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Microclimate Shifts and Leaf Miner Community Responses to Shelterwood Regeneration in Sessile Oak Forests

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Abstract: For forests to provide ecosystem services and function optimally, they need to be managed. Forest management measures can cause significant environmental changes, which sometimes appear extreme. The most notable disturbance caused by forest regeneration is the change in canopy cover. Alteration of the canopy cover is followed by the modifications of many microclimatic factors. These changes subsequently affect all the living organisms in the forest. The present study was conducted to determine how the changes caused by modifications of canopy closure by shelterwood regeneration affect the leaf-mining insect community on sessile oak (*Quercus petraea* (Matt.) Liebl.). We identified that the removal of the canopy significantly affects the microclimate, vegetation, and the leaf miner community. The insolation and temperature increased in the more open areas, while relative air humidity decreased. This affects the characteristics of the young oak plants, which grow taller and produce more leaves in the open-canopy areas. All these changes consequentially affect the leaf miner community. While the species richness and abundance per tree increased with the decrease in canopy closure, the species richness and abundance per leaf decreased. The opening of the canopy positively affected the leaf miners in the end by increasing the diversity and evenness of their community.

Keywords: biodiversity; forest management; *Quercus petraea*; species richness; forest disturbance; light availability; temperature and humidity

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1. Introduction

Forests are the most diverse and ecologically important terrestrial habitats on the planet, covering about 30% of the Earth's land surface [1]. They provide important ecosystem services, such as carbon sequestration, soil and water protection, and consequentially, mitigation of climate change [2]. Most forests require being managed, ideally in accordance with nature, to allow their normal functioning and to maximize the use of these ecosystem services [2,3]. However, regeneration and other forest management techniques might appear drastic and result in major environmental changes [4–6]. While these changes can negatively affect some ecosystem components, their long-term impact is generally positive, and without them, many existing forests could not survive [4,5]. The most significant disturbance caused by forest regeneration is the rapid change in canopy cover and light conditions caused by the removal of some or all of the trees in the area under regeneration [5,7]. As a consequence of these modifications, the microclimate in the regenerated areas changes significantly [8,9]. Without the protection of the canopy and/or forest edge, the climate becomes significantly drier and warmer [10]. The canopy is a major driver of

the natural regeneration process, influencing the spread of both woody and herbaceous plant communities [11–13]. The plants most affected by the changes in canopy conditions are those that develop under the closed canopy of mature trees [11–13].

Changes in habitat conditions caused by alterations of canopy closure can have a profound effect on forest insect communities [14–17]. It can affect them directly by altering their distribution in the forest, or indirectly by affecting the light availability, speed of nutrient cycling, and temperature [18–20]. Changes in environmental factors can also affect the insects' host plants and natural enemies in many ways [21–24]. In open canopy conditions, insects are more susceptible to predators and adverse abiotic conditions, like high insolation, intense precipitation, and powerful winds, which are typically buffered by the forest canopy [15,24–27]. Some authors claim that higher canopy closure increases herbivory rates [28], while according to others, the effect depends on the tree species [29].

Previous studies have found that different groups of insects respond differently to changes in the canopy closure [27–32]. For example, gallicolous insects and true bugs (Hemiptera, Heteroptera) benefit from a more open canopy [18,28], while ambrosia beetles are negatively affected by this change [33]. As the general trend of the impact of canopy closure on insect communities cannot be identified from the previous work on the topic, we decided to conduct this study, in which we tested the effect of changes in canopy closure caused by shelterwood regeneration on the leaf-mining insect community on sessile oak (*Quercus petraea* (Matt.) Liebl.).

The shelterwood regeneration method, which was applied in the study areas, incorporates elements of natural regeneration by gradually removing mature trees. In Southeastern Europe, where there is a rich tradition of managing natural forests, the system has been widely adopted [34]. This approach focuses on renewing the stand and planning for future forest composition, with all mature trees removed over a series of two to four fellings that span around 10 years. This contrasts with selective felling, which considers criteria such as size, age, and species of the trees to maintain a specific structure [35,36]. The shelterwood regeneration method gradually prepares young trees for the open canopy conditions, which increases their adaptation and survival rates and conserves diversity [37–39].

Leaf miners were used for the experiment as they are susceptible to the effects of environmental changes [16,40,41]. They are a diverse insect guild with members from four orders [41,42], which has been well-studied in Serbia [43,44]. Their larvae live within one leaf their entire life, so they are tied to one location in the forest [40,45]. As they cannot migrate, they are exposed to all the changes the forest is exposed to. They react to those changes directly and indirectly, through the changes in the host plants [25,41,46,47]. They are an ecologically important group because, on one hand, they can cause significant damage to plants, while on the other, they play a crucial role in food webs, serving as prey for birds, parasitoids, and predatory arthropods [24,42,48,49].

Sessile oak was chosen as a host plant because it is widely spread and valued in Europe as it provides many ecological and economic benefits, it reacts to changes in canopy closure and has a rich and diverse insect community [42,43,50–52]. Although extensive research was conducted on the effect of forest regeneration on insect communities [16,40,53–55], no studies have examined how changes in environmental conditions caused by shelterwood regeneration affect the leaf-mining insect community on young sessile oak plants.

Young forest plants are highly sensitive to environmental changes, particularly those caused by alterations in canopy closure. That is why we investigated how variations in canopy closure affect the young sessile oak plants, their growing environment, and the insects that interact with them. To achieve this, we aimed to determine how the changes in canopy closure affect: (1) the microclimatic conditions, (2) the characteristics

of the understory vegetation, and (3) the leaf-mining insect community on young sessile oak plants.

2. Materials and Methods

2.1. Study Sites

The research was conducted in 2020 on three locations in the northeastern part of Serbia (Majdanpek): Ujevac (44°25′ N; 21°52′ E), Crna reka (44°21′ N; 21°55′ E), and Ravna reka (44°26′ N; 21°59′ E). The average annual temperature at the study sites ranged from 9.3 to 10.3 °C, while during the growing season, it was between 15.9 and 17.0 °C. The average annual precipitation varied from 679 to 705 mm, with growing season precipitation averaging between 388 and 403 mm [7]. According to the Thornthwaite climate classification, the studied localities fall under a subhumid moist climate (C_2) [7]. In contrast, Lang's climate classification categorizes them as semi-humid, typical of low-altitude forests [7].

The stand at the locality Ujevac is phytocenologically defined as a community of sessile oak and hairy sedge (*Carex pilosa* Scop.) (Carici pilosae–Quercetum petraeae). It is situated at 270–290 m above sea level. The slope of the terrain is 20, and the exposition is western. The soil is deep eutric brown, formed on neutral and basic eruptive rocks, and weakly skeletal. The stand at the locality Crna reka is phytocenologically defined as a community of sessile oak and forest fescue (*Festuca drymeja* Mert. and W.D.J. Koch) (Festuco drymeiae—Quercetum petraeae). It is situated at 450–470 m above sea level. The slope of the terrain is 15° and the exposition is southwest. The soil is loamy ilimerized (luvisol), on a silicate substrate. The stand at the Ravna reka locality is phytocenologically defined as a community of sessile oak with hairy sedge (Carici pilosae—Quercetum petraeae). It is situated at 490–520 m above sea level. The slope of the terrain is 20° and the exposition is south–southwest. The soil is district brown, shallow to medium deep, and formed on gneiss [7].

2.2. Experimental Design

Three sites with different canopy closure were selected at each location (canopy cover classes). For closed canopy cover class, about 140-year-old stands where no management measures were conducted in the last 30 years were selected. Semi-open canopy cover class was represented by about 140-year-old stands in which the preparation cut of regeneration by shelterwood cutting was conducted in the last 5–10 years when the seed yield was abundant. Open canopy cover class was represented by stands in which the canopy of the about 140-year-old growth forest was removed by final cut of shelterwood cutting in the last 5–10 years after the regeneration has been deemed successful, and oak seedlings higher than the surrounding herbaceous vegetation were identified.

At each site, at each locality, five young (5–7-year-old) sessile oak trees were sampled. All of their leaves were counted twice during the vegetative season (June and August). The leaves with mines on them were separated, and brought to the Entomological Laboratory of Belgrade University, Faculty of Forestry where species causing them were identified based on Hering [56], Patočka and Turčani [57], Laštůvka et al. [58] and Ellis [42]

2.3. Environmental and Plant Characteristics

To analyze the canopy cover, hemispherical canopy photographs were taken at all experimental sites using a Nikon Coolpix 5000 camera (Nikon Corp., Tokyo, Japan) equipped with an FC-E8 hemispherical ("fish-eye" or open-sky) lens. At the experimental sites, photographs were captured on the same day between 9:00 and 12:00 AM, under cloudless sky conditions. During image acquisition, the camera was horizontally and vertically leveled at a height of 1.30 m above ground level. The hemispherical images were processed using

the software Gap Light Analyzer (GLA, Version 2.0) [59]. Image processing included registration and classification phases, followed by the calculation of relevant canopy structure parameters. For pixel classification, the threshold value for the image was determined with the aid of the shareware SideLook 1.1 [60] using all the offered color channels. To assess microclimatic conditions, we measured air temperature, relative humidity, and insolation in all experimental sites every two hours from 6 AM to 6 PM over three days in July, the sunniest month. The measurements were taken consecutively from 1–3 July 2020. Since July is the warmest month in the research area, the objective was to collect data on the mentioned climatic elements when differences in various forest canopies are most evident. We utilized a WS-GP1 portable automatic weather station (Delta-T Devices Ltd., Cambridge, UK), which allowed us to collect essential meteorological data at a height of 2 m during the specified time intervals. The cover of herbaceous and woody species was estimated visually from above and recorded in percentages to the nearest 10%, ranging from 10% to 100%, and after that to the nearest 1%, ranging from 1% to 9% [7]. The plant height was measured on all plants present within square sample plots measuring 10 × 10 m (0.01 hectares) on each locality in each canopy cover class, using a measuring tape with an accuracy of 0.5 cm.

2.4. Characteristics of the Leaf Miner Community Analyzed

Leaf mining insect community was quantified by the following parameters at the level of a single tree:

1. Species richness (number of species identified) per tree, and the number of species per 100 leaves, calculated as:
$$S_i = \frac{s_i}{l_i} * 100 \quad (1)$$
where s_i is the number of species found in one sample, l_i is the number of leaves per sample.
2. Total species richness of leaf miners (number of species identified on all trees).
3. The abundance of individual species (A_i) per tree, and the number of mines per 100 leaves, calculated as:
$$A_i = \frac{n_i}{l_i} * 100 \quad (2)$$
where n_i is the number of mines of one particular species found in one sample and l_i is the number of leaves per sample.
4. The total abundance of leaf miners (A_b) is calculated as a sum of all individual species' abundance.
5. Shannon's index of diversity (H'), calculated as:
$$H' = -\sum_{i=1}^{S_i} (p_i \times \ln(p_i)) \quad (3)$$
where S_i is the species richness and p_i is the proportion of individuals belonging to the i-th species in the dataset [61].
6. Buzas and Gibson's evenness index (Ev), calculated as:
$$Ev = \frac{e^H}{S_i} \quad (4)$$
where H is Shannon's index of diversity and Si is species richness [62].

2.5. Statistical Analysis

As the distribution of the analyzed parameters did not fit the normal distribution (Kolmogorov–Smirnov test), a generalized linear mixed model (GLMM) was used for

further analysis, with canopy cover class as a fixed factor and study sites as a random factor. Poisson distribution was assumed for the analysis of the number of miner species or individuals per tree, and gamma distribution was used for the rest of the data. The analyses were conducted with an identity link function, at the confidence level of 95%. An LSD post hoc test was used for comparison among means where the GLMM showed a significant difference. Diversity and evenness indices were calculated using PAST 5.2.2 [63]. Statistical analyses were conducted using IBM SPSS Statistics 26.0 [64].

3. Results

3.1. The Influence of Changes in the Canopy Cover on the Forest Microclimate

Canopy cover differed significantly between the sites at each locality (F = 2517.761, $p = 0.000$) (Figure 1). The differences in canopy cover caused significant changes in the microclimate. The insolation (F = 1063.681, $p = 0.000$) and temperature (F = 402.560, $p < 0.0001$) increased significantly from closed to open canopy conditions, while relative humidity decreased in the same manner (F = 512.479, $p < 0.0001$) (Figure 1).

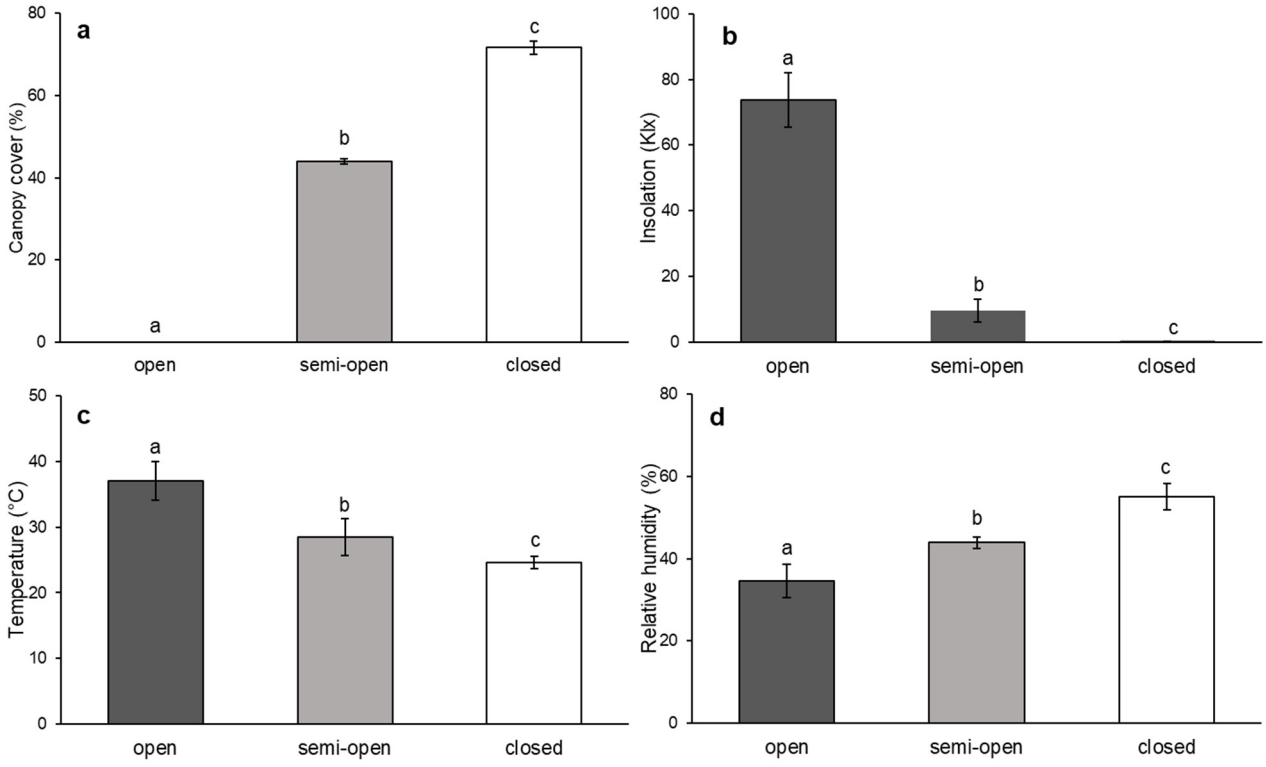


Figure 1. Differences in canopy cover (%) (**a**) and influence of canopy cover class on insolation (1×/1000) (**b**), temperature (°C) (**c**), and relative humidity (%) (**d**) (mean ± SD) assessed by the GLMM (letters above the columns indicate the grouping calculated by LSD post hoc test).

3.2. The Influence of Canopy Cover on Understory Vegetation

Seven woody and three herbaceous understory plant species were identified as dominant on the study sites in the following order: *Quercus petraea* (Matt.) Liebl. (59.4%), *Rubus hirtus* Waldst. and Kit. (12.8%), *Tilia tomentosa* Moench (8.3%), *C. pilosa* (5.0%), *F. drymeja* (4.4%), *Fraxinus ornus* L. (3.9%), *Acer campestre* L. (2.2%), *Carpinus betulus* L. (2.2%), *Cornus mas* L. (1.1%), and *Rosa arvensis* Huds. (0.6%) (Figure 2). The total understory plant cover showed a regularity where the highest amount of ground area covered by understory plants was in the open canopy cover class, slightly lower in the area with the semi-open canopy cover class, and significantly lower in the closed canopy cover class (Figure 2 and Table 1). The understory plant ground cover by plant species differed between different

canopy cover classes, although this was only significant for some species (Figure 2 and Table 1). Of the identified species, *Q. petraea* covered the greatest area, and dominated in the open class, compared to both the semi-open and closed canopy classes. From the rest of the identified species, only *F. ornus* and *A. campestre* covered a significantly greater ground area in the semi-open compared to the closed and open canopy classes (Figure 2 and Table 1).

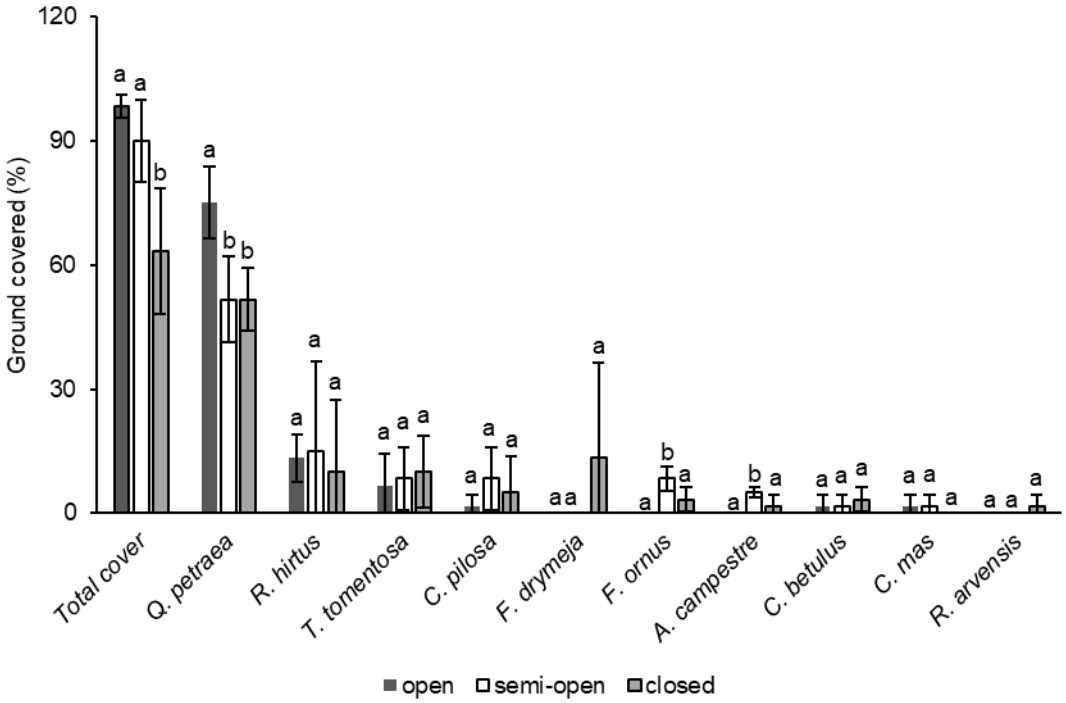


Figure 2. Differences in total ground cover by understory plants and ground cover by plant species (% of the ground area covered) (mean ± SD) assessed by the GLMM (letters above the columns indicate the grouping calculated by LSD post hoc test).

Table 1. Effect of canopy cover class on the ground cover area covered by understory vegetation assessed by the GLMM (bold values indicate statistically significant values).

	F	*p*
Total cover	**16.710**	**0.012**
Q. petraea	**6.759**	**0.029**
R. hirtus	0.072	0.931
T. tomentosa	2.736	0.267
C. pilosa	1.079	0.464
F. drymeia	1.000	0.422
F. ornus	**9.500**	**0.014**
A. campestre	**7.000**	**0.027**
C. betulus	1.000	0.444
C. mas	1.000	0.444
R. arvensis	1.000	0.422

The young oak plants that grew in the closed canopy conditions differed from the plants that grew in the semi-open or open canopy conditions. The height of the plants ($F = 63.308$, $p < 0.0001$), as well as the number of leaves ($F = 111.763$, $p < 0.0001$), differed significantly between different canopy cover classes. The plants' height, as well as the number of leaves, was highest in the open canopy cover class, lower in the semi-open, and lowest in the closed canopy cover class (Figure 3).

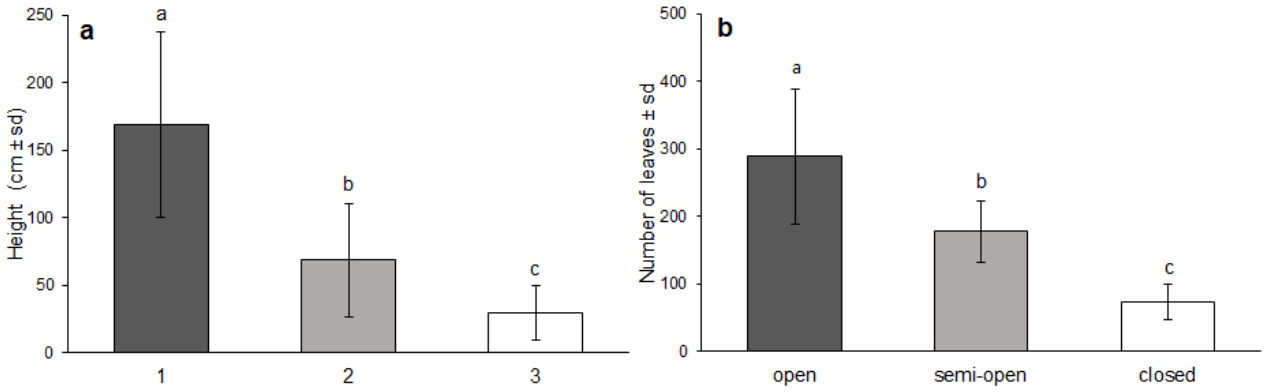


Figure 3. Influence of canopy cover class on the height (**a**) and number of leaves (**b**) of young sessile oak trees (mean ± SD) assessed by the GLMM (letters above the columns indicate the grouping calculated by LSD post hoc test).

3.3. The Influence of Canopy Closure on the Leaf Miner Community on Young Sessile Oak Plants

A total of 12 leaf miner species were identified on the leaves of the studied plants (Table 2). The most frequent and abundant of all the identified species were *Profenusa pygmaea* (Klug, 1816), *Phyllonorycter quercifoliella* (Zeller, 1839), and *Tischeria ekebladella* (Bjerkander, 1795).

Table 2. Leaf miner species identified on the young sessile oak plants in different canopy cover classes.

Species	Canopy Cover Class		
	Open	Semi-Open	Closed
Bucculatrix ulmella (Zeller, 1848)	✓	✓	
Caloptilia alchimiella (Scopoli, 1763)	✓	✓	✓
Coleophora flavipennella (Duponchel, 1843)			✓
Ectoedemia albifasciella (Heinemann, 1871)	✓	✓	
Phyllonorycter harrisella (Linnaeus, 1761)	✓	✓	
Phyllonorycter quercifoliella (Zeller, 1839)	✓	✓	✓
Phyllonorycter roboris (Zeller, 1839)	✓	✓	✓
Profenusa pygmaea (Klug, 1816)	✓	✓	✓
Stigmella basiguttella (Heinemann, 1862)	✓	✓	✓
Stigmella roborella (Johansson, 1971)	✓	✓	✓
Tischeria decidua (Wocke, 1876)	✓		
Tischeria ekebladella (Bjerkander, 1795)	✓	✓	✓
Σ	11	10	8

Canopy cover had a significant effect on the number of leaf miner species per tree ($F = 4.695$, $p = 0.012$), as well as per leaf ($F = 15.644$, $p = 0.000$). While the number of species per tree increased with the decrease in canopy cover, the number of species per leaf decreased (Figure 4a,b). The situation regarding the number of mines was the same. Canopy cover had a significant effect on the number of leaf mines per tree ($F = 7.310$, $p = 0.001$) as well as per leaf ($F = 10.263$, $p = 0.000$), and the number of mines varied in the same order (Figure 4c,d). Canopy cover also significantly affected the Shannon diversity index ($F = 16.052$, $p = 0.000$) and the Buzas and Gibson's evenness index ($F = 15.270$, $p < 0.0001$). Both of these indices increased in the direction from closed to open canopy cover classes (Figure 4e,f).

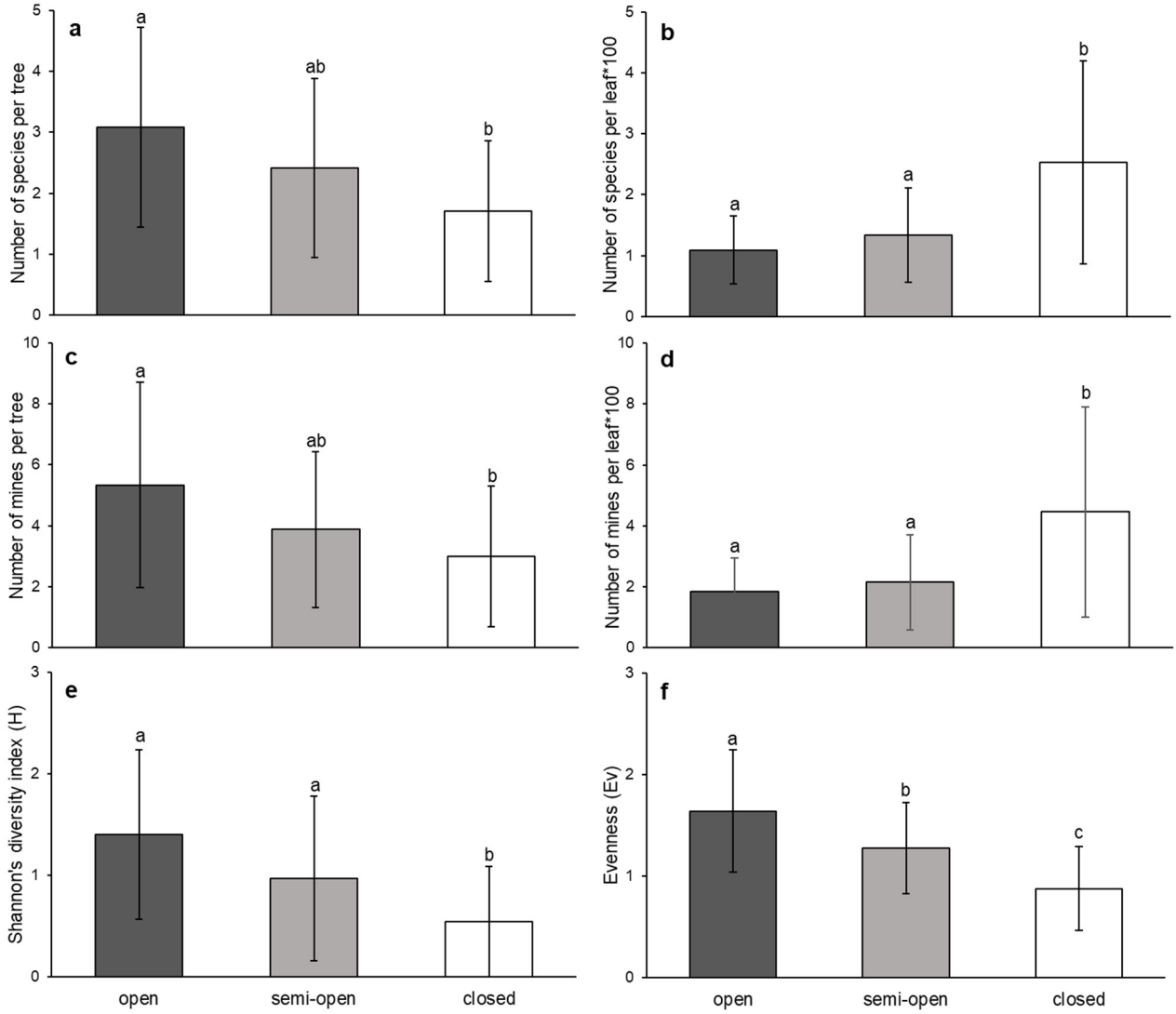


Figure 4. The influence of canopy cover class on the sessile oak leaf miner community (mean ± SD), represented by the number of species per tree (**a**), number of species per leaf × 100 (**b**), number of mines per tree (**c**), number of mines per leaf × 100 (**d**), Shannon's diversity index (**e**), and evenness (**f**), assessed by the GLMM (letters above the columns indicate the grouping calculated by LSD post hoc test).

4. Discussion

In this study, we found that shelterwood regeneration has a significant impact on the sessile oak forest microclimate, vegetation, and its leaf-mining insect community. The reduction in the canopy cover caused by the combined preparation–seed cut increased insolation by more than 17 times, while the final cut increased it by more than 133 times. These changes affected the vegetation characteristics both directly and indirectly by altering the microclimate characteristics, such as increasing the temperature and airflow and reducing air humidity. This consequentially contributed to plant growth as light intensity positively affected the rate of photosynthesis, biomass accumulation, and structural development [65,66]. On the other hand, they could negatively affect plants by increasing drought stress, negatively affecting soil microorganisms, and increasing the risk of pest outbreaks [67–69]. In the mosaic of different microclimate conditions, the areas with closed canopy may have served as climate buffers, preventing warm, dry air from entering other parts of the forest, thus mitigating drought stress and providing refuge for sensitive species [70–72]. These newly created conditions promote the growth of most plant

species, which is why shelterwood cutting is widely used in forestry to support natural regeneration [7,73,74].

After the combined preparation–seed cut and especially final-cut understory plant cover increased. Heliophilous plant species, including sessile oak, were particularly promoted. Besides the sessile oak cover, *F. Ornus* and *A. campestre* were significantly affected by the changes in canopy closure, although they were not present in the open canopy conditions where *Q. petraea* dominated. The oak plants that were exposed to more light also grew taller and produced greater leaf mass, as a consequence of enhanced photosynthesis due to more available light [7,75]. In contrast, shaded plants developed larger leaves to optimize light capture at the cost of reduced overall biomass [76].

The changes in forest cover also affected the leaf miner community. All the studied parameters per tree were significantly higher in open or semi-open conditions, compared to the closed canopy cover class. Leaf miners, like most herbivorous insects, prefer areas with higher insolation due to the associated increase in host plant quantity, quality, and microclimatic benefits for their development [77,78]. The change in canopy cover affected leaf miners both directly by modifying the microclimate and indirectly by altering host plant characteristics. The increased temperature most likely benefited the leaf miners as it accelerates insect metabolism and development, increasing their voltinism, and subsequently their survival rates [78–80]. Changes in microclimate could have affected the interactions of leaf miners with competitive herbivorous insect species, as well as their natural enemies [24,81,82]. Higher temperatures and insolation also affect leaf miners indirectly through their effects on host plants, by affecting their phenology, size, leaf mass, etc. [15,16,78,80]. Plants in open-canopy areas were significantly taller and had more leaves which emitted stronger chemical cues, making them easier to detect by the leaf miners [16,40]. This likely explains why all insect community parameters per tree were significantly higher in the open and semi-open cover classes. In contrast, shade-grown plants were smaller, produced fewer leaves, and emitted weaker chemical signals, making them less attractive. On the other side, sun-exposed plants produce more protective chemicals such as tannins and flavonoids, enhancing herbivore resistance, whereas shaded plants allocate fewer resources to chemical defense, making them more vulnerable [83–85]. Additionally, some leaf miner species prefer shaded environments where plants produce larger, more hydrated leaves which provide better feeding conditions for future larvae [86,87]. Overstory trees in those shaded areas also serve as reservoirs for colonizing species, as they can maintain a sustainable and more diverse population of leaf miners [16,88].

Leaf miner diversity and evenness were significantly higher in the areas with open and semi-open canopies compared to areas with closed canopies. From an ecological perspective, this is viewed as positive as increased biodiversity implies a more resilient ecosystem [89–91]. However, this study refers to only one insect guild on one host plant species, and the study was performed in a single forest location, so the results are hard to generalize in this context without analyzing other ecosystem members on a greater multitude of ecologically different localities, which is why it should serve as a reference point for future research. Nevertheless, shelterwood regeneration created a mosaic of diverse habitats with natural, reduced, and removed canopy cover [92–95]. The formation of these microhabitats allowed the survival of both sciophilous and heliophilous plant species and both the forest specialist and open-area insect species which feed on them in a relatively small area [39,94–97]. These mixed habitats accommodate greater forest species richness and diversity compared to both clear-cutting and selective cutting, which tend to homogenize environmental conditions over large areas [97–99]. The diverse forest structure can also boost carbon sequestration in the long term while maintaining ecological stability, as the forest is not completely removed at any moment, which is a significant advantage

compared to clear-cutting [5,100,101]. Forestry practitioners understand this, which is why forest regeneration methods incorporate diversity conservation as an important factor in recent years by leaving retention trees or groups of trees when applying clear-cutting, or reducing the area under regeneration when applying shelterwood regeneration [16,55,102]. If forests like the one in this study were left to regenerate passively, similarly to protected virgin oak forests, then shrub species, lime, hornbeam, or even invasive species like ghetto palm would probably dominate these forests [103–105]. In the long term (over a century), large forest complexes might gradually develop into mixed oak forests, but many of their ecological functions, including biodiversity conservation, would be lost [106]. This would result in significant ecological and economic losses [51,107].

5. Conclusions

Shelterwood regeneration of sessile oak forests causes changes in canopy cover which affect the forest microclimate by increasing insolation and temperature, and decreasing air humidity. This subsequently influences the plants in the regenerated areas, as well as the insect communities feeding on them. The increase in light availability contributes to an increase in the plants' height and production of increased leaf mass as a consequence of enhanced photosynthesis.

Sessile oak leaf miner species richness and abundance per tree, as well as diversity and evenness, were significantly higher in the open or semi-open canopy cover classes, while species richness and abundance per leaf decreased in the open or semi-open canopy cover classes. Leaf miners benefited from the increased insolation due to the increase in host plant quantity, quality, and microclimatic benefits for their development. The parameters calculated per leaf were higher in the shaded environment, probably due to the increased production of protective chemicals of the sun-exposed plants; the characteristics of the shaded plants which produce larger, more hydrated leaves; and overstory trees which can sustain an abundant leaf miner population and act as population reservoirs.

Either way, the shelterwood forest regeneration had a positive influence on the sessile oak and other understory plants as well as on the leaf miner community. It created a mosaic of diverse habitats that accommodated both young and mature sessile oak plants. This affected the oak age diversity positively, while also increasing the leaf miner species richness and diversity, allowing long-term forest stability and sustainability. This way, many other ecological functions to which oak forests contribute were enabled, while simultaneously allowing for economic profitability. As the study was performed in a single forest location, which had a single insect guild feeding on it, the extension of results to other forest formations, climatic zones, or insect groups can be constrained, which is why additional temporal, spatial, and species replications need to be conducted to confirm these conclusions.

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