

Effect of *Hedera pastuchovii* Woronow on soil and host tree characteristics along an elevation gradient in the Hyrcanian Forests

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Research Article

Keywords: Plant invasion, Microbial respiration, Nutrient cycling, Litter decomposition, Stomatal characteristics, Principal Component Analysis, Forest ecosystem functioning

Posted Date: June 23rd, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9975822/v1>

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Additional Declarations: No competing interests reported.

Abstract

Hedera pastuchovii Woronow, an evergreen climbing species widely distributed in the Hyrcanian forests, can alter forest structure and ecosystem functioning through its interactions with host trees and soil processes. This study investigated the relationships among elevation, host tree species, leaf functional traits, stomatal characteristics, litter quality, and soil physicochemical and microbial properties in relation to *H. pastuchovii* occurrence in the Lufur–Firozja forests of northern Iran. Sampling was conducted along an elevational gradient from 300 to 900 m a.s.l. in infested and non-infested stands. The results showed that elevation exerted a stronger influence on vegetation and soil characteristics than the presence of *H. pastuchovii*. The highest density of the species occurred at mid-elevations (450–600 m), coinciding with maximum soil organic matter, nitrogen, microbial biomass, respiration, and enzymatic activities. Higher elevations were characterized by lower nutrient availability, reduced microbial activity, and smaller leaf traits. Infestation significantly reduced leaf area, petiole length, lamina dimensions, stomatal density, stomatal size, and litter nutrient contents (C, N, P, Ca, and Mg). Although soil physicochemical properties were only slightly affected, microbial biomass and enzymatic activities declined markedly in infested stands. Host preference analysis revealed significant associations with *Diospyros lotus* L., *Acer velutinum* Boiss., *Carpinus betulus* L., and *Mespilus germanica* L. PCA confirmed clear separation among elevational classes and infestation conditions, highlighting elevation as the primary driver of soil ecological processes and plant functional responses. Overall, mid-elevational Hyrcanian forests provide the most favorable conditions for *H. pastuchovii* expansion, with its ecological impacts mediated mainly through changes in host plant performance, litter quality, and soil biological activity.

1. Introduction

Climbing plants constitute an influential component of forest ecosystems, shaping both structural complexity and ecological processes. By exploiting host trees to gain vertical access to light, these species intensify competition for aboveground resources and modify regeneration pathways and carbon allocation patterns within forest stands (Schnitzer and Bongers, 2002; Verbeeck et al., 2024). In some contexts, rapidly spreading climbers exhibit ecological behaviors comparable to invasive plants, which are recognized as major drivers of biodiversity loss worldwide (Wilcove et al., 1998). Such species may suppress native vegetation through competition for light, nutrients, space, and biotic interactions, thereby altering community composition and reducing diversity (Morales and Traveset, 2009; Valone and Weyersset, 2019). The impacts of dominance-forming plants extend beyond aboveground interactions. Through modifications in litter production, biomass accumulation, and root exudation, they can alter soil physicochemical properties, restructure soil microbial communities, and influence nutrient cycling processes (Meiners et al., 2017; Zhao et al., 2019). Such belowground alterations may generate feedback mechanisms that reinforce species persistence and increase ecosystem susceptibility to additional disturbances (Simberloff and Von Holle, 1999; Ma et al., 2020). Species of the genus *Hedera* (Araliaceae) exemplify climbers with high ecological plasticity, persistent evergreen foliage, and strong vegetative expansion capacity (Metcalf, 2005). Although several *Hedera* species are native within parts of their range, they may locally attain high abundance and substantially influence light availability, understory regeneration, and vegetation dynamics (Blinkova et al., 2023). Under conditions of high abundance, *Hedera* may gradually suppress surrounding vegetation through competition for light, space, and soil resources. Local dominance of this species has the potential to influence soil nutrient dynamics, as dense *Hedera* cover may alter organic matter inputs and compete with neighboring plants for both organic and mineral nutrients. Such competitive interactions can modify soil structure and physicochemical properties over time (Weand et al., 2026). Prolonged expansion of *Hedera* may therefore contribute to shifts in plant community composition and potentially affect associated faunal assemblages. Increased dominance of this climber may reduce local plant diversity and abundance, thereby influencing ecosystem functioning and productivity (Bunk et al., 2019). Despite its ecological prominence, comprehensive evaluations of its distribution patterns, host preferences, and interactions with soil properties and environmental gradients remain limited. Clarifying these plant–soil–host interactions is therefore essential for understanding the ecological role of climbing plants in these biodiverse forest ecosystems (Yıldırım et al., 2025).

The Hyrcanian forest, located in the Caspian region, serves as a natural green belt in northern Iran, stretching from the Alborz mountain range to the Caspian Sea. This forest spans approximately 110 kilometers in width and 800 kilometers in length, covering a total area of 2.1 million hectares, which accounts for 15% of the total forest area and 1.1% of Iran's land area. The Hyrcanian forests are recognized as one of the last temperate broadleaf forests globally (Sagheb Talebi et al., 2014), holding

significant ecological, social, economic, and cultural value. Recently, they have been designated as a UNESCO World Heritage site (Hosseini, 2019). *Hedera pastuchovii* Woronow is a native climbing species of Iranian forests, with its primary distribution concentrated in the Hyrcanian phytogeographical region of northern Iran. The species is widely distributed across the provinces of Gilan, Mazandaran, and Golestan, and it is also recorded in parts of the Arasbaran forests in northwestern Iran. This species typically establishes in humid and semi-humid broadleaf forests, particularly within the understory of temperate stands dominated by species such as *Fagus orientalis* Lipsky, *Quercus castaneifolia* C.A.Mey., *Acer velutinum* Boiss., and *Carpinus betulus* L. *Hedera pastuchovii* occurs across a broad elevational range, from lowland areas near sea level up to approximately 1800–2200 m above sea level. However, its highest abundance is generally observed at mid-elevations characterized by high humidity, organic-rich soils, and relatively dense canopy cover. The distribution and local dominance of this species are strongly influenced by environmental factors, including moisture availability, light conditions, soil characteristics, and forest stand structure. Under favorable ecological conditions, *H. pastuchovii* may become one of the dominant climbing elements within northern Iranian forest ecosystems (Sagheb-Talebi et al., 2014). Although *Hedera pastuchovii* Woronow is native and widespread in these forests, its distribution patterns in relation to site conditions, host tree identity, and soil properties are still insufficiently quantified, particularly when assessed jointly with ecophysiological traits (e.g., leaf morphology) along environmental gradients. Elevational gradients provide powerful natural experiments for testing plant–soil–environment relationships because temperature, moisture regimes, and soil development often vary predictably across relatively short spatial distances (Frindte et al., 2019). Integrating elevation with measurements of soil physicochemical and biological properties can clarify whether the occurrence and performance of climbers are primarily driven by abiotic constraints, host-tree availability, or their interaction. Therefore, this study investigates the distribution of *Hedera pastuchovii* and its associations with environmental conditions, soil properties (physical, chemical, and biological), and host tree characteristics along an elevation gradient in the Hyrcanian forests (Lufur–Firozja). In addition, we evaluate variation in leaf morphological traits of *H. pastuchovii* across elevation to improve understanding of its ecological strategies and potential ecosystem-level implications.

In line with the objectives of the present study, three hypotheses were formulated. The first hypothesis (H1) posits that leaf morphological traits of *Hedera pastuchovii* vary significantly along the elevation gradient, reflecting adaptive responses to changing environmental conditions. The second hypothesis (H2) suggests that the presence of *H. pastuchovii* is associated with reduced soil nutrient availability and enhanced soil microbial activity in host tree stands. The third hypothesis (H3) proposes that the distribution and infestation intensity of *H. pastuchovii* are strongly influenced by host tree species and site characteristics, with lower infestation rates on *Carpinus betulus* L. and higher dominance at mid-elevations, north-facing slopes, rough-barked trees, and larger-diameter hosts within the Hyrcanian forests.

2. Materials and Methods

2.1. Study area

The study area, locally known as the Lufur and Firozja forests, is located within the Central Alborz section of the Hyrcanian forest belt in northern Iran. The area falls under the administrative jurisdiction of the Natural Resources Offices of Savadkuh-e Shomali and Babol counties and is situated approximately 45 km southeast of Babol city. Geographically, the study site lies between 36°11'53" to 36°14'54" N latitude and 52°39'33" to 52°47'32" E longitude, covering an elevational range from 200 to 2500 m above sea level. This broad altitudinal gradient encompasses diverse topographic conditions, including variations in slope, aspect, and microclimate. The region is characterized by a humid temperate climate typical of the Hyrcanian forests, with relatively high annual precipitation and moderate temperatures. Environmental conditions vary markedly along the elevation gradient, creating distinct ecological zones that support diverse forest communities. structural modifications. The prevailing stands are primarily characterized by *Carpinus betulus*–*Parrotia persica* and *Parrotia persica*. –*Carpinus betulus* mixtures, accompanied by scattered individuals of *Alnus subcordata* C.A.Mey., *Acer velutinum* Boiss., *Quercus castaneifolia* C.A.Mey., *Parrotia persica* (DC.) C.A.Mey., and *Gleditsia caspica* Desf., with occasional occurrences of other broadleaf species. Overall, these stands exhibit moderate to low structural quality and reduced vitality, reflecting the legacy of past disturbances. Notably, the density and frequency of tree species hosting *Hedera pastuchovii* were considerable across the study sites, indicating substantial host availability within the altered forest structure.

2.2. Sampling method

The dominant forest type in the study area has largely been altered due to past disturbance factors and is now mainly characterized by hornbeam-dominated (*Carpinus betulus* L.) to persimmon–hornbeam (*Diospyros*–*Carpinus*) stands, accompanied by scattered individuals of alder (*Alnus subcordata* C.A.Mey.), poplar (*Populus caspica* Bornm.), Chestnut-leaved oak (*Quercus castaneifolia* C.A.Mey.), Persian ironwood (*Parrotia persica* (DC.) C.A.Mey.), maple (*Acer velutinum* Boiss.), and rarely other species. Overall, the forest stands were in relatively poor quantitative and qualitative condition. However, the density and abundance of tree species hosting *Hedera pastuchovii* were considerable. To examine the effects of slope, elevation changes, and the open-space influence of the existing access road within the study area, sampling was initiated at 300 m above sea level and extended up to 900 m, which represented the upper elevational limit of *Hedera pastuchovii* distribution (i.e., 300, 450, 600, 750, and 900 m a.s.l.). At each 100-m elevational interval, three sample plots were established on both sides of the road (the first plot at the roadside edge, the second 100 m from the first plot, and the third 100 m from the second plot), resulting in a total of six plots per 100-m elevational band. Square plots with dimensions of 20 × 20 m were used.

For the measurement of leaf, stomatal and soil variables at elevations of 300, 450, 600, 750, and 900 m a.s.l., three 1-ha plots (100 × 100 m) were selected. These plots included both *Hedera pastuchovii*-infested and non-infested areas, with inter-plot distances of approximately 300–400 m to ensure sample independence. Geological, physiographic, and climatic conditions were considered comparable across all sampling locations to control for environmental variation. Soil and litter samples were collected from the four corners of each plot using a 30 × 30 cm quadrat at a depth of 0–20 cm. A portion of the soil samples was air-dried for physicochemical analyses, while the remaining samples were stored at approximately 4 °C to preserve biological properties for microbiological assessments. This sampling design enabled a detailed evaluation of the effects of *Hedera pastuchovii* on soil and organic layer properties along an elevational gradient. Additionally, leaf morphological traits were assessed using samples collected from both infested and uninfested trees of comparable conditions (Fig. 1).

2.3. Laboratory analyses and calculations

Air-dried soil samples, consisting of broken aggregates, were processed through a 2 mm sieve. Prior to air drying, the soil samples were subjected to overnight drying at 105°C to evaluate the moisture content using the gravimetric method. The hydrometer method was utilized to determine soil texture, as outlined by Bouyoucos in 1962. Soil pH and electrical conductivity (EC) were assessed in a soil-to-water solution at a ratio of 1:2.5 (v/v) with the help of an Orion Ionalyzer Series 901 pH meter and an Orion Ionalyzer Series 901 EC meter, respectively. The Walkley-Black method was employed to ascertain the soil organic carbon content, as referenced by Allison in 1975, while total nitrogen was quantified using a semi-MicroKjeldahl technique, following the work of Bremner and Mulvaney (1982). Soil organic carbon (SOC) was calculated using the Walkley-Black method (Allison, 1975), and the organic matter (OM) content was derived using the formula ($OM \% = Organic\ C \% \times 1.724$) proposed by Ezeigbo et al. in 2013. The available phosphorus P was evaluated using the Olsen method, as described by Homer and Pratt in 1961, while the quantities of K and Mg were extracted at pH 9 with ammonium acetate, adhering to the procedure established by Bower et al., (1952). Basal respiration (BR) was quantified by measuring CO₂ release from soil samples over a three-day incubation period at 25°C (Alef, 1995). Substrate-induced respiration (SIR) was evaluated by combining the soil samples with 1% (w/w) glucose, and the rate of CO₂ production was also measured after three days of incubation (Anderson and Domsch, 1990). The fumigation-extraction technique was employed to assess the content of soil microbial carbon and nitrogen (MBC and MBN) (Brookes et al., 1985). The amount of microbial biomass phosphorus (MBP) was assessed by calculating the difference in extractable inorganic phosphorus between fumigated and non-fumigated soil (Brookes et al., 1982). The soil metabolic quotient (qCO₂) (BR/MBC), microbial ratio (MBC/C), and carbon availability index (BR/SIR) were derived from organic C, BR, SIR, and MBC data (Insam and Domsch, 1988; Anderson and Domsch, 1990; Cheng et al., 1996). Soil enzyme activity (i.e., urease, acid phosphatase, arylsulphatase, and invertase) was measured using the standard methods outlined by Schinner and Von Mersi (1990). To determine leaf area, five fully developed leaves were randomly chosen from each sample, and their surface area was measured with a leaf area meter. Stomatal characteristics, such as stomatal density, length, width, and area, were assessed using a light microscope at 400× magnification. Measurements were taken on prepared epidermal impressions, and mean values were calculated for each sample.

2.4. Statistical analysis

The normality of the data was assessed through the Kolmogorov-Smirnov test (p-value > 0.05) and the Levine test for variance homogeneity. Differences across elevational classes were evaluated using one-way analysis of variance (ANOVA). When significant treatment effects were identified, mean comparisons were conducted using Tukey's honestly significant difference test. Furthermore, the relationship between host tree species and the infestation rate of *Hedera pastuchovii* was analyzed using the chi-square (χ^2) test of independence. In addition, principal component analysis (PCA) was applied to soil data to identify patterns of significant change under varying pollution conditions by creating a correlation matrix in the PC-ORD software.

3. Results

3.1. Frequency and incidence of *Hedera pastuchovii* infestation

The results of infestation frequency and percentage analysis revealed considerable variation in *Hedera pastuchovii* infestation among host tree species. The highest infestation rate was recorded in *Diospyros lotus*, *Acer velutinum* Boiss. followed by *Carpinus betulus* L., *Mespilus germanica* L., which showed comparatively high infestation levels. In *Carpinus betulus* L., an infestation rate of 36.36% was observed, indicating a moderate level of infestation relative to the other species. Despite having the highest number of sampled individuals (n = 63), *Diospyros lotus* L. had 36 infested individuals, corresponding to an infestation rate of 57.14%. In contrast, *Crataegus monogyna* Jacq., *Morus alba* L., and *Ulmus minor* Mill., showed no infestation, resulting in a recorded infestation rate of zero (Table 1). Chi-square analysis revealed a significant positive association between the presence of *Diospyros lotus* L. and infestation by *Hedera pastuchovii* ($\chi^2 = 0.23$). This indicates that infestation frequency increased with increasing abundance of *Diospyros lotus* L. Similarly, a significant positive association was observed between the presence of *Acer velutinum* Boiss. and *H. pastuchovii* infestation ($\chi^2 = 0.22$), suggesting higher infestation levels in stands with greater abundance of this species. In contrast, no significant association was detected between infestation by *H. pastuchovii* and the presence of *Gleditsia caspica* Desf., *Carpinus betulus* L., *Mespilus germanica* L., *Crataegus monogyna* Jacq., *Morus alba* L., and *Ulmus minor* Mill., *Diospyros lotus* L., and *Alnus subcordata* C.A.Mey. (Table 2).

Table 1
Number and percent of trees polluted in *Hedera pastuchovii*

Species	Trees abundance	Abundance of polluted trees	Percentage of polluted trees (%)
<i>Gleditsia caspica</i> Desf.	8	0	0
<i>Diospyros lotus</i> L.	63	36	57.14
<i>Acer velutinum</i> Boiss	5	5	100
<i>Carpinus betulus</i> L.	22	8	36.36
<i>Mespilus germanica</i> L.	3	2	66.66
<i>Crataegus monogyna</i> Jacq.	1	-	-
<i>Morus nigra</i> L.	1	-	-
<i>Ulmus minor</i> Mill.	1	-	-
<i>Alnus subcordata</i> C.A.Mey.	18	5	27.77

Table 2
Frequency distribution and correlation between tree species and the incidence of *Hedera pastuchovii*

Species	Trees abundance	Value	Chi-square coefficient	Phi coefficient
<i>Gleditsia caspica</i> Desf.	8	1.49	0.26	-
<i>Diospyros lotus</i> L.	63	7.02	0.00	0.23
<i>Acer velutinum</i> Boiss	5	6.23	0.01	0.22
<i>Carpinus betulus</i> L.	22	4.46	0.02	0.20
<i>Mespilus germanica</i> L.	3	0.07	0.045	0.20
<i>Crataegus monogyna</i> Jacq.	1	0.83	0.35	-
<i>Morus nigra</i> L.	1	0.83	0.35	-
<i>Ulmus minor</i> Mill.	1	0.83	0.35	-
<i>Alnus subcordata</i> C.A.Mey.	18	2.67	0.10	-

3.2. Leaf and Stomatal Properties

The results of the two-way analysis of variance revealed that elevational classes and the presence of *Hedera pastuchovii* had significant effects on petiole length, lamina length, maximum lamina width, leaf width at 10% of lamina length, leaf width at 90% of lamina length, and leaf area at the 1% probability level (Fig. 2). The mean comparison analysis indicated that petiole length and leaf width reached their highest values at the 450 m elevation class and their lowest values at the 300 m elevation class. The greatest lamina width, as well as leaf width at 10% and 90% of lamina length, were also recorded at the 450 m elevation class, after which these traits exhibited a decreasing trend with increasing elevation. The highest leaf area was likewise observed at the 450 m elevation class. The findings of the present study further demonstrated that the presence of *Hedera pastuchovii* resulted in reductions in petiole length, lamina length, maximum lamina width, leaf width at 10% of lamina length, leaf width at 90% of lamina length, and leaf area in infected trees compared with healthy trees (Fig. 2). The results of the two-way analysis of variance examining the effects of elevation above sea level and the presence of *Hedera pastuchovii* revealed that elevational classes and the presence of *Hedera pastuchovii* had significant effects on stomatal length, stomatal width, and stomatal density. The results of the mean comparison analysis indicated that the greatest stomatal length, width, and area were observed at the 750 and 900 m elevation classes. The highest stomatal density was also recorded at the 900 m elevation class. In general, stomatal density was greater at higher elevational classes than at lower ones, whereas a decline in stomatal density was observed at intermediate elevations (Fig. 3–6). The presence of *Hedera pastuchovii* led to reductions in stomatal length, width, area, and density in the host species, and these differences were statistically significant (Fig. 3).

3.3. Litter Layer Properties

The results demonstrated that elevational classes had a significant effect ($p < 0.05$) on all organic soil layer indices, including organic layer thickness, litter carbon, nitrogen, carbon-to-nitrogen ratio, phosphorus, potassium, calcium, and magnesium, indicating that elevation plays a substantial role in altering litter layer characteristics. Moreover, the presence of *Hedera pastuchovii* also exerted a significant influence on all of these indices. Overall, these findings suggest that both elevation and the presence of *Hedera pastuchovii* can substantially affect the characteristics of organic soil layer properties (Table 4 and Fig. 4). According to the results of the present study, the presence of *Hedera pastuchovii* led to a reduction in organic soil layer properties, including carbon, nitrogen, carbon-to-nitrogen ratio, phosphorus, calcium, and magnesium (Table 4 and Fig. 4).

Table 4

Two-way analysis of variance (ANOVA) of litter and soil physical and chemical (mean $\pm$ standard error; n = 20) properties in relation to forest sites (as control without *Hedera pastuchovii*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

Soil properties	Evaluation above sea level		Hedera effects		Hedera effects $\times$ Evaluation	
	<i>F test</i>	<i>p value</i>	<i>F test</i>	<i>p value</i>	<i>F test</i>	<i>p value</i>
Litter Thickness	100.77	0.000	21.375	0.000	0.275	0.636
Litter C	207.767	0.000	17.326	0.000	0.385	0.816
Litter N	165.617	0.000	14.174	0.000	1.612	0.216
Litter C/N ratio	67.124	0.000	12.644	0.000	1.247	0.137
Litter P	83.634	0.000	8.326	0.000	0.353	0.872
Litter K	68.547	0.000	13.647	0.000	3.589	0.086
Litter Ca	37.634	0.000	11.785	0.000	1.297	0.643
Litter Mg	64.865	0.000	14.693	0.000	2.578	0.335
Soil moisture	17.755	0.000	12.788	0.000	0.094	0.997
Temperature	12.788	0.000	1.360	0.457	0.236	0.994
Bulk density	2.689	0.059	0.044	0.865	0.009	1.000
Particle density	0.889	0.998	0.010	0.976	0.005	1.000
Porosity	7.367	0.000	1.082	0.466	0.029	1.000
Sand	4.528	0.000	0.240	0.578	0.026	1.000
Silt	2.834	0.041	0.092	0.965	0.068	0.999
Clay	15.316	0.000	0.026	0.975	0.079	0.998
EC	102.284	0.000	0.895	0.467	1.344	0.287
pH	105.174	0.000	6.277	0.000	0.376	0.887
Organic carbon OC	92.183	0.000	8.158	0.000	0.322	0.920
Nitrogen N	71.217	0.000	10.589	0.000	0.094	0.906
C/N ratio	10.358	0.000	14.028	0.000	0.267	0.859
Soil organic matter SOM (%)	67.924	0.000	8.690	0.000	0.067	0.994
Available P	102.672	0.000	21.531	0.000	0.297	0.877
Available K	42.374	0.000	8.949	0.000	0.665	0.625
Available Ca	202.427	0.000	10.245	0.000	0.738	0.976
Available Mg	71.754	0.000	11.333	0.000	0.613	0.656
Basal respiration or BR	58.623	0.000	29.567	0.000	0.577	0.899
Substrate induced respiration or SIR	10.921	0.000	12.368	0.000	0.468	0.535
Microbial Biomass C MBC	18.494	0.000	8.966	0.000	1.574	0.375
Microbial Biomass N MBN	22.584	0.000	8.368	0.000	0.965	0.747
Bold and italic values indicate significant statistical differences.						

Soil properties	Evaluation above sea level		Hedera effects		Hedera effects × Evaluation	
	<i>F test</i>	<i>p value</i>	<i>F test</i>	<i>p value</i>	<i>F test</i>	<i>p value</i>
Microbial Biomass P MBP	20.172	0.000	17.457	0.000	0.568	0.434
MBC/MBN	0.691	0.678	1.497	0.353	0.678	0.907
Soil metabolic quotient	1.390	0.249	0.580	0.398	2.864	0.907
Microbial ratio	12.558	0.000	10.960	0.000	1.578	0.195
Urease	60.236	0.000	71.580	0.000	4.644	0.000
Acid phosphatase	39.360	0.000	45.680	0.000	2.433	0.036
Arylsulfatase	101.870	0.000	49.579	0.000	5.345	0.000
Invertase	55.556	0.000	34.779	0.000	4.356	0.000
Bold and italic values indicate significant statistical differences.						

3.4. Soil Physical and Chemical Properties

Analysis of variance (ANOVA) demonstrated significant differences among elevational classes in soil physical, chemical, and biological properties (Table 4). Soil physical parameters, including silt, clay, sand content, and soil moisture, varied significantly across elevations. Similarly, chemical properties, such as EC, pH, organic carbon, organic matter, total nitrogen, C/N ratio, K, Ca, Mg, and available P showed significant elevational variation. In addition, both basal and substrate-induced soil respiration differed significantly among elevational classes. In studied plots with *H. pastuchovii*, silt content ranged from 40.66% at 300 m to 42% at 600 m, showing relatively minor variation along the elevational gradient. In contrast, in plots without *H. pastuchovii*, silt values increased from 38.80% at 300 m to 40.00% at 600 m and remained relatively high at higher elevations. At lower elevations (300 and 450 m), silt content was higher in plots with *H. pastuchovii* compared to plots without the species. Clay content in plots with *H. pastuchovii* varied between 15.32% (900 m) and 34% (600 m), with the highest value observed at 600 m. In plots without *H. pastuchovii*, clay content was higher at lower elevations, reaching 32.60% at 300 m and 35% at 600 m, and then decreased progressively toward higher elevations (12.33% at 900 m). At 300 and 600 m, clay content was noticeably greater in plots without *H. pastuchovii*. Sand content increased with elevation in both treatments. In plots with *H. pastuchovii*, sand ranged from 28.88% at 300 m to 71% at 900 m. In plots without *H. pastuchovii*, sand content increased from 28.60% at 300 m to 76% at 900 m. The highest sand percentage was recorded at 900 m, particularly in plots without *H. pastuchovii*. Soil moisture showed clear elevational variation. In plots with *H. pastuchovii*, moisture increased from 23.23% at 300 m to 37.79% at 600 m, followed by a decline at higher elevations (16.28% at 900 m). In plots without *H. pastuchovii*, moisture decreased gradually with elevation, from 23.21% at 300 m to 15.23% at 900 m. Across most elevations, soil moisture tended to be higher in plots with *H. pastuchovii*, particularly at mid-elevations (600 and 750 m). The analysis of variance results indicated significant statistical differences in soil chemical properties, including electrical conductivity, pH, carbon, organic matter, nitrogen, carbon-to-nitrogen ratio, potassium, calcium, magnesium, and available phosphorus, across different elevation classes and *Hedera pastuchovii* presence conditions. The comparison of means (Tables 3 and 4) showed that soil chemical properties were significantly affected by elevation gradient, while the presence or absence of *Hedera pastuchovii* had comparatively limited effects. Soil organic matter and nitrogen increased from 300 to 600 m elevation, reaching their highest values at 600 m, and subsequently declined at higher elevations, with the lowest values recorded at 900 m. A similar trend was observed for exchangeable K and Ca, both peaking at 600 m. Exchangeable magnesium also exhibited its maximum concentration at 600 m and its minimum at 750 m. The C:N ratio reached its highest value at 750 m and its lowest at 600 m. In contrast, available P decreased with increasing elevation, with maximum values at 600 m and minimum values at 900 m. Overall, elevation gradient exerted a stronger influence on soil chemical properties than the presence of *Hedera pastuchovii* (Tables 3 and 4).

Table 3
Comparison of the mean $\pm$ standard error of the effect of altitude above sea level on *Hedera* density

Elevation above sea level (m)	F value	Sig	<i>Hedera</i> density
300 m	6.653	0.000	14.25 $\pm$ 1.24 b
450 m			66.66 $\pm$ 14.72 a
600 m			47.22 $\pm$ 13.36 a
750 m			50.65 $\pm$ 12.24 a
900 m			20.45 $\pm$ 5.56 ab
Different lower letters indicate significant ($p < 0.05$) differences inside the altitude above sea level on <i>Hedera</i> density			

3.5. Soil Microbial and Enzymic Properties

The analysis of variance (ANOVA) results concerning soil microbial and enzymatic properties indicated that all microbial characteristics, with the exception of the metabolic quotient, the ratio of basal respiration to substrate-induced respiration, the ratio of microbial biomass carbon to microbial biomass nitrogen, the ratio of microbial biomass carbon to microbial biomass phosphorus, and the ratio of microbial biomass nitrogen to microbial biomass phosphorus, exhibited significant variations in relation to elevation above sea level and the presence of *Hedera pastuchovii*. Moreover, the interaction between elevation above sea level and the presence of *Hedera pastuchovii* did not have a statistically significant effect on any of the soil microbial or enzymatic properties. (Table 4). The results of the mean comparison analysis indicated that the highest basal respiration was observed at the 450 and 600 m elevation classes in plots lacking *Hedera pastuchovii*, whereas the lowest basal respiration was recorded at the 900 m elevation class in plots containing *Hedera pastuchovii*. This difference was statistically significant. Likewise, the highest substrate-induced respiration was detected at the 600 m elevation class in plots without *Hedera pastuchovii*, while the lowest substrate-induced respiration occurred at the 900 m elevation class in plots with *Hedera pastuchovii*. Regarding microbial biomass carbon, nitrogen, and phosphorus, the greatest values were found at the 450 and 600 m elevation classes in plots lacking *Hedera pastuchovii*, whereas the lowest values were associated with the 900 m elevation class in plots containing *Hedera pastuchovii*. The differences noted were also statistically significant. Conversely, the metabolic quotient, which is the ratio of basal respiration to substrate-induced respiration, along with the ratios of microbial biomass carbon to microbial biomass nitrogen, microbial biomass carbon to microbial biomass phosphorus, microbial biomass nitrogen to microbial biomass phosphorus, and the microbial quotient of carbon, did not show statistically significant differences. Additionally, the results of this study concerning soil enzymatic activity indicated that the highest levels of urease, acid phosphatase, arylsulfatase, and invertase enzymes were recorded at the 450 and 600 m elevation classes in plots devoid of *Hedera pastuchovii*. Conversely, the lowest soil enzymatic activities were recorded at the 900 m elevational gradient in plots containing *Hedera pastuchovii*, with these differences being statistically significant (Tables 4 and 5).

Table 5

Litter and soil physical, chemical and biological (mean $\pm$ standard error; n = 20) properties in relation to forest sites (as control without *Hedera pastuchovii*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

Soil properties	Studied sites with soil sampling location in different elevation									
	300 m		450 m		600 m		750 mm		900 m	
Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	
Soil moisture (%)	53.64 $\pm$ 3.62a	47.43 $\pm$ 3.35 b	50.76 $\pm$ 3.67 a	45.43 $\pm$ 3.65 b	48.64 $\pm$ 3.76 b	44.56 $\pm$ 3.45 c	45.66 $\pm$ 3.45 c	38.35 $\pm$ 3.46 cd	32.78 $\pm$ 3.33 d	29.35 $\pm$ 3.23 e
Temperature (%)	34.35 $\pm$ 3.57a	33.34 $\pm$ 3.23ab	32.35 $\pm$ 2.36a	31.86 $\pm$ 3.57b	28.46 $\pm$ 3.44b	26.75 $\pm$ 3.47c	27.37 $\pm$ 3.75c	25.34 $\pm$ 3.22d	24.57 $\pm$ 3.24d	23.65 $\pm$ 3.43e
Bulk density (g cm ⁻³)	1.54 $\pm$ 0.05a	1.58 $\pm$ 0.04a	1.53 $\pm$ 0.06a	1.52 $\pm$ 0.05a	1.40 $\pm$ 0.06ab	1.41 $\pm$ 0.04ab	1.38 $\pm$ 0.04b	1.43 $\pm$ 0.03b	1.49 $\pm$ 0.05a	1.51 $\pm$ 0.04a
Particle density (g cm ⁻³)	2.45 $\pm$ 0.03	2.43 $\pm$ 0.04	2.42 $\pm$ 0.05	2.44 $\pm$ 0.04	2.45 $\pm$ 0.06	2.46 $\pm$ 0.06	2.43 $\pm$ 0.05	2.41 $\pm$ 0.04	2.44 $\pm$ 0.06	2.43 $\pm$ 0.04
Porosity (%)	36.76 $\pm$ 3.56b	34.56 $\pm$ 3.46b	40.73 $\pm$ 3.44b	37.57 $\pm$ 3.55b	47.34 $\pm$ 3.24a	45.33 $\pm$ 3.55a	45.89 $\pm$ 3.65a	42.35 $\pm$ 3.26a	38.86 $\pm$ 3.79b	36.78 $\pm$ 3.12b
Sand (%)	39.90 $\pm$ 3.44ab	37.45 $\pm$ 4.53b	31.43 $\pm$ 2.56c	34.25 $\pm$ 2.48c	29.01 $\pm$ 2.65c	31.29 $\pm$ 2.48c	34.24 $\pm$ 3.34b	35.24 $\pm$ 3.58b	43.43 $\pm$ 2.56a	44.01 $\pm$ 2.54a
Silt (%)	27.23 $\pm$ 3.32b	29.45 $\pm$ 3.23b	35.40 $\pm$ 3.46a	33.22 $\pm$ 3.22a	37.02 $\pm$ 3.43a	34.41 $\pm$ 3.46a	32.13 $\pm$ 3.32a	33.13 $\pm$ 3.24a	27.30 $\pm$ 3.23b	26.01 $\pm$ 2.35b
Clay (%)	32.87 $\pm$ 3.47a	33.10 $\pm$ 2.36a	33.17 $\pm$ 3.46a	32.53 $\pm$ 3.36a	34.03 $\pm$ 3.87a	34.30 $\pm$ 3.49a	33.63 $\pm$ 3.27a	31.63 $\pm$ 3.44a	29.27 $\pm$ 3.21b	30.03 $\pm$ 3.32b
EC (dS m ⁻¹)	256.66 $\pm$ 5.8b	223.89 $\pm$ 9.89a	335.01 $\pm$ 5.46a	225.23 $\pm$ 4.76a	220.63 $\pm$ 5.3ab	215.62 $\pm$ 5.76ab	205.32 $\pm$ 5.32b	201.35 $\pm$ 5.25b	190.07 $\pm$ 6.75c	118.46 $\pm$ 4.22c
pH (1:2.5 H ₂ O)	7.76 $\pm$ 0.01 a	7.11 $\pm$ 0.06 b	7.32 $\pm$ 0.03 a	6.20 $\pm$ 0.08 c	7.24 $\pm$ 0.02 a	6.94 $\pm$ 0.01 c	7.02 $\pm$ 0.01 ab	6.83 $\pm$ 0.09 c	5.89 $\pm$ 0.06 d	5.35 $\pm$ 0.05 e
Carbon (%)	4.56 $\pm$ 0.28b	4.11 $\pm$ 0.43a	4.76 $\pm$ 0.46a	4.55 $\pm$ 0.43b	4.89 $\pm$ 0.35a	4.43 $\pm$ 0.43b	3.92 $\pm$ 0.35c	3.78 $\pm$ 0.56c	3.66 $\pm$ 0.47c	3.98 $\pm$ 0.35c
Nitrogen (%)	0.49 $\pm$ 0.03b	0.42 $\pm$ 0.04c	0.44 $\pm$ 0.05c	0.39 $\pm$ 0.03d	0.57 $\pm$ 0.04a	0.55 $\pm$ 0.06ab	0.41 $\pm$ 0.05b	0.37 $\pm$ 0.04d	0.35 $\pm$ 0.03d	0.3 $\pm$ 0.04e
C/N ratio	9.31 $\pm$ 0.91c	9.78 $\pm$ 0.13c	10.82 $\pm$ 0.16b	11.66 $\pm$ 0.22ab	8.57 $\pm$ 0.17d	8.05 $\pm$ 0.13d	9.56 $\pm$ 0.16c	10.21 $\pm$ 0.15b	10.16 $\pm$ 0.17b	13.26 $\pm$ 0.16a
SOM (%)	7.86 $\pm$ 0.11b	7.10 $\pm$ 0.12b	8.32 $\pm$ 0.15a	7.65 $\pm$ 0.14b	8.60 $\pm$ 0.15a	7.56 $\pm$ 0.13b	6.75 $\pm$ 0.16c	6.52 $\pm$ 0.16c	6.08 $\pm$ 0.15c	6.86 $\pm$ 0.13c
Available P (mg kg ⁻¹)	10.80 $\pm$ 0.35b	9.82 $\pm$ 0.46c	10.11 $\pm$ 0.34b	9.02 $\pm$ 0.43c	11.14 $\pm$ 0.12a	10.16 $\pm$ 0.23b	9.53 $\pm$ 0.13c	8.56 $\pm$ 0.13d	8.13 $\pm$ 0.15d	7.15 $\pm$ 0.12e
Different capital letters indicate significant (p < 0.05) differences among forest stand as control without <i>Hedera</i>) and forest under <i>Hedera pastuchovii</i> in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.										

Soil properties	Studied sites with soil sampling location in different elevation									
	300 m		450 m		600 m		750 mm		900 m	
Soil without <i>Hedera</i>	Soil under	Soil without	Soil under	Soil without	Soil under	Soil without	Soil under	Soil without	Soil under	
	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	<i>Hedera</i>	
Available K (mg kg ⁻¹)	40.66 ± 1.33a	32.33 ± 1.66c	32.66 ± 2.40c	28.33 ± 2.35d	44.66 ± 3.26a	38.04 ± 3.21b	34.33 ± 2.22c	28.33 ± 2.35d	13.33 ± 1.45e	10.66 ± 0.88f
Available Ca (mg kg ⁻¹)	566.66 ± 11.66b	490.78 ± 12.12c	562.60 ± 12.41b	482.53 ± 12.7c	681.7 ± 10.43a	580.7 ± 12.85b	573.57 ± 8.96b	490.50 ± 9.06c	241.36 ± 17.2d	210.6 ± 16.34e
Available Mg (mg kg ⁻¹)	86.90 ± 6.92b	70.33 ± 7.04c	104.23 ± 5.66a	90.87 ± 6.23b	117.17 ± 4.35a	95.56 ± 3.25b	60.33 ± 3.26d	55.33 ± 2.16e	73.92 ± 3.46c	60.33 ± 2.35e
Basal respiration (mg CO ₂ g ⁻¹ day ⁻¹)	0.45 ± 0.01c	0.36 ± 0.03d	0.53 ± 0.04b	0.45 ± 0.03c	0.63 ± 0.02a	0.52 ± 0.04b	0.47 ± 0.05c	0.37 ± 0.06d	0.25 ± 0.04e	0.19 ± 0.02f
Substrate induced respiration	1.16 ± 0.12c	1.11 ± 0.14d	1.54 ± 0.13b	1.22 ± 0.11c	1.63 ± 0.12a	1.30 ± 0.11c	1.25 ± 0.12c	1.08 ± 0.10d	0.97 ± 0.08e	0.88 ± 0.06f
(mg CO ₂ g ⁻¹ day ⁻¹)										
Microbial Biomass (mg kg ⁻¹)	447.25 ± 76.2b	340.33 ± 52.2c	600.46 ± 50.4a	520.25 ± 44.5ab	638.67 ± 65.5a	569.25 ± 54.5ab	448.58 ± 67.7b	356.33 ± 34.5c	330.33 ± 43.5c	308.83 ± 32.5d
Microbial Biomass (mg kg ⁻¹)	49.12 ± 3.44	39.98 ± 3.24	55.34 ± 3.46	44.42 ± 3.26	60.19 ± 3.46	48.16 ± 3.44	47.54 ± 3.57	37.98 ± 3.24	37.58 ± 3.67	22.41 ± 3.24
Microbial Biomass (mg kg ⁻¹)	60.75 ± 6.54	40.55 ± 6.46	65.58 ± 5.47	55.91 ± 4.68	72.50 ± 5.78	60.41 ± 6.46	58.25 ± 4.46	37.91 ± 3.45	37.58 ± 3.46	32.41 ± 3.56
MBC/MBN	9.16 ± 3.17	8.71 ± 1.02	10.94 ± 2.36	11.90 ± 1.24	10.63 ± 1.33	11.85 ± 1.35	9.59 ± 2.35	9.40 ± 1.45	10.62 ± 2.35	13.15 ± 2.35
Soil metabolic quotient	1.55 ± 0.23	1.17 ± 0.22	1.59 ± 0.21	1.20 ± 0.12	1.17 ± 0.14	1.23 ± 0.15	1.62 ± 0.13	1.19 ± 0.21	1.28 ± 0.14	1.06 ± 0.11
Microbial ratio (MBC/Corg)	98.02 ± 16.44b	71.44 ± 6.78c	182.66 ± 12.35a	114.25 ± 10.44ab	182.67 ± 14.34a	115.41 ± 11.35ab	114.28 ± 15.46b	75.76 ± 6.78c	70.81 ± 6.54c	61.83 ± 5.46d
Urease (µg NH ₄ ⁺ -N g ⁻¹ 2 h ⁻¹)	24.21 ± 1.17a	20.61 ± 2.13b	25.20 ± 1.55a	19.84 ± 1.23b	28.15 ± 1.35a	22.67 ± 2.23b	21.70 ± 2.56b	16.74 ± 1.26c	16.81 ± 2.21c	13.10 ± 2.15d
Acid phosphatase (µg PNP g ⁻¹ h ⁻¹)	380.2 ± 12.34b	305.3 ± 13.25c	445.27 ± 12.34a	335.91 ± 11.23b	487.66 ± 10.34a	375.92 ± 11.23b	360.12 ± 12.34b	310.68 ± 11.24c	330.66 ± 11.65c	270.91 ± 10.45d
Different capital letters indicate significant (p < 0.05) differences among forest stand as control without <i>Hedera</i>) and forest under <i>Hedera pastuchovii</i> in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.										

Soil properties	Studied sites with soil sampling location in different elevation									
	300 m		450 m		600 m		750 mm		900 m	
Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	Soil without <i>Hedera</i>	Soil under <i>Hedera</i>	
Arylsulfatase ($\mu\text{g PNP g}^{-1} \text{ h}^{-1}$)	210.58 $\pm$ 23.35b	176.08 $\pm$ 12.44c	240.83 $\pm$ 22.35ab	209.65 $\pm$ 23.46b	274.56 $\pm$ 21.25a	217.45 $\pm$ 20.21b	215.83 $\pm$ 21.45b	170.56 $\pm$ 15.34c	152.83 $\pm$ 16.47d	129.77 $\pm$ 16.46e
Invertase ($\mu\text{g Glucose g}^{-1} \text{ 3 h}^{-1}$)	260.56 $\pm$ 22.36b	225.83 $\pm$ 25.83c	302.67 $\pm$ 10.94a	276.92 $\pm$ 5.34b	312.5 $\pm$ 6.36a	288.67 $\pm$ 7.46b	255.08 $\pm$ 7.43b	215.09 $\pm$ 8.35c	205.08 $\pm$ 6.53d	178.46 $\pm$ 7.45e

Different capital letters indicate significant ($p < 0.05$) differences among forest stand as control without *Hedera*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

3.6. Relationship Between Altitudinal Gradient and Leaf, Stomatal, and Soil Characteristics in Hedera

Principal component analysis (PCA) was performed using leaf traits, stomatal characteristics, litter layer attributes, and soil physicochemical and microbial properties to evaluate the effects of elevation and the presence of *Hedera pastuchovii* across the studied elevational gradient. The first two principal components (64.96% and 17.54%) explained a major proportion of the total variance, representing the dominant environmental and biological gradients associated with elevation and *Hedera pastuchovii* infestation (Figs. 5 and 6). The PCA ordination clearly separated lower and intermediate elevation classes from higher elevations, indicating substantial variation in vegetation and soil characteristics along the elevational gradient. Intermediate elevations, particularly 450 and 600 m, were associated with higher values of leaf morphological traits, soil organic matter, microbial biomass, basal respiration, substrate-induced respiration, and soil enzymatic activities. In contrast, higher elevations, especially the 900 m elevation class, were characterized by lower soil nutrient availability, reduced microbial and enzymatic activities, and smaller leaf and stomatal traits. Plots without *Hedera pastuchovii* were generally associated with greater values of leaf area, petiole length, stomatal density, soil organic carbon, nitrogen, exchangeable nutrients, microbial biomass carbon, nitrogen and phosphorus, as well as higher urease, acid phosphatase, arylsulfatase, and invertase activities. Conversely, plots containing *Hedera pastuchovii* were positioned separately in the ordination space and were associated with reduced leaf morphological traits, lower stomatal properties, and diminished litter and soil quality indices. These findings indicate that the presence of *Hedera pastuchovii* substantially altered both plant functional traits and soil ecological processes. Among the elevational classes, the 450 and 600 m elevations exhibited the highest biological activity and nutrient availability, suggesting that these elevations provide more favorable environmental conditions for plant growth and soil microbial functioning. In contrast, the 900 m elevation class showed the lowest values for most soil biological and enzymatic properties, reflecting harsher environmental conditions and reduced ecosystem activity at higher elevations. Overall, the multivariate analyses demonstrated that elevation gradient exerted a stronger influence on soil physicochemical and biological properties than the presence of *Hedera pastuchovii*, although infestation by this species significantly contributed to reductions in vegetation performance and soil ecological quality.

4. Discussion

4.1. Frequency and incidence of Hedera pastuchovii infestation

The level of infestation by *Hedera pastuchovii* showed considerable variation among tree species, indicating that its distribution is strongly associated with host-specific traits. The highest infestation rate was observed in *Acer velutinum* Boiss., suggesting high suitability of this genus as a favorable host for the establishment of *Hedera pastuchovii*. This suitability is likely related to

traits such as relatively soft bark, higher stem surface moisture, and favorable conditions for the adhesion and establishment of adventitious roots. In contrast, *Diospyros lotus* L. exhibited relatively low infestation levels despite its abundance, indicating a degree of resistance to *Hedera pastuchovii* establishment. This resistance may be attributed to rough bark texture, periodic bark shedding, and/or the presence of inhibitory chemical compounds in bark tissues that limit root attachment. *Alnus subcordata* C.A.Mey. showed moderate infestation levels, which may be explained by differences in bark characteristics, vascular structure, and stem-associated microclimatic conditions. Overall, these patterns indicate that the establishment of *Hedera pastuchovii* is not random but reflects a clear selective host preference mechanism (Castagneri et al., 2013). The absence of infestation in species such as *Crataegus*, *Morus*, and *Zelkova*, suggests that these taxa are either structurally unsuitable for attachment or occur under environmental conditions unfavorable for establishment. These findings support the view that the distribution of *Hedera pastuchovii* is primarily governed by host biological and ecological traits and is restricted to specific tree species (Press & Phoenix, 2005; Blinkova et al., 2025). Correlation analysis between host presence and infestation intensity revealed a positive and significant relationship for *Diospyros lotus* L., *Acer velutinum* Boiss., and *Alnus subcordata* C.A.Mey., indicating their role as suitable hosts for *Hedera pastuchovii* establishment. These results suggest that the distribution of *Hedera pastuchovii* in the study area is strongly influenced by forest species composition, with *Diospyros lotus* L. and *Acer velutinum* Boiss. playing key roles in facilitating its establishment. This pattern further confirms that *Hedera pastuchovii* does not exhibit a random distribution but instead shows selective establishment on specific host species. Host selection in hemiparasitic plants is generally driven by traits such as xylem conductivity, bark structure, and local moisture conditions around the host stem (Zuber, 2004). The lack of significant correlation between infestation and species such as *Zelkova*, *Crataegus*, *Morus*, and other minor associated species indicates that these taxa are either physiologically or structurally unsuitable hosts or contribute minimally to the establishment process. This finding is consistent with previous studies demonstrating that the success of hemiparasitic plant establishment strongly depends on host traits, and that susceptibility varies substantially among species (Chaudron et al., 2021). From an ecophysiological perspective, species with higher hydraulic conductivity, thinner bark, and greater surface moisture provide more favorable conditions for haustorial penetration. Establishment of *Hedera pastuchovii* on susceptible hosts may lead to competition for water and nutrients, potentially reducing leaf water potential, stomatal conductance, and photosynthetic rates in host trees (Press & Phoenix, 2005). Overall, these findings highlight that both host identity and forest structure jointly determine the spatial pattern of *Hedera pastuchovii* occurrence, rather than random colonization or forest degradation alone.

4.2. Leaf and Stomatal Characteristics

Leaf, as the primary photosynthetic organ of plants, exhibits high plasticity and responds rapidly to environmental changes such as light availability and temperature fluctuations. Leaf morphological traits are strongly influenced by environmental variability, and such changes are generally interpreted as adaptive responses to ecological conditions. In this context, leaf functional traits can reflect specific adaptive strategies employed by plants under particular environmental constraints (Xing et al., 2023). Elevation above sea level has been shown to exert a substantial influence on leaf morphology and physiology within species. The results of the present study demonstrated that with increasing elevation, leaf lamina width, leaf width, and leaf area decreased significantly. Previous studies have reported that the morphology and physiology of species occurring at higher elevations differ markedly from those at lower elevations, and that traits such as leaf length, width, perimeter, and area generally decline with increasing altitude (Ouisse et al., 2020), which is consistent with the findings of the present study. It has also been suggested that part of the variation in leaf morphological traits is driven by differences in climatic and edaphic conditions across habitats, including mean annual temperature and humidity, length of dry season, soil fertility, as well as genetic variation among populations (Liu et al., 2020). The present study further revealed that the presence of *Hedera pastuchovii* leads to a reduction in leaf traits of the host species. Members of the genus *Hedera* are climbing plants that, through their growth and spread over host stems and canopies, can modify light availability, microclimatic conditions, and water–carbon resource dynamics, thereby indirectly inducing morphological and physiological responses in host leaves and stomata. By forming a dense canopy over host crowns, these plants reduce the amount of photosynthetically active radiation reaching the leaves, which typically results in morphological adjustments such as changes in specific leaf area and reductions in leaf thickness (Metcalf, 2005).

Stomata are one of the most important structures in vascular plants, playing a key role in gas exchange between the external environment and the mesophyll cells of leaves. They are responsible for regulating transpiration and carbon dioxide uptake during photosynthesis. The opening and closing of stomata directly influence the balance between water loss and biomass production in plants (Büssis et al., 2006). Even under conditions where soil moisture is not a limiting factor for plant growth, the regulation of water loss through excessive transpiration is particularly critical, especially in tall trees (Koch et al., 2004). Stomatal density varies among leaves, plants, and even within a single species, and is influenced by environmental factors such as atmospheric CO₂ concentration, air humidity, light intensity, and water availability in the root zone (Saeedi et al., 2015). Plants adjust stomatal density per unit leaf area under different site conditions to maintain a balance between carbon dioxide uptake and water loss (Körner et al., 1986). The results of the present study indicated that stomatal length and width increased with increasing elevation. The lowest stomatal area was observed at the 450 m elevation class. Stomatal density was higher at both low and high elevations compared with mid-elevation zones, where a reduction in stomatal density was recorded. Overall, increasing elevation generally leads to a reduction in atmospheric CO₂ concentration, and under lower CO₂ availability, stomatal density tends to increase as a compensatory response (Givnish, 1988). An increase in stomatal density with elevation has also been reported in species such as beech (*Fagus orientalis* Lipsky) (Saeedi et al., 2015) and lime (*Tilia begonifolia* Steven) (Yousefzadeh et al., 2010). Although an inverse relationship between stomatal density and stomatal size has been reported in some studies, the response of stomatal area to elevation remains inconsistent due to the combined influence of multiple environmental factors such as CO₂ concentration, temperature, light intensity, and humidity. Consequently, elevational effects may vary across different regions and ecological conditions (Woodward & Kelly, 1995). Some researchers have also reported a significant decrease in stomatal area with increasing elevation in Oriental beech (*Fagus orientalis* Lipsky) (Saeedi et al., 2015). The presence of *Hedera* can exert significant indirect effects on the stomatal characteristics of host plants through alterations in microclimatic conditions and resource availability rather than through direct physiological interaction with stomatal structures. By forming a dense canopy over host stems and crowns, *Hedera* reduces the amount of photosynthetically active radiation reaching host leaves and modifies the surrounding microenvironment, typically increasing humidity while reducing temperature fluctuations. These changes can influence stomatal development, as stomatal traits are highly sensitive to light intensity and vapor pressure deficit during leaf ontogeny. Under reduced light conditions, host plants often exhibit adjustments in carbon assimilation capacity, which may lead to modifications in stomatal density and size to optimize the balance between CO₂ uptake and water loss. In addition, the altered microclimate created by *Hedera* can affect transpiration demand, thereby influencing stomatal conductance and long-term stomatal patterning in newly developed leaves. Moreover, potential competition for water resources, particularly under dense infestations, may impose mild to moderate physiological stress on host trees. Such water-related constraints can further contribute to adjustments in stomatal behavior and structure, including reductions in stomatal size or alterations in stomatal density as part of an adaptive response to maintain hydraulic balance (Blinkova et al., 2024). Overall, the impact of *Hedera* on stomatal traits is best interpreted as an indirect consequence of its influence on host environmental conditions and physiological status. These combined effects highlight the role of climbing and hemiparasitic vegetation in shaping functional leaf traits of host trees, particularly through long-term modifications of microclimate and resource dynamics (Castagneri et al. 2013).

4.3. Litter layer properties

The results of this study indicated that the presence of *Hedera helix* can lead to a reduction in nutrient concentrations in the soil litter layer. One of the primary mechanisms underlying this pattern is related to the chemical composition of *Hedera* leaves, which are characterized by high lignin content and a high carbon-to-nitrogen (C/N) ratio. These traits generally result in slower decomposition rates and reduced nutrient release from organic matter, thereby limiting the short-term availability of key nutrients such as nitrogen and phosphorus to plants (Blinkova et al., 2024). In addition, the dense canopy formed by *Hedera* may modify soil microenvironmental conditions by reducing light penetration and oxygen availability at the soil surface. Such changes can suppress microbial activity, thereby constraining organic matter decomposition and nutrient mineralization processes (Shdaimah et al., 2023). Consequently, the overall cycling of nutrients within the litter layer becomes slower and less efficient. Although *Hedera* litter may decompose relatively faster in the presence of soil mesofauna, the high spatial dominance and coverage of this species can still reduce the overall contribution of microbial processes to nutrient cycling, ultimately leading to a net decline in soil nutrient availability (Roeder et al., 2022). Therefore, the observed reduction in litter nutrient content under *Hedera* influence is likely driven by a combination of litter chemical quality, alterations in microbial activity, and

physical effects of dense vegetation cover. These findings highlight the importance of managing dominant invasive or competitive species such as *Hedera* to maintain ecosystem functioning, nutrient cycling dynamics, and soil biodiversity. In mature forest ecosystems that rely heavily on rapid nutrient turnover, extensive expansion of *Hedera* may have long-term consequences for ecosystem processes and native plant diversity. Furthermore, the results demonstrated that the impact of *Hedera* on litter nutrient content varied along the elevational gradient. The highest nutrient concentrations were observed at elevations of 450 and 600 m, while lower values were recorded at both lower and higher elevations. This pattern may be attributed to elevation-related environmental variations, including temperature, moisture availability, solar radiation, and microbial activity. Mid-elevation zones typically provide more favorable conditions for microbial processes, which enhance decomposition rates and facilitate nutrient return to the soil system (Chen et al., 2026). Moreover, the interaction between elevation and *Hedera* presence suggests that the strength of its effect is not uniform across the landscape. In more favorable mid-elevation conditions, microbial activity may partially buffer the negative effects of *Hedera* litter quality, whereas in low- or high-elevation environments, harsher climatic conditions may amplify nutrient limitation by further suppressing decomposition processes. Overall, these results indicate that the influence of *Hedera helix* on litter nutrient dynamics is strongly context-dependent and modulated by elevation-driven environmental gradients.

4.4. Soil Physical and Chemical Properties

Soil texture components exert important physical effects on plant growth by either facilitating or restricting root development and by regulating water and oxygen availability. Clay is considered the most reactive mineral fraction of soil due to its high capacity for alkaline cation adsorption, thereby enhancing soil fertility and nutrient retention for plant uptake (Habibi Kilak et al., 2020). The results of the present study showed that soil clay content increased significantly with elevation up to 600 m, but declined at higher elevations, reaching its minimum at 900 m. Consistent with the present findings, Yang et al. (2008) reported that mid-elevations often provide favorable conditions for soil development and fine-particle accumulation, while increased erosion at higher elevations may limit clay retention. Therefore, the reduction in clay content at the highest elevation may indicate weakened soil-forming processes and enhanced downslope translocation of fine particles. Silt, as another fine soil fraction, plays an important role in improving soil structure and water-holding capacity; however, it is more susceptible to erosion than clay. The findings of this study demonstrated that soil silt content increased with elevation up to 600 m and then significantly decreased at higher elevations, with the lowest value recorded at 900 m. This result is consistent with the findings of Mishra and Francaviglia (2021), who attributed reduced silt content at higher elevations to intensified erosion and removal of fine particles. In the present study area, lower silt content at higher elevations may also reflect reduced soil stability and diminished water storage capacity. In contrast, soil sand content showed an increasing trend with elevation, reaching its highest value at 900 m. Increased sand content is generally associated with the selective removal of finer particles and the residual accumulation of coarser fractions. This finding agrees with the results reported by Samie et al. (2022), who demonstrated that reduced vegetation cover at higher elevations enhances surface erosion and consequently increases soil sand content. In the current study, the higher sand percentage at upper elevations may indicate poorer soil physical quality in terms of water and nutrient retention. Soil moisture is among the most important physical properties influencing biological activity and soil chemical processes, and its variation is strongly controlled by soil texture and organic matter content. The results revealed that soil moisture was highest at 600 m elevation and declined at higher elevations. Previous studies have shown that soils with higher organic carbon content and finer particles possess greater moisture retention capacity (Beiranvand et al., 2021). Moreover, soils with greater organic carbon storage generally exhibit lower bulk density, which further enhances their water-holding capacity (Wang et al., 2014). In the present study, the simultaneous occurrence of maximum clay content and soil moisture at 600 m suggests that finer soil texture played a key role in improving water retention at this elevation. Conversely, the decline in soil moisture at higher elevations may be attributed to lower clay and silt contents, higher sand content, and reduced organic matter, all of which decrease the soil's capacity to store water. Furthermore, the presence of the nurse species did not significantly affect soil physical properties.

Changes in elevation significantly affected soil chemical properties and nutrient dynamics. Soil electrical conductivity (EC) increased up to 600 m elevation and declined thereafter. The higher EC at mid-elevation coincided with greater clay content, suggesting enhanced cation retention and nutrient storage capacity. Similar reductions in EC at higher elevations have been attributed to increased leaching and erosion of base cations such as Ca and Mg under conditions of higher precipitation (Praeg

et al., 2020; Seyoum et al., 2020). Soil pH also varied significantly along the elevational gradient. Soil reaction remained nearly neutral up to 600 m but shifted toward alkaline conditions at 750 m, possibly due to erosion exposing CaCO_3 -rich subsurface horizons (Moghimian et al., 2019). However, at 900 m elevation, soil pH decreased to acidic levels. Previous studies similarly reported a negative relationship between elevation and soil pH, mainly as a consequence of increased rainfall, enhanced leaching of base cations, and greater H^+ activity at higher elevations (Wang et al., 2018; Zebire et al., 2019; Ratier Backes et al., 2021; Hailemariam et al., 2023). The highest soil organic carbon and organic matter contents were recorded at 450 and 600 m elevations. Favorable temperature and moisture conditions at these elevations likely promoted vegetation growth, litter accumulation, and organic matter inputs to soil (Khalilpour, 2013). Soil organic matter plays a critical role in nutrient supply, water retention, and soil permeability (Liu et al., 2020). In contrast, the lowest carbon and organic matter contents occurred at 900 m elevation, where lower temperatures and reduced vegetation productivity may limit litter production and decomposition processes (Hailemariam et al., 2023). Variations in microbial activity, litter quantity, root distribution, and soil texture along elevation gradients have also been identified as key drivers of soil organic matter dynamics (Tolessa and Senbeta, 2018). Furthermore, higher clay content can enhance carbon stabilization in soil (Saiz et al., 2012), which may explain the greater carbon accumulation observed at 600 m elevation. Nitrogen content followed a similar trend, with the highest values observed at 450 and 600 m and a significant decline at higher elevations. Greater nitrogen availability at lower elevations may be associated with higher litter inputs and denser vegetation cover. Previous studies demonstrated that reduced vegetation density at high elevations increases runoff and erosion, leading to lower soil carbon and nitrogen contents (Hou et al., 2019; Han et al., 2022). In addition, the soil C:N ratio increased significantly with elevation, indicating slower decomposition and mineralization rates under colder high-elevation conditions (Han et al., 2022). Exchangeable Ca, K, and Mg contents decreased with increasing elevation, likely due to greater precipitation and nutrient leaching at upper elevations (Sharma and Sharma, 2013). Similar declines in soil potassium and magnesium along elevational gradients have been reported previously (Karamian and Hosseini, 2016; Sapkota, 2017). Available phosphorus also reached its minimum at 900 m elevation, which may be related to increased leaching of soluble phosphorus compounds and reduced mineralization rates under colder conditions (Misaghi and Golchin, 2024). The presence of *Hedera pastuchovii* significantly influenced soil nutrient dynamics. Plots containing *Hedera* showed lower organic matter, nitrogen, and nutrient contents compared with plots without the species. Canopy coverage by *Hedera* likely reduced light availability and photosynthetic activity of host trees, thereby decreasing litter production and organic matter inputs to soil (Augusto et al., 2003). In addition, secondary compounds released during *Hedera* litter decomposition may suppress microbial activity and slow nutrient cycling processes (Berg and McClaugherty, 2020). Increased competition for water and nutrients between *Hedera* and host trees may further intensify nutrient limitations and alter decomposition dynamics (Yıldırım et al., 2025). Consequently, long-term establishment of *Hedera* may negatively affect soil fertility, nutrient balance, and forest ecosystem stability (Taylor et al., 2025).

4.5. Soil Microbial and Enzymic Properties

Soil microbial properties, including basal respiration, substrate-induced respiration, and microbial biomass, are widely used indicators of soil biological activity and ecosystem functioning. Microbial activity plays a key role in the decomposition of organic matter and nutrient cycling processes (Rasouli Sedeghiani et al., 2016). The results of the present study showed that microbial activity increased up to 450–600 m elevation and declined significantly at 900 m. Higher microbial activity at mid-elevations was likely associated with greater litter accumulation and higher carbon availability, which provided favorable conditions for microbial growth and metabolism (Kara and Bolat, 2007). In addition, suitable soil moisture and a balanced texture characterized by higher clay and silt contents at these elevations improved water retention and soil aeration, thereby enhancing microbial processes. In contrast, reduced vegetation density, lower litter input, decreased soil moisture, and lower temperatures at 900 m likely restricted microbial metabolism and reduced basal respiration (Feng et al., 2021). Increased sand content and lower clay percentages at higher elevations may also have reduced the soil's capacity to retain water and nutrients, further limiting microbial activity. Therefore, the observed pattern of basal respiration appears to reflect the combined influence of vegetation cover, soil organic matter, moisture availability, and soil texture along the elevational gradient (Chen et al., 2021; Zeng et al., 2022). Substrate-induced respiration, an important indicator of active microbial populations and biologically available carbon, followed a similar trend, increasing significantly up to 600 m and declining at higher elevations. Greater accumulation of fresh organic residues and root-derived carbon at mid-elevations likely provided more accessible substrates for heterotrophic microorganisms, thereby stimulating microbial respiration (Anderson and Domsch, 1978; Xue Sha et al.,

2011). Adequate soil moisture at these elevations may also have promoted microbial activity by facilitating organic matter dissolution and nutrient transport. Conversely, lower moisture content and higher sand percentage at upper elevations likely constrained microbial respiration (Feng et al., 2021). The quality and composition of soil organic matter also strongly influenced SIR patterns. Organic materials at mid-elevations were probably fresher and more decomposable, whereas lower temperatures at higher elevations may have promoted the accumulation of more recalcitrant organic compounds, resulting in lower microbial respiration rates (Pietikäinen et al., 2005). In addition, differences in microbial community composition along the elevational gradient may partly explain the observed variation, as microbial abundance and metabolic efficiency are often greater at intermediate elevations than at colder, high-elevation sites (Siles et al., 2016). Soil microbial biomass, a sensitive indicator of ecosystem management and soil quality, is strongly affected by vegetation cover and litter characteristics. Previous studies demonstrated that changes in vegetation structure and plant residue inputs can substantially alter microbial biomass and activity (Saviozzi et al., 2002; Bini et al., 2013). In the present study, the presence of *Hedera pastuchovii* may have contributed to reduced microbial biomass. Dense canopy cover formed by climbing species can modify litter accumulation patterns and alter microbial processes in surface soils. Although litter produced by these species enters the soil organic pool, increased competition for nutrients and shading effects on host vegetation may reduce microbial activity and disrupt nutrient cycling processes (Jiménez-Hernández et al., 2023). Soil organic matter, fertility, and microbial and enzymatic activities are recognized as major indicators of soil functional quality (Kooch et al., 2020). Cheng et al. (2013) reported that soil enzymatic activity is strongly influenced by vegetation type as well as soil pH, nitrogen, and phosphorus contents. Reduced activities of key soil enzymes, such as urease and phosphatase, may limit organic matter decomposition and nutrient recycling, thereby affecting soil fertility and ecosystem functioning (Nannipieri et al., 2012). Such combined effects may alter both soil physicochemical properties and biological processes, ultimately affecting host plant health and ecosystem stability. Overall, the findings of the present study demonstrated that infestation by *Hedera* significantly affected soil physical, chemical, microbial, and enzymatic properties. Soils without *Hedera* contained significantly higher levels of carbon, organic matter, nitrogen, calcium, potassium, and magnesium than soils under *Hedera* presence. Similar findings were reported by Weand and Green (2026), who observed significant differences in soil nutrients and seed germination between invaded and non-invaded sites. Shdaimah (2023) also reported that *Hedera* reduced the release rates of nitrogen, phosphorus, and magnesium in forest ecosystems. Furthermore, Metcalfe (2005) suggested that *Hedera* negatively affects soil health by reducing light penetration and soil oxygen availability, decreasing beneficial microbial diversity, lowering soil fertility, and suppressing plant growth. These observations are consistent with the results of the present study and highlight the potential ecological impacts of climbing species on forest soil functioning and ecosystem sustainability.

5. Limitations of the study and recommendations

Although this study provides valuable insights into the distribution of *Hedera pastuchovii* along an elevational gradient and its relationship with soil and host tree characteristics, several limitations should be acknowledged. First, the study was conducted within a specific geographic region of the Hyrcanian forests; therefore, caution should be exercised when generalizing the findings to other forest ecosystems with different climatic and structural conditions. Second, soil sampling was carried out during a single period, and seasonal variations in soil chemical and biological properties were not assessed. Since microbial activity and nutrient dynamics are strongly influenced by temporal fluctuations, multi-seasonal sampling would provide a more comprehensive understanding. Although correlations between *Hedera pastuchovii* presence and environmental variables were identified, the observational nature of the study limits the ability to fully disentangle causal relationships. Future controlled experiments could provide further insight into whether the observed soil variations are drivers or consequences of species establishment. Furthermore, physiological responses of host trees were evaluated using structural indicators; incorporating detailed physiological measurements such as photosynthetic rate, water potential, and nutrient allocation could provide deeper insight into host–ivy interactions. Future research should therefore (i) expand sampling across broader climatic and structural gradients, (ii) incorporate long-term and seasonal monitoring of soil and vegetation parameters, (iii) apply experimental removal or manipulation studies to assess causal mechanisms, and (iv) integrate eco-physiological measurements to better understand host tree responses. Such approaches would contribute to developing more effective management strategies for maintaining ecological balance in Hyrcanian forest ecosystems.

6. Conclusions

The present study demonstrated that both elevation gradients and the presence of *Hedera pastuchovii* significantly influence soil properties, leaf morphological traits, stomatal characteristics, and soil microbial and enzymatic activities in temperate forest ecosystems. Mid-elevation zones (particularly 450–600 m a.s.l.) provided more favorable conditions for soil biological activity and nutrient availability, whereas higher elevations were generally associated with reduced microbial and enzymatic functioning. The presence of *Hedera pastuchovii* consistently led to significant reductions in soil organic layer nutrients, microbial biomass, enzymatic activities, and key leaf functional traits of host trees. These effects are mainly attributed to changes in microclimatic conditions, including reduced light availability, altered temperature and humidity regimes, and modifications in litter quality and decomposition processes. In addition, infestation by *H. pastuchovii* altered stomatal characteristics and reduced leaf size and area, indicating strong morphological and physiological responses of host trees to infestation pressure. Species-specific variation in infestation intensity further indicated that *H. pastuchovii* exhibits selective host preference, with certain tree species providing more suitable structural and physiological conditions for establishment. This non-random distribution highlights the importance of host identity and forest composition in determining infestation patterns. In line with the objectives of the study, three hypotheses were tested. The first hypothesis (H1), stating that leaf morphological traits of *Hedera pastuchovii* vary significantly along the elevation gradient as an adaptive response to environmental variation, was supported. The second hypothesis (H2), proposing that the presence of *H. pastuchovii* is associated with reduced soil nutrient availability and changes in soil microbial and enzymatic activity, was also supported. The third hypothesis (H3), suggesting that the distribution and infestation intensity of *H. pastuchovii* are strongly influenced by host tree species and site characteristics with lower infestation in *Diospyros lotus* L. and higher occurrence at mid-elevations, north-facing slopes, rough-barked trees, and larger-diameter hosts was likewise supported. Overall, *Hedera pastuchovii* acts as a key ecological modifier in these forest ecosystems, influencing nutrient cycling, soil biological processes, and host plant functional traits. These findings highlight the importance of considering both environmental gradients and host-specific factors in understanding its ecological impacts and in developing effective forest management strategies.

Abbreviations

C: Carbon; N: Nitrogen; OM: Organic Matter; Ca: Calcium; K: Potassium; P: Phosphorus; Mg: Magnesium; Mois: Moisture; BR: Basal Respiration; SIR: Substrate-Induced Respiration; BD: Bulk Density; Pd: Particle Density; Poro: Porosity; Acidphos: Acid Phosphatase; Arylsul: Arylsulfatase; MBC: Microbial Biomass Carbon; MBN: Microbial Biomass Nitrogen; MBP: Microbial Biomass Phosphorus; MBC/MBN: Microbial Biomass Carbon / Microbial Biomass Nitrogen; qCo2: Metabolic Quotient; LTi: Litter Thickness; OCL: Organic Carbon Litter; NL: Nitrogen Litter; PL: Phosphorus Litter; KL: Potassium Litter; CaL: Calcium Litter; MgL: Magnesium Litter; PLL: petiole length leaf; LbL: leaf blade length; MLBW: maximum leaf blade width; LWOTL: leaf width at one-tenth of its length; LWNTL: leaf width at nine-tenths of its length; LA: Leaf area; SPL: stomatal pore length; SPW: stomatal pore width; SPA: stomatal pore area; SD: stomatal density; PCA: Principal Component Analysis.

Declarations

Acknowledgment

The authors greatly acknowledge the financial contribution to the study of Tarbiat Modares University.

Credit author statement: Naser Ebrahimi Malekshah: Sampling and laboratory analysis, Writing-original draft; Seyed Mohsen Hosseini: Statistics, Writing-original draft, Supervision; Yahya Kooch: Statistics; Writing-original draft; Omid Esameilzadeh: Writing-revision and editing.

Conflict of Interests: The authors declare that they have no conflict of interest.

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Figures

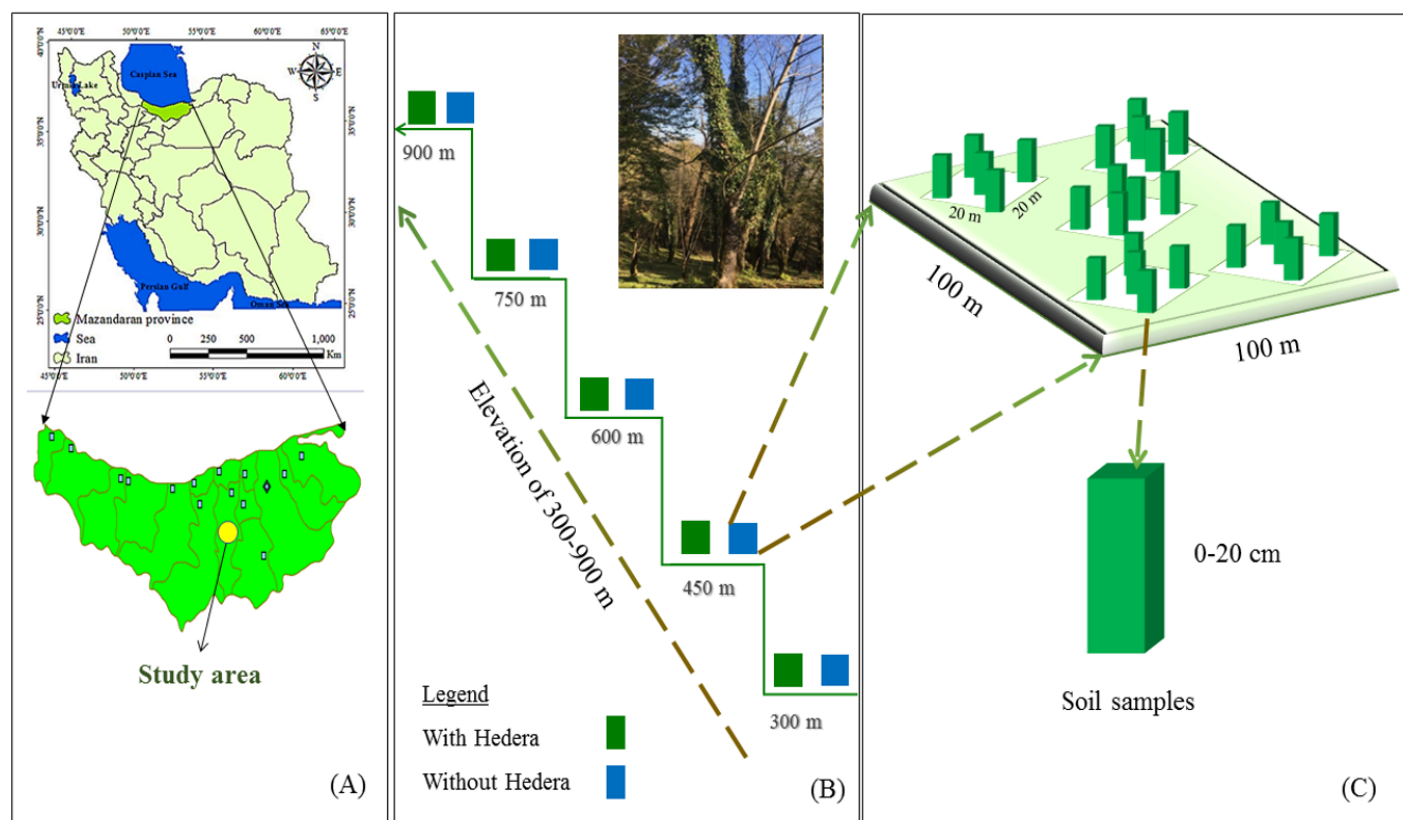


Figure 1

Geographical location of the study area in the north of Iran, Mazandaran province (A). Schematic representation of the spatially separated sites, and experimental design adopted for soil sampling in the study sites (B and C). Figures not to scale.

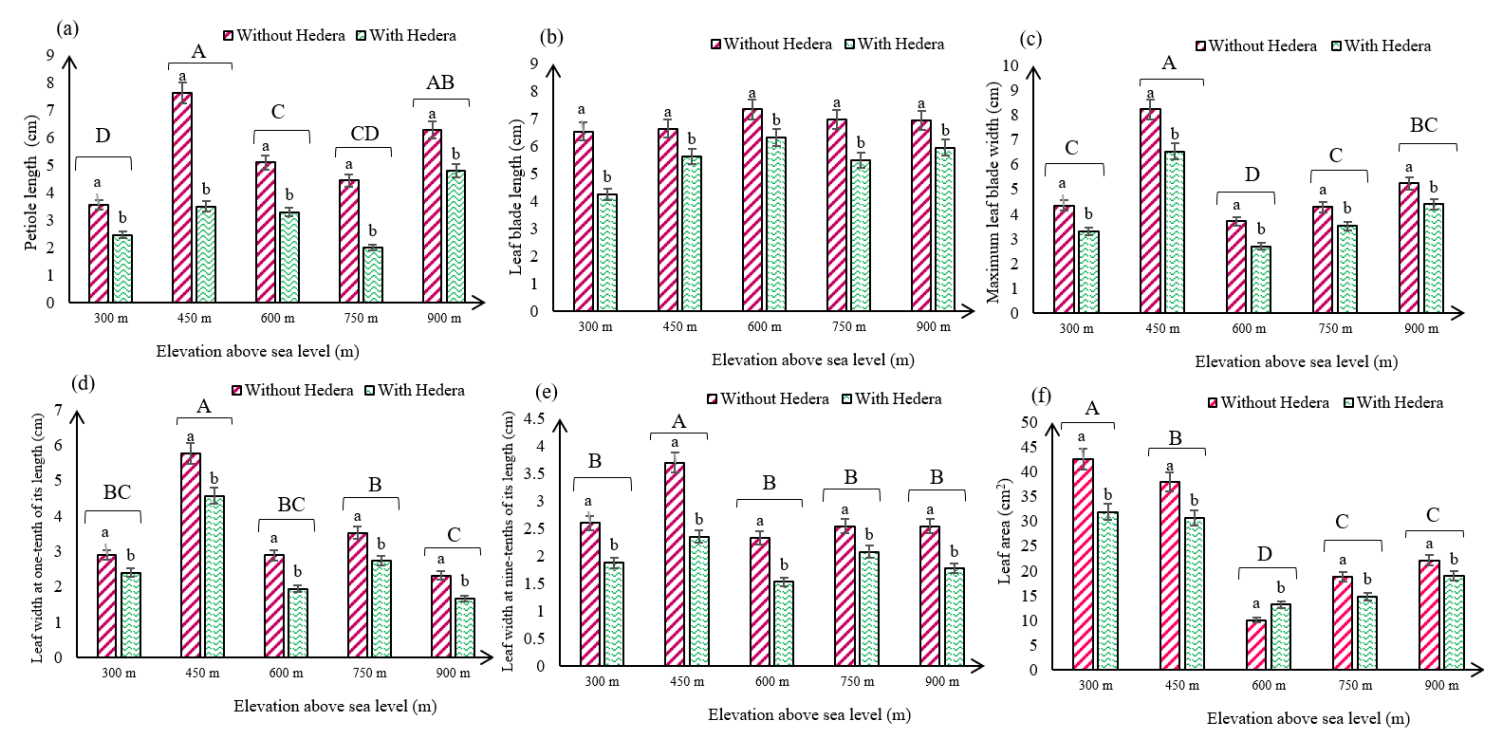


Figure 2

Mean ($\pm$ standard error; $n=12$) of leaf petiole length (a), leaf blade length (b), maximum leaf blade width (c), leaf width at one-tenth of its length (d), leaf width at nine-tenths of its length (e), Leaf area (f) properties in relation to forest sites (as control without *Hedera pastuchovii*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest. Different lowercase letters indicate significant ($p < 0.05$) differences between the two *Hedera* conditions (control and forest under *Hedera pastuchovii*) and different capital letters indicate significant ($p < 0.05$) differences inside the five elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

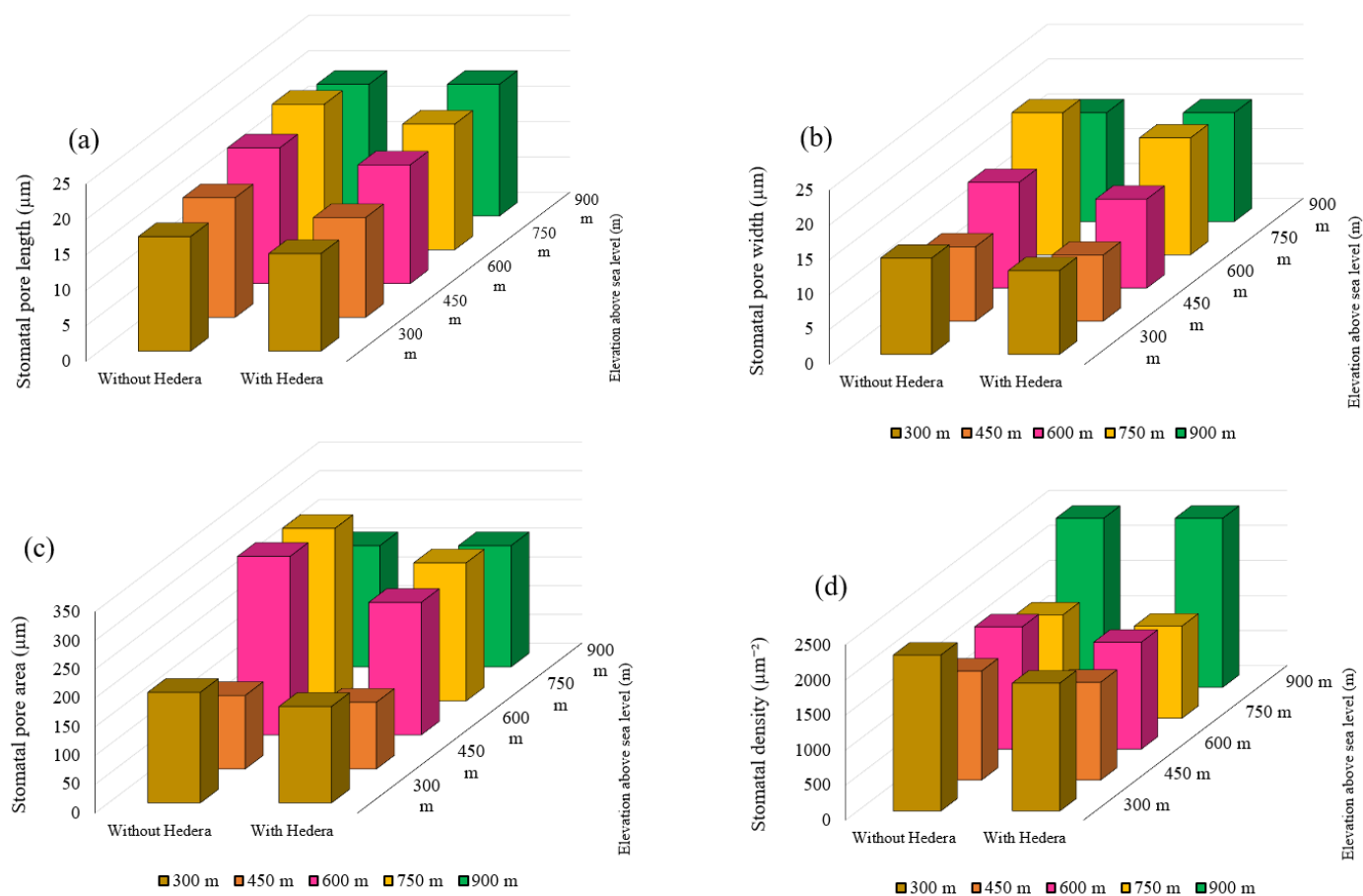


Figure 3

Mean ($\pm$ standard error; $n=12$) of stomatal pore length (a), stomatal pore width (b), stomatal pore area (c), stomatal density (μm^{-2}) (d) properties in relation to forest sites (as control without *Hedera pastuchovii*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

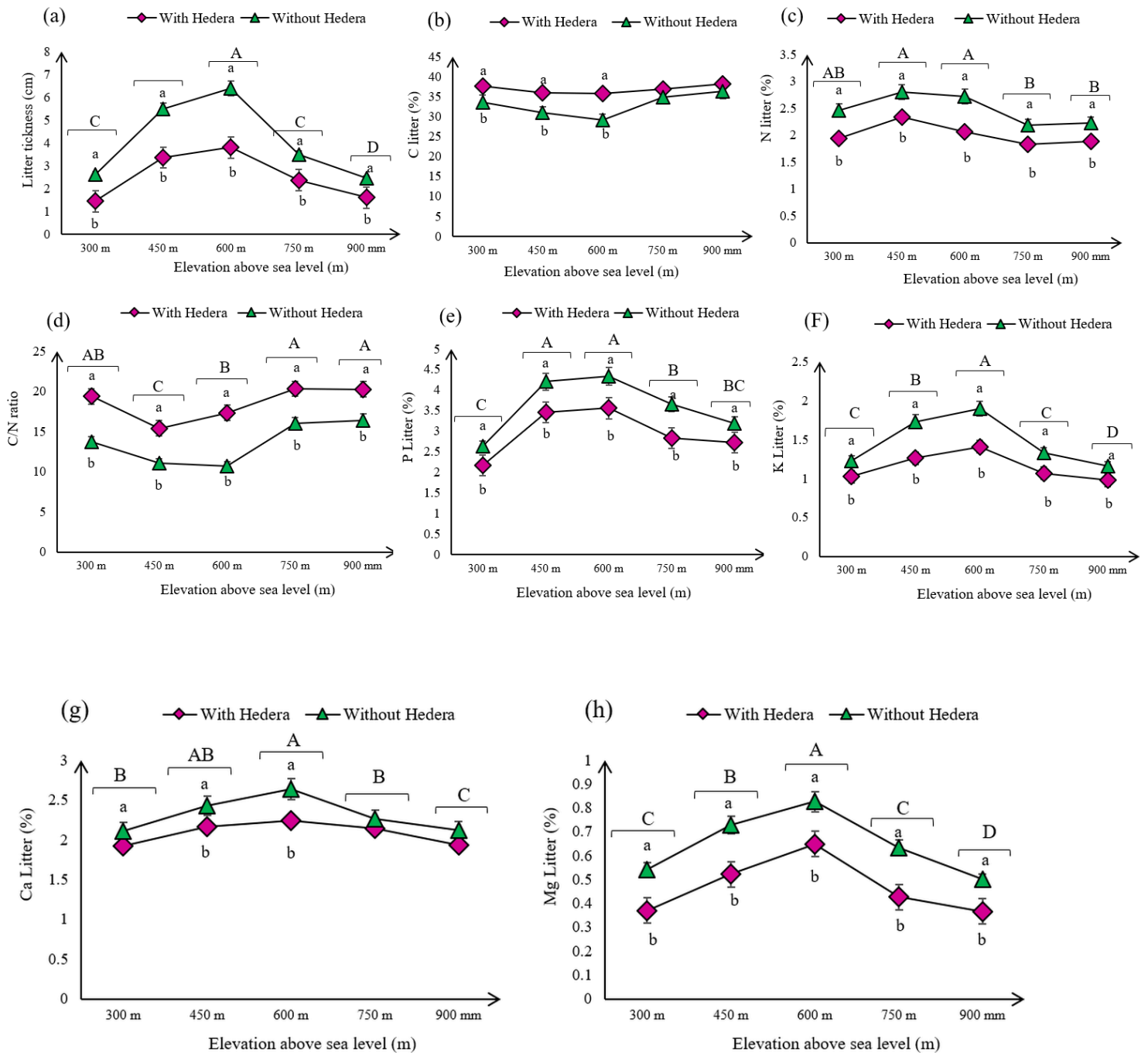


Figure 4

Mean ($\pm$ standard error; $n=12$) of litter thickness (a), carbon (b), nitrogen (c), carbon to nitrogen ratio (d), phosphorous (e), potassium (f), calcium (g), and magnesium (h) properties in relation to forest sites (as control without *Hedera pastuchovii*) and forest under *Hedera pastuchovii* in the different elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest. Different lowercase letters indicate significant ($p < 0.05$) differences between the two Hedera conditions (control and forest under *Hedera pastuchovii*) and different capital letters indicate significant ($p < 0.05$) differences inside the five elevation (300 m, 450 m, 600 m, 750 m and 900 m above sea level) in Hyrcanian Forest.

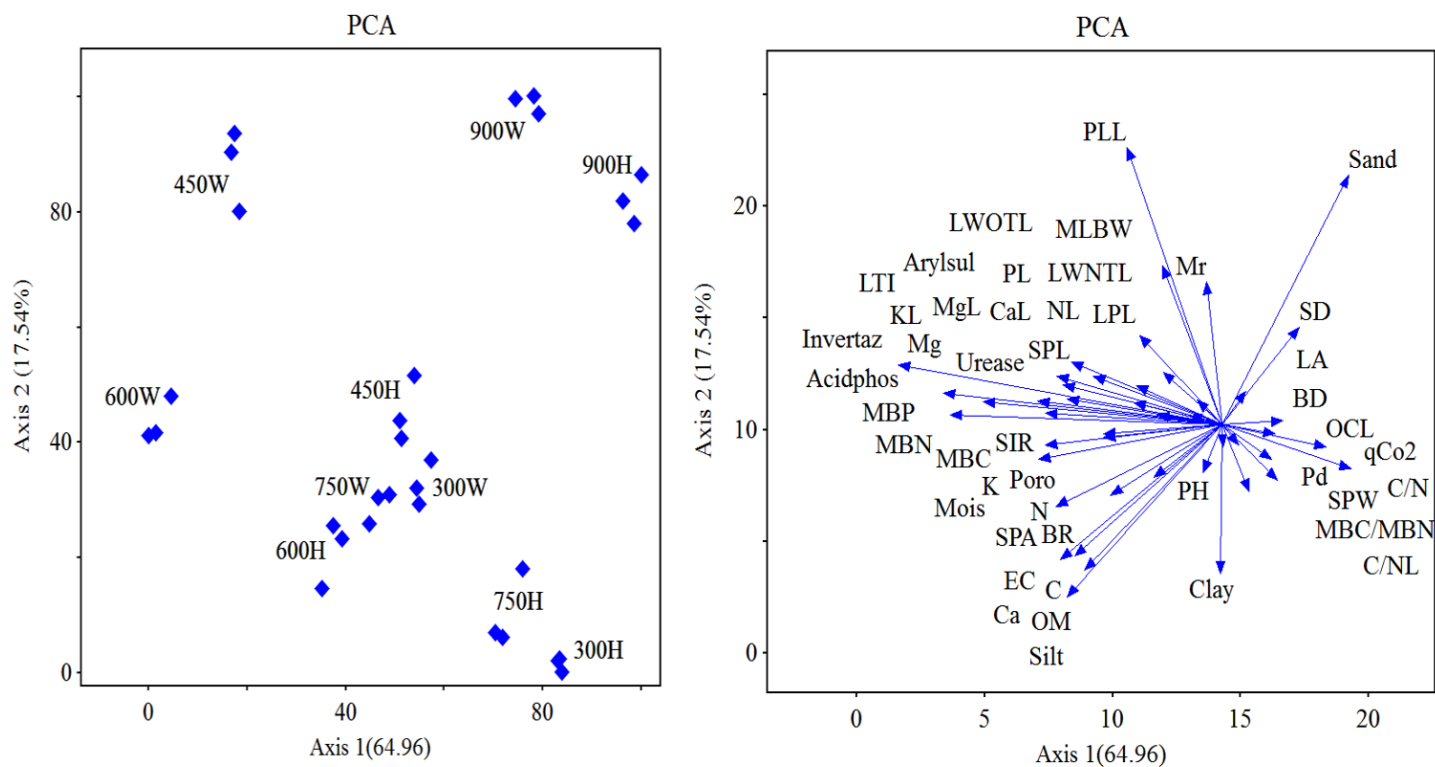


Figure 5

PCA (axis 1: 64.96 % and axis 2: 17.54 %) based on the correlation matrix of the studied sites and leaf, stomata and soil properties.

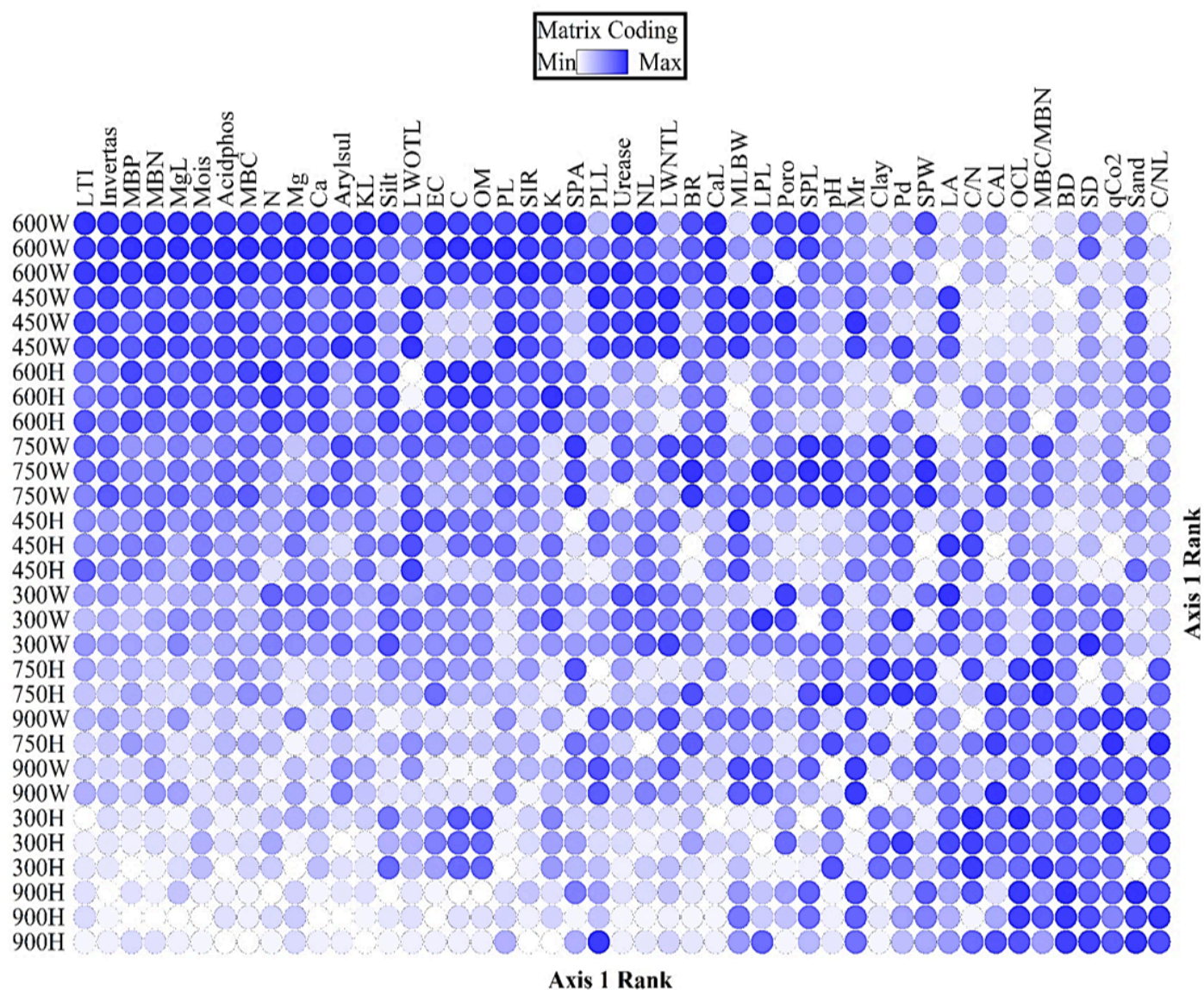


Figure 6

Ranking of based on the correlation matrix of the studied sites and leaf, stomata and soil properties of principal component analyses (PCA).

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