtained a relatively high percentage of singletons in the forest, oil palm, and cornfield at 28.6, 29.2, and 38.8%, respectively. This outcome suggests an incomplete species inventory and probably a much larger species richness of the sampling habitats, that the estimated richness. Under these circumstances, the species accumulation curve did not approach an asymptote, indicating that considerable portions of the individual fauna were unsampled. Based on the Jackknife 1 estimator, the maximum species richness (128) occurred in the forest and oil palm habitats, while the cornfield recorded the minimum species (99). Therefore, further samplings appear necessary, although spider assemblages are difficult to completely sample, mainly due to the large number of rare species obtained during surveys (Haddad et al. 2009). A high proportion of singleton has also been observed by other research (Rubio et al. 2008; Horvarth et al. 2014). The large quantity of singletons in this study is not synonymous with rarity, but tends to be cryptic or present in patchy distributions and thus inadequately sampled (Rubio et al. 2008).

Table 5. Indicator values (IV) of spider species in the forest, oil palm, and corn habitats

Habitat	Indicator species	Family	Guild*	IV (%)	Randomized IV		P**
					Mean	SD	
Forest	<i>Eriovixia laglaizei</i>	Araneidae	OW	72.9	29.6	8.69	0.0008
Forest	<i>Cyrtophora moluccensis</i>	Araneidae	OW	87.5	22.4	8.53	0.0002
Forest	<i>Ctenus javanus</i>	Ctenizidae	FR	78.9	25.6	8.95	0.0008
Forest	<i>Nephila pilipes</i>	Nephilidae	OW	74.0	31.9	7.63	0.0002
Forest	<i>Belisama</i> sp.	Pholcidae	SW	87.5	22.7	8.96	0.0004
Forest	<i>Smeringopus pallidus</i>	Pholcidae	SW	75.0	20.9	8.70	0.0008
Forest	<i>Hygropoda</i> sp.	Pissauridae	SW	71.9	25.6	8.81	0.0006
Forest	<i>Epeus falcobilineatus</i>	Salticidae	FR	96.2	25.5	8.77	0.0002
Forest	<i>Heteropoda venatoria</i>	Sparassidae	FR	84.3	28.2	8.41	0.0002
Forest	<i>Opadometa fastigata</i>	Tetragnathidae	OW	100.0	23.7	8.81	0.0002
Forest	<i>Leucauge celebesiana</i>	Tetragnathidae	OW	75.2	25.6	8.82	0.0006
Forest	<i>Tylorida ventralis</i>	Tetragnathidae	OW	100.0	23.7	8.76	0.0002
Forest	<i>Leucauge vibrabunda</i>	Tetragnathidae	OW	86.7	26.9	8.65	0.0002
Forest	<i>Parasteatoda mundula</i>	Theridiidae	SW	87.5	22.7	8.91	0.0002
Oil palm	<i>Neoscona nautica</i>	Araneidae	OW	87.9	26.7	8.39	0.0002
Oil palm	<i>Cyrtophora beccari</i>	Araneidae	OW	75.0	20.7	8.75	0.0004
Oil palm	<i>Pardosa nigriceps</i>	Lycosidae	GR	91.1	28.3	8.60	0.0002
Oil palm	<i>Lysania</i> sp.	Lycosidae	GR	100.0	23.8	8.73	0.0002
Oil palm	<i>Passiena spinicrus</i>	Lycosidae	GR	81.5	24.0	8.83	0.0006
Oil palm	<i>Oxyopes lineatipes</i>	Oxyopidae	FR	95.4	25.3	8.37	0.0002
Oil palm	<i>Oxytate virens</i>	Thomisidae	FR	75.0	20.8	8.71	0.0006
Corn	<i>Allocosa</i> sp.	Lycosidae	GR	75.0	20.9	8.91	0.0008
Corn	<i>Draposa tenasserimensis</i>	Lycosidae	GR	75.0	20.5	8.69	0.0002
Corn	<i>Oxyopes javanus</i>	Oxyopidae	FR	75.0	20.9	8.89	0.0008

Note: *FR: foliage runner; GR: ground runner; GW: ground weaver; OW: orb weaver; SW: space weaver. **Monte Carlo test of significance of the observed maximum indicator value for species

The results also represented the significant effect of vegetation habitats on the composition of spider guilds. Previous investigations demonstrated the impacts of habitat structure on the distribution and abundance of distinct spider guilds (Cunha et al. 2012; Rodrigues et al. 2014; Stokmane and Spungis 2016; Avila et al. 2017). Web-buildings that anchor prey-capture webs to the substrate and hunting spiders that are actively pursuing or using a sit-and-wait strategy for prey capture, demonstrated separate interactions with the habitat structure (Podgaiski and Rodrigues 2016). The physical environment structure exhibits a significant influence on the habitat preference for spiders, particularly the web-building families (Foelix 2011). This statement validates the present study data, due to the more abundant nature of orb weavers in forests, than oil palm and cornfield habitats. Forest habitat has a dense shade and high vertical stratification, with strong potentials to offer additional physical structures for web attachment, including different branch types (Hore and Uniyal 2008). Meanwhile, complex vegetations provide extensive options for micro-habitat selection and prey capture, especially among web-builders (Haddad et al. 2009). The relative predominance of orb weavers was very minimal both in oil palm and cornfield, without adequate physical structure for web attachment. Less availability of web-anchoring structure significantly limited the web-building spiders in open habitats (Gomez et al. 2016). Conversely, higher proportions of ground runners were observed in oil palm and more particularly in cornfields. Khan and Rather (2012) also reported a high proportion of ground runners in a cornfield in Kashmir, India.

Based on the NMDS analysis, a considerable difference in spider assemblages was observed among vegetation habitats. Spiders interact indirectly with the vegetation, indicating a structural support availability for webs and active hunting, as well as prey accessibility, influence species composition (Fourie et al. 2013). Various research recorded a correlation between the structural complexity of habitats and species diversity (Moorhead et al. 2013; Nogueira et al. 2016; Stokmane and Spungis 2016; Avila et al. 2017; Haddad and Butler 2018). According to a habitat heterogeneity hypothesis, plant communities with more functional biodiversity offer additional ecological niches and a greater possibility of resource exploitations by the fauna (Benitez-Malvido et al. 2020). Higher spider species richness in forest and oil palm plantations is possibly due to a wider vegetation diversity, leading to an enhanced habitat complexity comprising several territorial niches (Fourie et al. 2013; Nardi and Marini 2021). Cornfield habitats appear relatively uniform in structure, which tends to limit the availability of separate niches. Furthermore, vegetation architecture plays an important role in spider composition in structurally complicated habitats and vegetations, with the ability to sustain a higher spider abundance and diversity. Consequently, enhancing understory vegetation complexity in oil palm plantations potentially increases spider abundance and diversity (Stokmane and Spungis 2016; Ashton-Butt et al. 2018; Spear et al. 2018; Romero et al. 2019; Benitez-Malvido et al. 2020; Hood et al. 2020; Luke et al. 2020; Pashkevich et al. 2020).

Apart from habitat structure and complexity, other environmental factors, including rainfall, humidity, and temperature tend to also influence the composition of spider assemblages, since certain species are only adaptable to specific environmental conditions (Coddington et al. 1996). The high canopy density, particularly in forests, provides a shelter for the lower layers against extreme temperatures, wind, rain, or other climatic determinants. As a consequence, the microclimatic situations appear relatively constant throughout the year, possibly allowing for easy coexistence of diverse species (Cardoso et al. 2007). Ordination analysis revealed that forest species prefer cooler temperatures and higher humidity, whereas open habitat species prefer warmer temperatures and lower humidity. Meanwhile, the majority of orb-weaver spiders are associated with more stable microclimatic conditions under more closed canopies. Araneidae and Tetragnathidae are major orb weavers with a strong dependence on relative humidity (Peres et al. 2014). The prey-capture threads in most spider orb webs greatly depend on viscous droplets for their stickiness, and therefore, the droplet extensibility becomes more intense with increasing humidity (Opell et al. 2011). Furthermore, the composition of spider communities is affected by the quantity of litter (Potapov et al. 2020). The species richness also increases with both litter depth and complexity (Podgaiski et al. 2016). Krashevskaya et al. (2015) reported that the amount of litter in oil palm plantations is minimal, compared to the rainforest. In the present study, the oil palm and cornfield habitats obtained greater species diversity in Lycosidae. This statement matched the results by Uetz (1979), where litter reduction increased the dominance of Lycosidae. The lycosids are known to forage on flat open surfaces and are, therefore, most prevalent in shallow and compacted litters (Ossamy et al. 2016). The frequency of anthropogenic disturbance has the ability to also influence species assemblages (Barriga et al. 2010; Baldissera et al. 2020). This disturbance generally decreases the spider species richness and density (Lo-Man-Hung et al. 2011). In the present study, habitat disturbance was not measured and the forest was relatively undisturbed, while oil palm and cornfields experienced heavy human activities, including planting, weeding, pruning, and harvesting. Perennial crops, such as oil palms, do not demonstrate a high level of physical disturbance common to annual crops, although they are disturbed through pruning and harvesting. Accordingly, spider assemblages in oil palm are more stable, compared to cornfield habitats.

Several studies have reported the use of spiders as environmental and ecological indicators (Haddad et al. 2009; Barriga et al. 2010; Ossamy et al. 2016; Rubio 2016). Apparently, out of the spiders evaluated in the present study, several species emerged as the best indicators. The results implied that specific spider species were associated with certain vegetation habitats, while other spider species were generalists, occurring in most of vegetation habitats. Subsequently, an indicator species analysis was used to examine whether the species produced any affinity for the different vegetation habitats. This process further identified three species as the perfect

indicators (IV=100%). Tetragnathids *O. fastigata* and *T. ventralis* were associated with forests, while *Lysania* sp. existed in oil palms. In general, web-builders serve as indicators of the dense and complex vegetation structure of the undisturbed forest, while the active hunting species were indicators of more-opened vegetation habitats (Hadad et al. 2009). Lycosidae is, however, assumed as an excellent environmental indicator of forest degraded areas (Bonaldo and Dias 2010).

In conclusion, structurally more diverse vegetations, such as forest and oil palm, support a higher number of spider species. This could be due to a greater variety of available niches within more complex vegetation, than the cornfield habitats. The results further confirmed that these structurally complex habitats provide a wider selection of web-attachment sites, leading to increased habitat suitability for the web-builders spiders. As a consequence, the present study offered a very comprehensive insight into spider habitat selections and their interactions with the plant communities. However, a need for future studies that quantifies habitat characteristics and disturbance factors appears necessary to depict how these features influence the spider community, in terms of structure and composition.

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