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Effect of Combined Factors on Moth Communities in Western Hungarian Sessile Oak–Hornbeam Forests

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Abstract: The many publications on forests and moth communities accomplished in different sampling regions and habitat types have produced diverse results and conclusions. The multiplicity of outcomes requires regional or local investigations on forest traits and herbivores to determine optimal management methods to maintain biodiversity and ecological stability in woodlands. Our study focused on sessile oak–hornbeam forests, which are economically and ecologically significant in many European countries. Samplings were performed in 2011–2012 using portable light traps in a highly forested area in western Hungary. We used 16 variables for PCA from the sampling of vascular plants and the local forest management plan document. These newly created variables (i.e., principal components) were related (used generalized linear models) to different groups of sampled moth communities: Macrolepidoptera, Microlepidoptera, and ecological groups (according to the host vegetation layer). Based on these significant relations, thinning activity may have various effects on moth communities, through the changed light regime and microclimate conditions. Temperature growth in the gaps could lead to the increasing abundance of heat-preferred Lepidoptera species; however, the decreasing species richness of trees (as a result of thinning) is less favourable for moth assemblages. Increasing herb coverage supports moth communities in the investigated forest stands, which may also be induced by the lower canopy closure. Besides the increasing coverage in the lower vegetation layers, plant species richness is also an important element for moth communities; this was demonstrated by the negative relation between the PC4, PC6 (weighted toward coverage), and Lepidoptera groups. Our results supported the fact that a single study on forest management practice or on vegetation traits is not sufficient to indicate their exact effect on moth communities, because their influence is complex. In order to halt the loss in diversity of the examined forest type, we suggest an overall approach to define the optimal forest management practice and tree mixture rate, regarding a larger area.

Keywords: Lepidoptera; macromoth; micromoth; thinning; *Quercus petraea*; vegetation; species richness; abundance; light trap

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1. Introduction

Forests are immensely complex ecosystems that sustain large masses of herbivores, especially phytophagous insects [1]. Moths are critical components of many interactions. They are a food base for higher trophic levels, and their defoliation activities induce the chemical defences of trees. Furthermore, moth caterpillars often host parasitoids and moth imagoes pollinate many plants [2–6]. Moths are also excellent habitat disturbance indicators [7,8]; however, they can be major biotic disturbances of forest ecosystems [9].

Intensive forest management, particularly clearcutting, is a significant anthropogenic disturbance factor [10,11]. However, it potentially creates ecotones at forest edges for nocturnal Lepidoptera species, which could support unique moth assemblages [12]. Single-tree selection harvest disturbs the forest less than clearcutting, leaving a higher moth abundance [10]. Several authors have confirmed the advantages of selective logging over clearcutting concerning their effects on Lepidoptera [13–15]. However, moth community responses to logging can vary. In the selectively logged stands, the increasing floristic diversity can support Lepidoptera species richness [16]. Nevertheless, Chey et al. [17] proved less difference in moth species richness between harvested and undisturbed stands. Moon et al. [18] found decreased community indices in managed forests compared to no-cutting areas.

The influence of forest management on moth communities is not limited to clearcutting and logging. Thinning for the improvement in main tree species also has various effects, such as increasing the density of understorey vegetation [19], altering microhabitat density [20], or influencing arthropod communities [21,22]. Taki et al. [22] established that the effect of thinning on moth assemblages is under-investigated; this observation remains valid.

Besides the management and harvesting methods, many biotic and abiotic factors can also influence forest Lepidoptera, such as vegetation structure, host–plant resources, soil productivity, and stand size [22–24]. These factors are often affected by the silviculture. For instance, thinning creates new microhabitats and increases the heterogeneity of vegetation [25].

The results from past investigations on factors that influence moth communities vary; however, there are some agreements in the importance of the scale of disturbance [26], woodland size [27], biogeographical threats [28], and environmental factors [29,30]. The numerous results require regional investigations (on many forest types) to establish which major factors influence moth assemblages. Clarification is important in supporting biodiversity and ecological stability in forests.

Oak forests represent high value in Central Europe in economical and nature conservation terms [31]. They play an important role in herbivore insect community maintenance as well. In Hungary, altogether, 630 species can develop on oak trees, including approximately 310 Lepidoptera species of which, ca., 32% are specialised to *Quercus* sp.; this is higher than on other tree species [32,33]. Oak forests are often under pressure from intensive management practice, which may greatly influence vegetation and moth communities. Thinning is a generally used method in oak forests to improve the growth of the main tree species. Therefore, thinning is more frequently used as the tree stands ages [34].

This study focuses on a poorly investigated question: how can combined factors (vegetation traits and forest treatment) influence moth communities in sessile oak–hornbeam forests. We assumed that various environmental factors have a mixed influence on moth communities, such as thinning practice, vegetation composition, foliage cover, age of the forest stand, and the mixture rate of trees. These variables are often related [35] and may affect the ecological and taxonomical groups of moths differently. In the present study, a two-year-long investigation was conducted on sessile oak–hornbeam forest sites. We wanted to determine which factors have significant influence on moth communities and what kind of effects they have.

2. Materials and Methods

2.1. Study Site

This investigation was conducted in the Sopron Mountains in the Lower Austroalpides on the western border of the Carpathian Basin. The area—comprising approximately 18,500 hectares—is divided between Austria (two-thirds) and Hungary (one-third) [36]. Study sites were selected in the Hungarian side of the region, which is a highly forested area (approximately 90% coverage) [37] (henceforward, Sopron Mountains refers only to the Hungarian part of the study area). One of the most common forest types in the Sopron Mountains today is sessile oak–hornbeam woodlands. Sessile oak (*Quercus petraea* agg. (Matt. Liebl.)) and Hornbeam (*Carpinus betulus* (Linnaeus)) dominate these forests. Other deciduous and coniferous species are also present in the tree layer. The most common additional deciduous species are Small-leaved Lime *Tilia cordata* (Miller), European Chestnut

(*Castanea sativa* (Miller)), Beech (*Fagus sylvatica* (Linnaeus)), and Sweet Cherry (*Cerasus avium* (Linnaeus)). Coniferous tree species, European Larch (*Larix decidua* (Miller)), Scots Pine (*Pinus sylvestris* (Linnaeus)), and Norway Spruce (*Picea abies* (Linnaeus)), occur in low proportions. The high shade level of the canopy strongly affects the understorey. The shrub layer is usually not dense and comprises young tree species and some mesic shrub species (typically Common Dogwood (*Cornus sanguinea* (Linnaeus)) and European Hazelnut (*Corylus avellana* (Smith)). The herb layer varies according to ecological conditions, but general and mesic forest species elements compose the undergrowth [36,38].

We focused on nine *Quercus petraea* agg.-dominated forest stands divided into different ages (old forests: Sites 1–3, middle-age forests: Sites 4–6, young forests: Sites 7–9). The main criteria for site selection were the following: (i) a low proportion of conifers, (ii) similar relief conditions, and (iii) no human disturbances during the sampling period (e.g., forest management intervention). The study sites laid relatively close to each other within a 1500-hectare block, keeping at least 500 m of distance between them. Table 1 presents the most important study site characteristics. Based on the local forest management plan document, thinning practice mainly focuses on the mixture of trees and shrub species. It is more intensive in middle-age and older forests; however, the investigated young stands were avoided by thinning.

Table 1. Variables in each forest stand that potentially influence Lepidoptera communities. The listed variables were used for PCA.

	Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**
S (vascular plants)	16	7	32	28	16	48	13	16	17
S (trees)	3	3	4	3	3	3	4	6	8
Canopy cover (%)	70.31	95.5	90.02	90.03	90	80.02	96.11	85.23	85.07
S (shrubs)	2	1	3	4	4	4	0	0	0
Cover of shrub layer (%)	0.02	0.5	50.02	5.03	0.04	20.03	0	0	0
S (herbs)	2	1	3	4	4	4	7	10	9
Cover of herb layer (%)	45.68	0.05	0.3	0.26	0.1	0.45	0.07	0.1	10.06
S (understorey)	13	5	31	28	13	46	12	15	15
Cover of understorey (%)	45.7	0.55	50.32	5.29	0.14	20.48	95.1	5.14	85.11
FHD indices	0.72	0.26	0.71	0.03	0.7	0.55	0.23	0.03	0.46
Age	109	106	82	66	45	51	14	15	14
Area (ha)	6.2	6.8	6.6	5.4	5.1	3.8	4.2	2.1	4.2
Stem number/ha	230	550	410	1030	1570	1220	7900	5700	6100
Thinning activity	3	2	2	1	1	3	0	0	0
Thinning intensity (m^3)	80	70	30	200	160	205	0	0	0
Average thinning area (ha)	6.2	6.8	6.6	5.4	5.1	2.57	0	0	0

S—species richness; Thinning activity—number of thinning periods in the last 10 years; Thinning intensity—volume of removed stems during thinning in the last 10 years.

2.2. Moth Sampling

Lepidoptera species were collected using portable light traps installed with UV light sources (peak wavelength, 400–410 nm) [39,40]. Based on Truxa and Fiedler [41], we chose a minimum distance of 30 m from the forest edge and used low-power LEDs as light sources (3 W, operated by a 4.5 V battery) to avoid collecting from the neighbouring forest stands as far as possible; however, most moth species fly well, so collection from neighbouring forests was not entirely avoidable.

Two traps were used within each sampling site, always positioned on the same spot on the ground 50 m apart to prevent light interference [42]. Light trapping was regularly performed at night (from sunset to sunrise) and suspended during heavy rain. Samplings were performed 15 times annually in 2011 and 2012, from the end of March to early November. Sixty samples were collected from each forest stand.

Collected individuals were identified at the species level by macro-morphological features, except *Eupithecia* spp., *Mesapamea* spp., and damaged specimens, which were identified by extracted genitalia.

2.3. Environmental Variables

Different variables from each forest were collected by sampling vascular plants and from the local forest management plan document.

Vascular plant species were surveyed in May 2012, which was an optimal period to find species both from spring and summer aspects. The survey followed the Braun–Blaquet method [43]. We used one piece of 20 × 20 m random quadrate for the sampling unit in each stand. Herb, shrub, and tree species were recorded in each quadrate. Moreover, we estimated the foliage cover (%) of each vegetation storey by the summarised species coverage. The single occurrences of each species were recorded as 0.01% cover. Different vegetation layers were defined by the following interpretation: tree layer—woody plants over 5 cm in Diameter at Breast Height (DBH, measured at 130 cm height) and over 180 cm in height; shrub layer—woody plants under 5 cm in DBH and 50–180 cm in height; and herb layer—herbs and woody plants under 50 cm in height. We used the nomenclature of Király [44] for taxonomy direction.

Foliage Height Diversity indices (FHD) were calculated based on the vascular plant sampling. FHD indices were used to characterise vegetation structure established on the coverage of different storeys [45].

As listed in Table 1, we used 16 variables in each forest stand for analysis.

2.4. Data Analysis

We focused on the species richness and abundance of moth assemblages, in each sampling site.

This study analysed (a) the overall captured moth communities and different groups of moths, such as (b) taxonomical groups (Macroheterocera and Microheterocera) and (c) ecological groups based on the known foodplant of each species. We separated three ecological groups according to the host vegetation storey (hosted in the herb layer, shrub layer, and tree layer). Some species could be hosted on multiple vegetation layers. These appear in both ecological groups where they were potentially hosted.

We used principal component analysis (PCA)—a linear transformation to generate new, independent variables (principal components)—to reduce and combine the numerous environmental factors [46,47].

We applied a generalized linear model (GLM) to define the relation between dependent and independent variables [48]. The GLM considered different groups of collected moths as dependent variables and included the principal components as independent variables into the quantitative models. The Poisson distribution fitted our data best, so we used the Poisson family and log link function to evaluate the parameters. The GLM was derived by stepwise regression based on the Akaike information criterion (AIC) [49]. The significance level was set at $p < 0.05$.

The above statistical evaluation was performed in R (version 4.3.2) [50]. For calculations and visualisation, we used psych [51], devtools [52], ggbiplot [53], and readr [54] packages.

3. Results

A total of 41,436 Lepidoptera individuals from 791 species were collected, including 31,735 specimens from 442 macromoth species and 9701 individuals from 349 micromoth species (Table S1). The most abundant ecological group was tree-hosted (can develop on trees) Lepidoptera, with 25,463 individuals from 344 species, followed by herb-hosted moths, with 15,108 individuals from 406 species, and shrub-hosted moths, with 4119 individuals from 138 species. Table 2 presents the species number and abundance of Lepidoptera communities in each forest site.

Table 2. Species richness, abundance, and diversities of Lepidoptera in each forest site. Numerical values of different hosting layers are also represented.

	Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**
S (total)	429	353	371	362	436	414	299	416	332
N (total)	5087	4661	5269	5203	5585	4954	2220	4820	3667
S (macro)	266	226	239	226	268	254	168	245	192
N (macro)	4014	3745	4432	4215	4451	3985	1215	3453	2225
S (micro)	163	127	132	136	168	160	131	171	140
N (micro)	1073	916	837	988	1134	969	1005	1367	1442
S (tree-hosted)	195	195	182	195	199	201	167	201	184
N (tree-hosted)	3083	3803	4060	3331	3087	3083	1653	3302	2514
S (shrub-hosted)	92	73	76	65	85	84	72	92	84
N (shrub-hosted)	586	489	644	465	660	444	423	841	594
S (herb-hosted)	189	130	150	139	178	182	99	169	113
N (herb-hosted)	1235	656	812	1113	1370	1290	490	1118	942
S (understorey)	255	179	203	183	241	238	150	235	174
N (understorey)	1715	1007	1371	1477	1918	1641	717	1759	1336
S (macro-tree)	122	121	116	122	116	121	89	118	102
N (macro-tree)	2670	3191	3563	2788	2489	2544	882	2409	1468
S (micro-tree)	73	74	66	73	83	80	78	83	82
N (micro-tree)	413	612	497	543	598	539	771	893	1046
S (macro-shrub)	47	42	40	34	47	43	33	43	36
N (macro-shrub)	401	323	482	329	475	314	180	450	267
S (micro-shrub)	45	31	36	31	38	41	39	49	48
N (micro-shrub)	185	166	162	136	185	130	243	391	327
S (macro-herb)	129	97	108	98	126	124	63	110	73
N (macro-herb)	828	429	584	808	1018	960	269	780	549
S (micro-herb)	60	33	42	41	52	58	36	59	40
N (micro-herb)	407	227	228	305	352	330	221	338	393
S (macro-understorey)	163	127	138	122	163	153	88	141	101
N (macro-understorey)	1180	711	1035	1089	1422	1235	400	1158	752
S (micro-understorey)	92	52	65	61	78	85	62	94	73
N (micro-understorey)	535	296	336	388	496	406	317	601	584

S—Species richness of Lepidoptera in the samples; N—abundance of Lepidoptera in the samples; total—complete Lepidoptera in the samples; macro—macromoths in the samples; micro—micromoths in the samples; tree-hosted—Lepidoptera species which develop on trees; shrub-hosted—Lepidoptera species which develop on shrubs; herb-hosted—Lepidoptera species which develop on herbs; understorey—Lepidoptera species which develop on the underlayer vegetation, including shrubs and herbs as well.

We found a total of 96 vascular plant species in the samples. *Q. petraea* agg. was the dominant tree species in the canopy layer whose coverage varied between 70 and 95%. Further tree species represented a very low proportion. The most abundant mixture of tree species was the *C. betulus*. The shrub layers usually had a low density, except in Site 3, Site 7, and Site 9. In Site 7 and Site 9, the parameters of stand-forming tree specimens (height, DBH) did not fit the tree layer criteria; however, they fit the shrub layer (specified in the Materials and Methods—Environmental Variables subsection), which resulted in a higher density of shrubs. In Site 3, *C. betulus* had high coverage in the shrub layer. The herb layers also represented a low coverage, except in Site 1, where the Wood Melick (*Melica uniflora*) Retzius was the dominant species. Coverage details of the vascular plants are listed in Table S2.

We identified several highly correlated variables (Figure S1), which supported the need to use PCA. We chose ten variables from our study on vascular plants and six variables from the local forest management plan. The PCA created nine components, of which eight explained the total variance (Table 3). The components that had explanatory power did not correlate with each other (Figure S2).

Table 3. Loadings (i.e., correlations between components and variables) of principal components.

Environmental Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Species richness of vascular plants	−0.156	**−0.490**	0.168	0.050	−0.055	0.170	0.071	−0.116	**0.342**
Species richness of trees	0.289	−0.027	0.219	0.095	**−0.318**	**−0.389**	**0.469**	**−0.503**	−0.177
Canopy cover (%)	0.104	0.008	**−0.521**	**0.413**	0.189	0.055	−0.034	−0.129	−0.031
Species richness of shrubs	−0.293	−0.259	−0.094	−0.083	0.299	−0.255	0.249	**0.310**	0.047
Cover of shrub layer (%)	−0.161	−0.246	0.130	**0.556**	**−0.313**	−0.081	−0.090	**0.377**	−0.160
Species richness of herbs	**0.336**	−0.172	0.093	−0.088	−0.109	−0.184	0.106	0.221	**0.543**
Cover of herb layer (%)	−0.091	**0.305**	**0.465**	−0.277	0.022	0.128	0.212	**0.330**	−0.089
Species richness of understorey	−0.145	**−0.498**	0.144	0.066	−0.086	0.214	0.123	−0.052	−0.294
Cover of understorey vegetation (%)	0.170	0.067	**0.376**	**0.373**	**0.438**	**0.406**	0.245	−0.028	−0.016
FHD indices	−0.189	0.050	**0.384**	0.194	**0.416**	**−0.581**	**−0.361**	−0.159	−0.083
Age	**−0.311**	0.259	−0.002	0.035	−0.285	0.179	0.058	−0.083	−0.283
Area (ha)	−0.259	0.298	−0.055	0.319	0.109	0.044	**0.397**	−0.148	**0.422**
Stem number/ha	**0.354**	−0.034	0.042	0.041	0.219	0.191	−0.131	0.086	−0.151
Thinning activity in the last 10 years	**−0.326**	0.007	0.197	−0.057	−0.128	0.232	**−0.390**	**−0.398**	**0.326**
Thinning intensity (m^3)	−0.247	−0.246	−0.175	**−0.342**	**0.343**	0.009	0.267	−0.235	−0.190
Average thinning area (ha)	**−0.327**	0.190	−0.130	0.105	−0.110	−0.150	0.199	0.207	0.050
Percentage of explained variances	46.6%	19.0%	14.2%	9.9%	4.0%	3.3%	1.9%	1.1%	0%

Bold highlights mark the heavily represented environmental variables is each dimension.

The first dimension (PC1) accounted for 46.6% of the variance, which can be seen to represent thinning factors (thinning activity and area, stem number), with young forests at the high end and middle-aged and old forests at the low end. It was also weighted toward the species richness of herbs (Figure 1, Table 3). The second dimension (PC2) accounted for 19.0% of the variance and was heavily weighted toward the species richness of vascular plants, understorey vegetation, and herb layer coverage. In this dimension, middle-aged forests are opposed to old forests (Figure 1, Table 3). The third dimension (PC3) explained 14.2% of the total variance. It most heavily represented the canopy covarage and was strongly weighted to herb coverage. Furthermore, PC3 significantly considered the coverage factors of understorey coverage and FHD indices (Figure S3, Table 3). The fourth dimension (PC4) elucidated 9.9% of the variance and was weighted heavier on coverage of the canopy layer, shrub layer, and undersotrey vegetation. It also represented the stand area and thinning intensity (Figure S4, Table 3). The fifth dimension (PC5) accounted for 4% of the variance and mainly represented the coverage factors (shrub layer, understorey cover, FHD indices), species richness of trees, and thinning intensity (Figure S5, Table 3). The sixth dimension (PC6) explained 3.3% of the variance. Similar to PC5, it was heavily weighted toward coverage factors such as understorey coverage and FHD indices. It also represented the relevance of tree species richness (Figure S6, Table 3). The rest of the dimensions (PC7—1.9%, PC8—1.1%) explained a very low ratio of the variance. Both PC7 and PC8 were heavily weighted to the species richness of trees and represented some other significant factors (Figures S7 and S8, Table 3).

The GLM results (subjected to model selection) showed a higher number of Lepidoptera groups correlated with PC1 (21), PC3 (16), PC4 (20), and PC6 (21) (Figure 2), which require further discussion. Therefore, we found that PC2, PC5, PC7, and PC8 represented negligible relations with Lepidoptera groups or explained the quite low ratio of the total variances.

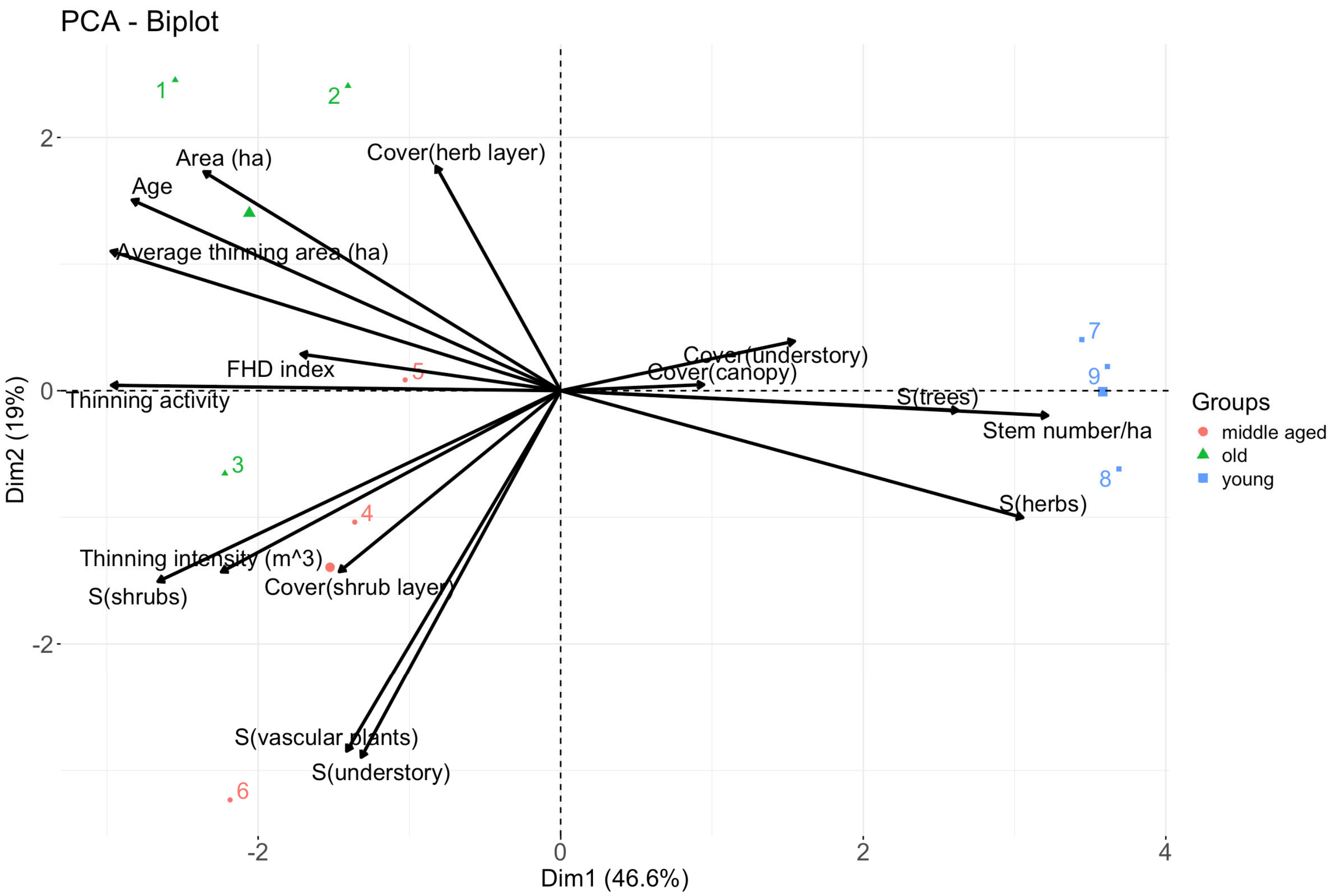
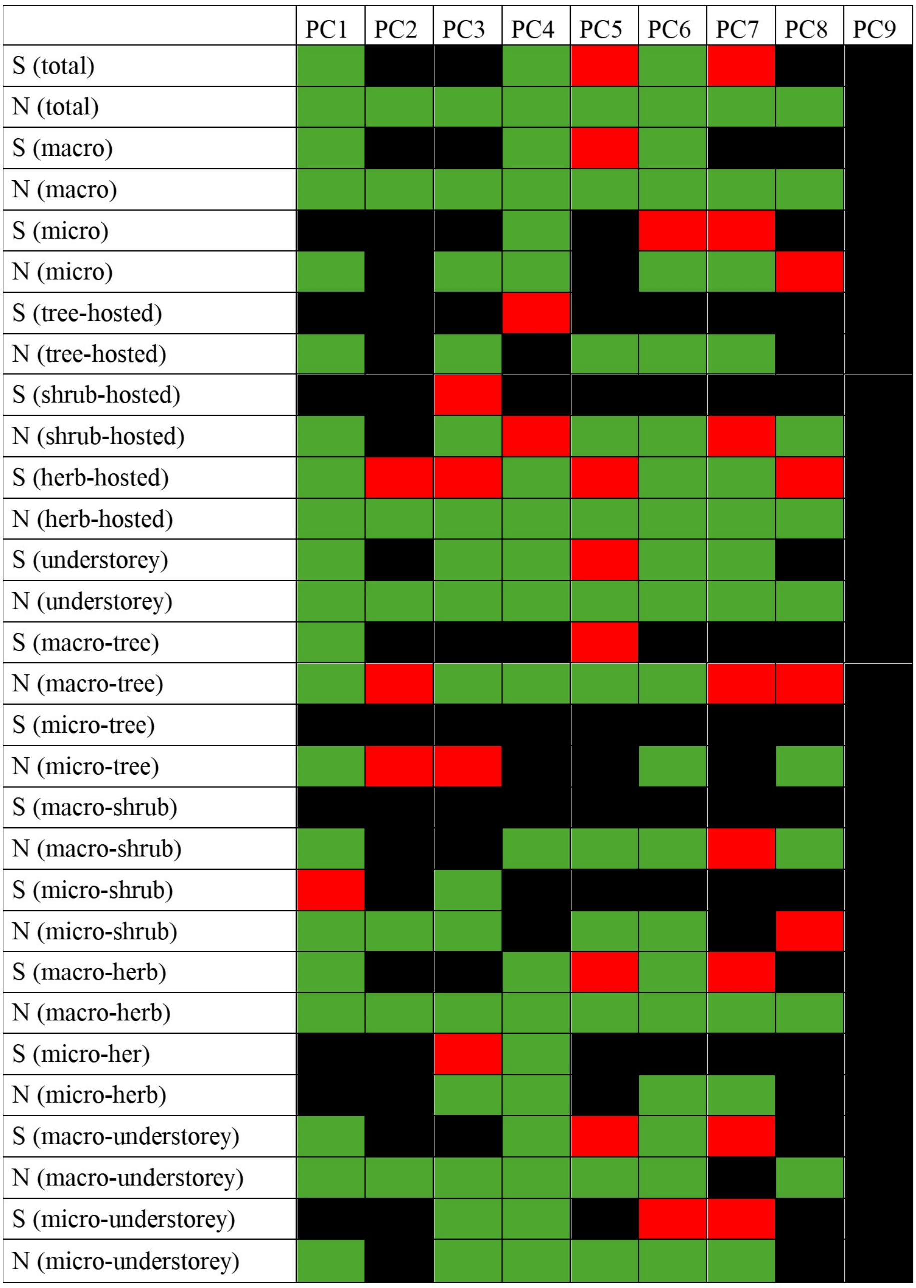


Figure 1. Two-dimensional principal component analysis shows the ordinations of the original environmental variables. The first and second axes explained 46.6% and 19.0% of the variability. The numbered points represented the sampling sites.



	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
S (total)	🟩	⬛	⬛	🟩	🟥	🟩	🟥	⬛	⬛
N (total)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
S (macro)	🟩	⬛	⬛	🟩	🟥	🟩	⬛	⬛	⬛
N (macro)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
S (micro)	⬛	⬛	⬛	🟩	⬛	🟥	🟥	⬛	⬛
N (micro)	🟩	⬛	🟩	🟩	⬛	🟩	🟩	🟥	⬛
S (tree-hosted)	⬛	⬛	⬛	🟥	⬛	⬛	⬛	⬛	⬛
N (tree-hosted)	🟩	⬛	🟩	⬛	🟩	🟩	🟩	⬛	⬛
S (shrub-hosted)	⬛	⬛	🟥	⬛	⬛	⬛	⬛	⬛	⬛
N (shrub-hosted)	🟩	⬛	🟩	🟥	🟩	🟩	🟥	🟩	⬛
S (herb-hosted)	🟩	🟥	🟥	🟩	🟥	🟩	🟩	🟥	⬛
N (herb-hosted)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
S (understorey)	🟩	⬛	🟩	🟩	🟥	🟩	🟩	⬛	⬛
N (understorey)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
S (macro-tree)	🟩	⬛	⬛	⬛	🟥	⬛	⬛	⬛	⬛
N (macro-tree)	🟩	🟥	🟩	🟩	🟩	🟩	🟥	🟥	⬛
S (micro-tree)	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
N (micro-tree)	🟩	🟥	🟥	⬛	⬛	🟩	⬛	🟩	⬛
S (macro-shrub)	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
N (macro-shrub)	🟩	⬛	⬛	🟩	🟩	🟩	🟥	🟩	⬛
S (micro-shrub)	🟥	⬛	🟩	⬛	⬛	⬛	⬛	⬛	⬛
N (micro-shrub)	🟩	🟩	🟩	⬛	🟩	🟩	⬛	🟥	⬛
S (macro-herb)	🟩	⬛	⬛	🟩	🟥	🟩	🟥	⬛	⬛
N (macro-herb)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
S (micro-her)	⬛	⬛	🟥	🟩	⬛	⬛	⬛	⬛	⬛
N (micro-herb)	⬛	⬛	🟩	🟩	⬛	🟩	🟩	⬛	⬛
S (macro-understorey)	🟩	⬛	⬛	🟩	🟥	🟩	🟥	⬛	⬛
N (macro-understorey)	🟩	🟩	🟩	🟩	🟩	🟩	⬛	🟩	⬛
S (micro-understorey)	⬛	⬛	🟩	🟩	⬛	🟥	🟥	⬛	⬛
N (micro-understorey)	🟩	⬛	🟩	🟩	🟩	🟩	🟩	⬛	⬛

Figure 2. Result of GLM using PCs and Lepidoptera groups as independent and dependent variables. GLM was subjected to model selection, and the table includes both the significant/non-significant and eliminated results. Significance level $p < 0.05$. Green squares represent significant relations that were included in the final model. Red squares represent non-significant relations that were also included in the final model. Black squares show the dimensions that were excluded during model selection. Detailed results of the model selection are presented in Supplementary File S1. S—Species richness of Lepidoptera in the samples; N—abundance of Lepidoptera in the samples; total—complete Lepidoptera in the samples; macro—macromoths in the samples; micro—micromoths in the samples; tree-hosted—Lepidoptera species which develop on trees; shrub-hosted—Lepidoptera species which develop on shrubs; herb-hosted—Lepidoptera species which develop on herbs; understorey—Lepidoptera species which develop on the underlayer vegetation, including shrubs and herbs as well.

4. Discussion

Our results reveal that Lepidoptera communities were most affected by PC1 (weighted toward forest age, thinning factors, and herb species richness). The effects were negative for different groups of macromoths and the total detected moths with a very few exceptions. In our interpretation, the thinning factors were not favourable for macromoth communities in the investigated forest stands. Forest age was also heavily weighted in PC1 and we revealed a mainly negative effect on Lepidoptera. The intensity of thinning was related to the forest age: the older forests were affected more and the younger forests were affected less or avoided by thinning. Consequently, the cumulated thinning effect grew with forest age. Our findings on forest age and thinning activity were supported by the local forest management plan document (including the performed managements in the forest sites) and even by Figure 1 (young forest sites were well separated from the others along PC1).

However, PC3 (representing primarily coverage factors) showed mainly positive relations with many Lepidoptera groups (especially with the moth abundance), pointing to the fact that higher vegetation coverage can support moth density in the investigated forest stands (S1—detailed GLM results). Nevertheless, we need to note that six Macrolepidoptera species had extreme high abundance in the samples (over 1000 specimens per species; representing more than 43% of the total macromoth abundance), definitely affecting the positive relation between vegetation coverage and moth abundance.

Thinning can generate heterogeneity through microhabitat diversification and create canopy gaps and a less limited light regime; it can also affect the diversity of various species, such as pioneer trees [55], understorey vegetation [19,56], small mammals [57], ground spiders [21], and even insect assemblages [22]. It has been previously shown that microhabitat heterogeneity influences the number of Lepidoptera species [25]. The created gaps facilitate the growth of various photophilous plants typically absent from the shaded underlayer. Increasing plant species diversity can even enhance the species richness of macromoths [58]. More intensive thinning (which typically focused on the mixture of trees and shrubs in the investigated forests) can result in a more abundant herb layer [59] and less abundant canopy layer. In addition, thinning can increase the biomass and volume productivity of vegetation [60]. Consequently, in our study, the thinning itself is less favourable for moth species richness, due to the decrease in resources; however, the increasing density or productivity of some vegetation layers—as a result of thinning—supported the Lepidoptera abundance.

We found fewer relations between micromoth groups and the principal components. Micromoths form the majority (2/3) of the Heterocera fauna of Hungary along fairly diverse ecological requirements [61]. Moreover, they have a high proportion of host plant and habitat specificity [62]. Despite the various habitat demands of micromoths, their species richness was less correlated with PC1. However, we found mainly positive relations between PC1 and micromoth abundances, which can be explained by the high proportion of two oak feeding species: Yellow Oak Tortix (*Aleimma loefligianum* (Linneaus 1758)) (known pest species in Hungarian oak forests) and Oak Longhorn (*Carcina quercana* (Fabricius, 1775)). These two species represented 31% of the total abundance of micromoths which potentially develop on trees (Table S1). Furthermore, *A. loefligianum* and *C. quercana* prefer warmer conditions during larval development [63]. Thinning affects microclimate conditions due to increasing light penetration and temperature gradients [64,65]; therefore, warmer microclimatic conditions in the gaps (created by thinning) should be more favourable for *A. loefligianum* and *C. quercana* larval development, which may result in their higher abundance; this can explain the positive relation between PC1 and tree-hosted micromoth abundance. However, the precise clearing of this question requires further investigations using vertical microclimatic measurements.

Negative correlations appeared between PC4, PC6 (strongly represented coverage factors), and most of the Lepidoptera groups (S1—detailed GLM results before and after the model selection, Table 3). The study sites are characterised by upper (composed of larger trees, especially *Q. petraea*) and lower canopy layers (composed mainly of *Carpinus betulus*), resulting in high shade levels in the forest interior. Therefore, shade affected the lower vegetation layers more intensively. The shaded forest inside is less tolerated by plants, causing less species and lower coverage of the understorey vegetation [66,67]. However, within some sampling sites, we found a dense yet species-poor shrub-layer. Moth fauna have a high proportion of habitat specificity [62], which can explain the negative response to PC4; e.g., the Site 3 shrub-layer coverage was 50.02%, strongly dominated by *C. betulus* (50%) (Table S2 and Table 1). We suggest that the species richness of Lepidoptera groups would only increase with higher shrub coverage, or that understorey cover also involves the increasing number of plant species and more diverse structure. These criteria were not met in the sampling sites. Several studies supported the correlation between plant structural diversity and moth species richness (e.g., [68–70]). In addition, we need to consider that PC4 and PC6 explained the very low proportion of the variance (9.9% and 3.3%).

5. Conclusions

Our result has shown that moth communities in sessile oak–hornbeam forests are affected both by vegetation traits and management practice. Thinning is a generally used forest management method to reduce tree density, enhance forest health, and promote growth of the remaining trees; however, it has an obvious effect on the vegetation, e.g., it creates microhabitats, changes the light regime, and influences the growth of photophilous plants. Through thinning, the changes in vegetation composition and structure have various effects on moth communities. In the studied forest type, thinning reduced resources for tree-hosted Lepidoptera species; however, it affected microclimate conditions due to the increased light penetration and temperature, which, in turn, resulted in an increased abundance of heat-preferred species. Due to the less limited light regime, the increased herb layer also supported the Lepidoptera assemblages.

Furthermore, the canopy was composed mainly by *Quercus petraea* agg. and *Carpinus betulus* within the study sites and included only few mixture tree species. A lower species richness of trees was less favourable for moth communities (as a result of their high proportion of habitat and food–plant specificity) and might cause a lower stand-level abundance and species richness of some Lepidoptera groups. A dense yet species-poor shrub layer was also not favourable for moth communities. A high coverage of shrubs was always made up by the young growth of *C. betulus*.

Our final conclusion supports the fact that thinning activity per se in sessile oak–hornbeam forests is less favourable for many groups of moths; however, it can ensure the maintenance of moth communities through the increasing herb density. Furthermore, a dense yet species-poor shrub layer is also not favourable for moths. Consequently, thinning can affect Lepidoptera assemblages through the changes in the canopy structure and lower vegetation layer as well. We concluded that a single study on forest management practice or on vegetation traits is not suitable in indicating their exact effect on moth communities; therefore, their combined study is required.

In order to avoid the decrease in diversity of nocturnal Lepidoptera in the examined forest type, we suggest an overall approach to define the optimal forest management practice and tree mixture rate, regarding a wide scale of forest sites within a larger area.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15060896/s1.

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