Patterns of Leaf Morphological Traits of Beech (*Fagus sylvatica* L.) along an Altitudinal Gradient

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Abstract: Broadleaved tree species in mountainous populations usually demonstrate high levels of diversity in leaf morphology among individuals, as a response to a variety of environmental conditions associated with changes in altitude. We investigated the parameters shaping leaf morphological diversity in 80 beech individuals (*Fagus sylvatica* L.), in light and shade leaves, growing along an elevational gradient and under different habitat types on Mt. Paggeo in northeastern Greece. A clear altitudinal pattern was observed in the morphological leaf traits expressing lamina size and shape; with increasing altitude, trees had leaves with smaller laminas, less elongated outlines, and fewer pairs of secondary veins. However, this altitudinal trend in leaf morphology was varied in different habitat types. Furthermore, the shade leaves and light leaves showed differences in their altitudinal trend. Traits expressing lamina shape in shade leaves were more related to altitude, while leaf size appeared to be more influenced by habitat type. While the altitudinal trend in leaf morphology has been well documented for numerous broadleaved tree species, in a small spatial scale, different patterns emerged across different habitat types. This morphological variability among trees growing in a mountainous population indicates a high potential for adaptation to environmental extremes.

Keywords: *Fagus sylvatica*; Fagaceae; Greece; leaf morphometrics; leaf traits; altitude; plasticity; adaptation; habitat

1. Introduction

The morphological attributes of plant leaves are the fundamental functional traits for balancing light capture and transpiration [1] and are, for this reason, very important for the plant's ability to adapt to the ongoing environmental change [2]. Considering that leaf morphology varies greatly among taxa, these differences have been used for classification purposes in plant systematics [3]. However, leaf morphological traits show patterns of large diversity within the same species as well, even within the same individual genotypes, especially in cases of large trees, according to the position of leaves within the canopy [4–8]. Several studies have drawn conclusions about the environmental impact on leaf size and shape using the response of the leaf morphological traits of certain tree species to environmental signals [9,10].

Shifts in leaf morphology have usually been associated with altitude in many broadleaved species, e.g., in [11]. Most authors explain this as a result of plasticity due to the declining temperature with an increasing altitude [12–14], but also because of other stressful conditions characteristic of higher altitude habitats, such as low water availability, limited nutrient supply, wind exposure, and intense solar irradiation [11,13,15–18]. As a result, the leaves usually decrease in size with an increasing altitude [19,20], but this correlation is not simple and straightforward. Besides the multitude of environmental factors that change along an altitudinal cline, plants often demonstrate variation in leaf traits as part of more complex, physiological size/number trade-offs, including shifts in leaf, shoot and whole plant traits [21,22].

In most broadleaved trees, the leaves directly exposed to sunlight (light leaves hereafter) usually become smaller in size than the leaves inside the canopy (shade leaves hereafter). This variation in leaf morphology is described as a plastic response of the leaves to the heterogeneous light and stress conditions that exist within a tree canopy, especially during leaf formation [9,23]. At the same time, this leaf morphological variation within the canopy of the same individual tree can be an outcome of its overall adaptive strategy to optimize the balance between different resource limitations and to cope with ontogenetic restrictions [3,24]. This adaptive strategy is considered to be largely of a genetic nature [4] and is thought to play a crucial role in the survival of tree species under global environmental change [25,26].

The aim of this study is to investigate the parameters shaping the diversity patterns of leaf morphological traits in the European beech (*Fagus sylvatica* L.), in light and shade leaves, along an elevational gradient on Mt. Paggeo in northeastern Greece. Altitudinal gradients offer an appropriate experimental setting for the observation of changes in tree leaf traits as a response to environmental conditions in a relatively short space [27]. The European beech is an important, widespread, and morphologically diverse tree species in Europe that occupies the mountainous habitats in the southern part of its distribution, hosted in numerous different ecosystems. Leaf morphological traits are well studied in this species and have been used mainly for systematic purposes between the various existing ecotypes, postglacial lineages, and subspecies, e.g., in [24,28–30], and are less used for describing their adaptive pattern according to their altitude and other environmental parameters. The beech forests of Mt. Paggeo have been chosen for this study because they cover an almost uniform elevation gradient from 600 to 1800 m als, covering different habitat types and thus different environmental conditions.

2. Materials and Methods

2.1. Area of the Study and Sampling

Mt. Paggeo is located in north-eastern Greece and its southern side faces the Aegean Sea (Figure 1). It is relatively isolated from the other mountains harboring beech forests in the region, by lowland areas to the north and by sea to the south. Beech forests on Mt. Paggeo occur in an altitudinal range from 600 to 1800 m als, mainly on gneiss–schist, marble and, more rarely, on granite.
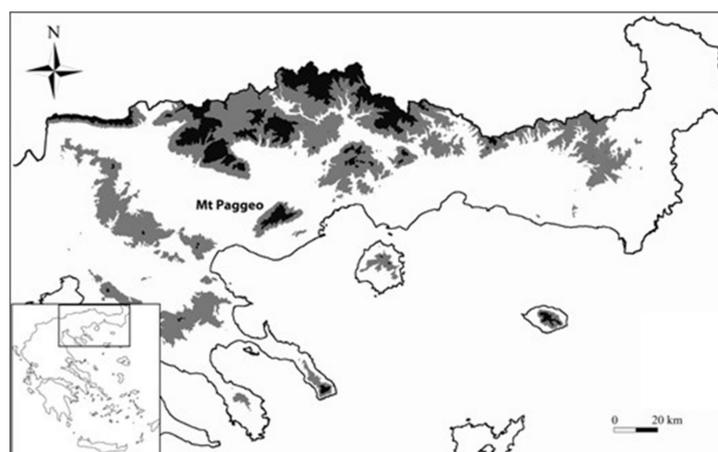
Figure 1. Orientation map of Mt. Paggeo in N.E. Greece. Grey colored areas have an altitude of 500–1000 m and black colored areas represent elevations above 1000 m.

According to the 92/43/EEC Directive and the Interpretation Manual of European Union Habitats [31], four beech forest habitat types occur on Mt. Paggeo [32,33]:

1. Thermophytic beech forests (*Quercus frainetto* Ten. woods—code: 9280) that mainly occur at the low elevations of the south-eastern slopes of the mountain, on gneiss–schist substrates and in a forest patch in the north-eastern part of the mountain on granite; these forests are similar to the units 5 and 6 according to Tsiripidis et al. [33], and to the *F. sylvatica* subsp. *orientalis* (Lipsky) Greuter & Burdet community [34];
2. Acidophytic forests (*Luzulo–Fagetum* beech forests—code: 9110), on gneiss–schist at higher elevations (above 1000 m als); they correspond to the unit 3 according to Tsiripidis et al. [32], and the *Calamagrostis arundinacea* (L.) Roth—*F. sylvatica* community [33];
3. Basiphytic forests (Cephalanthero–Fagion beech forests—code: 9150) on marble, also at higher elevations; they are similar to the unit 4 according to Tsiripidis et al. [32], and to *Brachypodium pinnatum* (L.) P.Beauv.—*F. sylvatica* community [33];
4. Beech forests that grow in a gorge on the north-eastern part of Mt. Paggeo, from 400 to 1600 m als (*Tilio–Acerion* forests of slopes, screes and ravines—code: 9180), that represent a rare vegetation type of high conservation value, belonging to the *Tilio–Acerion* alliance [32,33,35] and a possible local glacial refugium for beech [36].

Sampling occurred in late June of 2006. As many as 1600 leaves were collected from 80 beech individuals on an altitudinal transect from the lower elevations on the eastern side of Mt. Paggeo (800 m als) to the upper plateau of the mountain, reaching 1760 m als (Figure 2). Sampling was designed according to the forest coverage of beech in the study area and took place in four forest patches, representative of altitude and the three main habitat types of Mt. Paggeo (thermophytic, basiphytic and acidophytic; Table 1) [32].

Table 1. Description of the forest patches where sampling occurred.

Forest Patch	Altitude Range (m)	Soil Substrate	Habitat Type	Number of Trees Sampled
1	805–1100	gneiss–schist	Thermophytic	21
2	1100–1300	gneiss–schist	Acidophytic	20
3	1400–1500	marble	Basiphytic	19
4	16,601,760	marble	Basiphytic	20
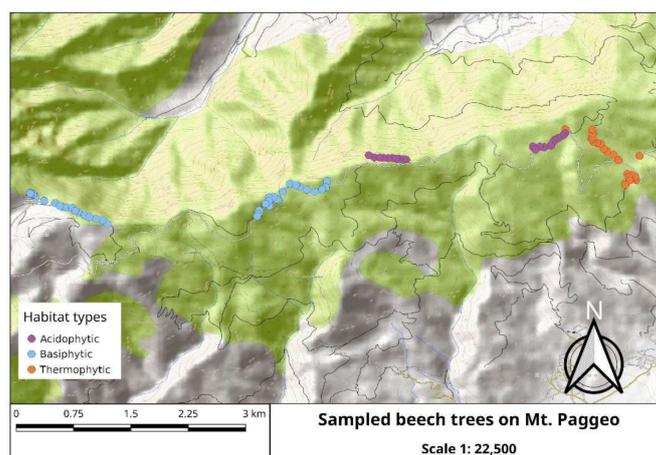
Figure 2. Map with the location and the habitat type of beech trees sampled on Mt. Paggeo.

Adult trees with a symmetrical and fully grown canopy, located at least 100 m away from each other, were selected within each patch. From each tree, ten typical, healthy, and fully expanded leaves were randomly collected from the outer part of the canopy at a height between two and three meters on the tree (light leaves), and ten more from the inner part of the tree canopy at the same height (shade leaves). For each tree, the geographical coordinates and the altitude were recorded, as well as the soil substrate and the habitat type where each individual tree belongs [32]. In addition, based on the altitude, the inclination, and the exposure to the sun that characterizes the specific location where each tree grows, a heat and a radiation coefficient were scored by applying the third equation from McCune and Keon [37].

2.2. Leaf Traits and Data Analysis

The leaves were dried and stored and then digitally scanned and saved as images. In each leaf image, 15 traits were measured, using Image-Pro Plus (MediaCybernetics®, Rockville, MD, USA). Three traits expressed lamina size, ten more were used to describe lamina shape, and finally two traits considered petiole attributes (Table 2). Average values of leaf traits within each tree were estimated for each shading level. Means between light leaves and shade leaves were compared using one-way ANOVA with R package Rcmdr [38,39].

We tested for the effects of soil type, habitat type, altitude, heat and radiation on all measured leaf size, leaf shape and petiole traits, separately for light and shade leaves, using generalized linear models. In all cases, we used Gaussian (normal) errors with an identity link through the 'glm' function [40]. In all model designs, we included all two-way interaction terms, and we simplified models by minimizing the Akaike Information Criterion (AIC), always retaining the non-significant main effects involved in higher order interactions, to satisfy the principle of marginality. We conducted post-hoc multiple comparisons, using the Tukey HSD function with adjustment for multiple comparisons, to further explore trait variations among habitat types. For non-normal model residuals, we used the 'BoxCox' function of the 'car' package [41] to carry out Box–Cox transformations on non-normally distributed variables. To visualize our models, we used the 'visreg' function in the 'VISREG' package [42] and the 'ggplot' function of the 'ggplot2' package [43].

Table 2. Morphological leaf traits measured.

Trait	Unit	Method
LENGTH	cm	Length of leaf lamina
WIDTH	cm	Maximum width of leaf lamina
PERIMETER	cm	Lamina perimeter
Leaf Index (LI)		(LENGTH/WIDTH) × 100
Maximum Width Index (MWI)		(The distance between the lamina basis and the point of maximum width on the primary axis/LENGTH) × 100
RadiusRatio (RR)		The maximum distance possible connecting the center of the lamina with the perimeter/the minimum distance possible connecting the center of the lamina with the perimeter
ROUNDNESS		PERIMETER/(4π × lamina area)
AREABOX		The lamina area/the area of its imaginary bounding box
DFINDEX		The longest caliper (feret) length within the lamina area/average caliper (feret) length within the lamina area
Perimeter Ratio (PR)		Ratio of the convex perimeter of the lamina/PERIMETER
Fractal Dimension (FD)		The fractal dimension of the lamina's outline
ANGLE	degrees	Angle between the primary axis of the lamina and the first secondary nerve on the left side
VEINS		Number of secondary nerves of the lamina
PETIOLE	cm	Length of the leaf petiole
Petiole Index (PI)		PETIOLE/LENGTH

To further evaluate the effects of soil type, habitat type, altitude, heat, and radiation on all measured traits, separately for light and shade leaves, we grouped these traits into three functional syndromes (leaf size, leaf shape and petiole traits), and used principal components analysis (PCA; 'vegan' R package) on each syndrome to produce three composite variables using the first principal component (PC1), each explaining 55–89% of the variation in the data. We used the scores of these three 1st principal component axes as response variables to perform a redundancy analysis (RDA), to discriminate the significance of the explanatory factors. The analysis was performed using the "vegan" package of R-Studio while the best permuted model (999 permutations) was described using the function "ordiR2step" in forward mode, in R-Studio [44]. RDA was performed separately for light and shade leaves.

3. Results

3.1. Light Leaves and Shade Leaves

The average values of the light and shade leaves were significantly different from each other for the traits expressing leaf size (LENGTH, WIDTH, PERIMETER), ROUNDNESS and AREABOX, ANGLE, VEINS, PETIOLE and PI (Table 3). Leaf shape traits, such as LI, MWI and RR were not significantly different between the light and shade leaves. The light leaves were smaller than the shade leaves, with a smaller angle between the main axis and the first secondary vein and with fewer vein pairs. The petiole of the light leaves was longer and the PI was much larger (Table 3).

Table 3. Mean values, coefficients of variance (CV%) and analysis of variance of morphological leaf traits at light and shade leaves. Numbers in bold symbolize statistical significance.

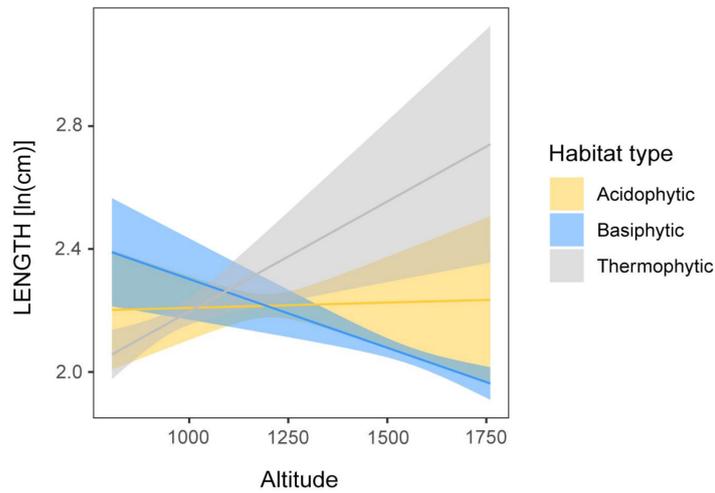|	Light Leaves		Shade Leaves		ANOVA	
Trait	**Mean**	**CV%**	**Mean**	**CV%**	**F**	**p (>F)**
LENGTH	7.76	15.21	8.37	11.83	12.72	**<0.001**
WIDTH	4.75	14.95	5.08	11.22	10.32	**0.002**
PERIMETER	19.43	14.46	20.87	10.92	12.65	**<0.001**
Leaf Index (LI)	164.08	8.04	165.58	8.11	0.51	0.476
Maximum Width Index (MWI)	50.15	4.71	49.65	4.83	1.78	0.184
RadiusRatio (RR)	1.714	8.58	1.748	8.70	2.16	0.143
ROUNDNESS	1.144	3.58	1.161	3.79	5.969	**0.016**
AREABOX	0.679	2.06	0.670	2.09	16.51	**<0.001**
DFINDEX	0.933	1.93	0.928	1.94	2.97	0.087
Perimeter Ratio (PR)	1.000	0.20	0.999	0.10	0.34	0.562
Fractal Dimension (FD)	1.006	0.10	1.006	0.10	1.51	0.221
ANGLE	35.95	8.71	37.61	8.67	10.73	**0.001**
VEINS	17.35	10.37	18.15	9.37	8.314	**0.004**
PETIOLE	0.950	17.89	0.770	22.08	48.63	**<0.001**
Petiole Index (PI)	12.40	16.13	9.17	18.10	123.50	**<0.001**

3.2. Generalized Linear Models

3.2.1. Size Traits

In both the light and shade leaves, the LENGTH differed between habitat types ($F_{2.74}$ = 5.66; $p < 0.01$ and $F_{2.73}$ = 10.53; $p < 0.001$, respectively), with the basiphytic type always supporting the shortest light and shade leaves (Figure 3). On average, the LENGTH of both the light and shade leaves decreased with increased altitude ($F_{1.74}$ = 4.54; $p < 0.05$ and $F_{1.74}$ = 4.33; $p < 0.05$). In the case of the shade leaves, the habitat type affected the response of the LENGTH along altitude (Habitat type x Altitude interaction: $F_{1.73}$ = 11.31; $p < 0.001$; Figure 4). The PERIMETER significantly differed between the habitat types for both the light ($F_{1.74}$ = 6.66; $p < 0.01$) and shade ($F_{1.74}$ = 15.15; $p < 0.001$) leaves, with trees distributed in a basiphytic habitat type always having low perimeter leaves. There was a marginal tendency of the light leaves to reduce the PERIMETER with increasing altitude ($p = 0.08$), while for the shade leaves, the habitat type affected the response of the PERIMETER along altitude (Habitat type x Altitude interaction: $F_{2.74}$ = 8.44; $p < 0.001$).

3.2.2. Shape Traits

Differences between the habitat types affected the response of the LI along altitude for both the light and shade leaves (Habitat type x Altitude interaction: $F_{2.72}$ = 5.19; $p < 0.01$ and $F_{2.72}$ = 6.84; $p < 0.05$, respectively; Figure 5). In addition, the shade leaves significantly decreased their LI with increasing altitude ($F_{2.72}$ = 6.97; $p < 0.01$). A significant interaction emerged between the habitat type and altitude ($F_{2.72}$ = 5.03; $p < 0.01$) for the light leaves, indicating that differences between habitat types affect the response of the MWI along altitude. On the other hand, the shade leaves, on average, decreased their MWI with increasing altitude ($F_{1.74}$ = 4.84; $p < 0.05$).

(**a**)

(**b**)
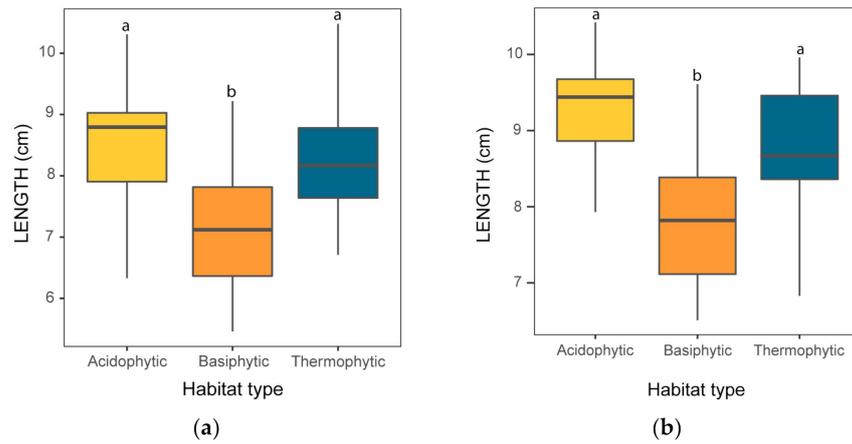
Figure 3. Comparison of LENGTH in different habitat types, for (**a**) light and (**b**) shade leaves. 20 leaves were measured per tree and the absolute frequency of the trees in each habitat type is: Thermophytic 21, Acidophytic 20 and Basiphytic 39. The central horizontal line in the box plots represents the median of the samples, the box plot edges represent the first and third quartile. The interquartile range (IQR) within the boxes represent the central 50% of the values. The whiskers show the range of observed values and the locations of the minimum and the maximum values.

Figure 4. Correlation graphs between LENGTH and altitude for shade leaves in three different habitat types.


(**a**)

(**b**)
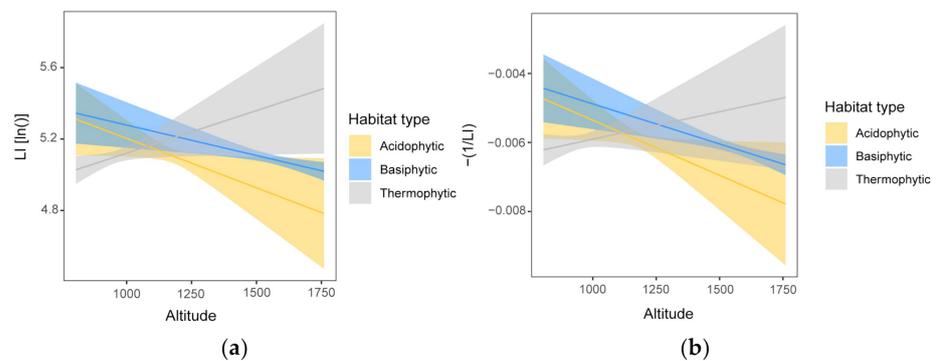
Figure 5. Correlation graphs between LI and altitude for (**a**) light leaves and (**b**) shade leaves in three different habitat types.

ROUNDNESS, on average, decreased with increasing altitude for both the light ($F_{1.72}$ = 5.84; $p < 0.05$) and shade leaves ($F_{1.73}$ = 8.05; $p < 0.01$), while differences between habitat types affected how round the leaves would be along altitude (Habitat type ×Altitude interaction: Light leaves, $F_{2.72}$ = 7.01; $p < 0.01$ and shade leaves, $F_{2.73}$ = 4.35; $p < 0.05$, respectively). In addition, the light leaves significantly decreased their ROUNDNESS with increasing radiation ($F_{1.72}$ = 4.23; $p < 0.05$).

3.3. Redundancy Analysis

RDA analysis generally showed moderate ratios of variance affected by the explanatory factors (20.83% and 17.21% for light and shade leaves, respectively). Altitude and habitat type showed the most significant effect on both the light and shade leaves regarding their size and shape. Additionally, the effect of the substrate proved significant but only for the shade leaves (Figure 6)

(**a**)   (**b**)
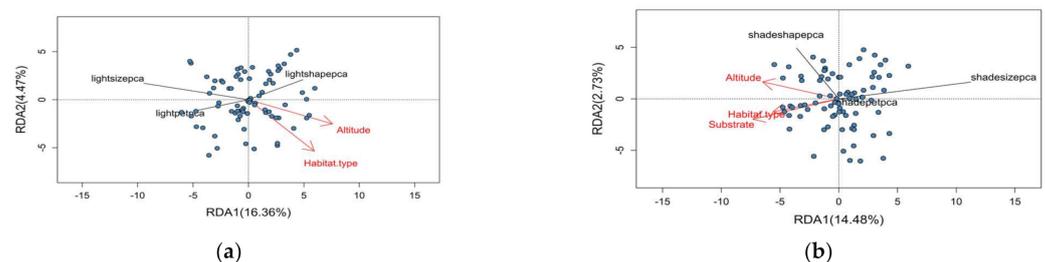
Figure 6. RDA biplot of most significant factors on response variable categories for (**a**) light leaves and (**b**) shade leaves. The variable categories are: lightsizepca (leaf size), lightshapepca (leaf shape) and lightpetpca (petiole size) for light leaves and shadesizepca (leaf size), shadeshapepca (leaf shape) and shadepetpca (petiole size) for shade leaves.

4. Conclusions

4.1. An Altitudinal Pattern in Leaf Morphology

The results of this study indicate that the altitude is an important factor shaping leaf morphology in the European beech. Trees growing in high altitudes, generally had leaves with smaller lamina size, less elongated outlines, fewer pairs of secondary veins, and shorter petioles. This altitudinal trend in leaf morphology was stronger for leaf size and the number of secondary veins, especially for leaves directly exposed to sunlight. A negative correlation of altitude with leaf size for trees growing in the same mountain has been described in several studies, e.g., for *Fagus* in [24,30] and for other broadleaved plant species [11,19,21,45,46], as well as in studies concerning broader geographical regions for several tree species, such as *Ulmus glabra* Mill., *Alnus incana* (L.) Moench subsp. *incana*, *Carpinus betulus* L., etc. [47–49].

The altitudinal trend in leaf morphology observed in this study was not uniform for all traits or shading classes, as is indicated by the interaction between the altitude and habitat type. This pattern indicates that leaf size was probably influenced by a set of complex environmental factors that do not change similarly with increasing altitude, such as levels of irradiation, temperature, water availability, and soil nutrient content [11,50]. Such complex trends in leaf size reduction due to altitude have been observed among plant species and among individuals of the same species [21,51]. Comparisons between the leaf morphological traits in beech populations along a precipitation gradient in Germany have indicated that—among a multitude of environmental factors—temperature is the main driver influencing leaf size, but its effect varies along different precipitation regimes [52]. This variation is therefore expected to be more intense in the mountainous beech forests of the Mediterranean region, such as the ones studied here.

In this study, the altitudinal trend in leaf size possibly indicates the increase of stress in leaves' development at the lowest and highest altitudes. Trees growing on sites with lower elevation are located on the southern slopes of Mt. Paggeo, where an increase in altitude

possibly improved the growing conditions for the beech, since the stress caused by heat and intense evapotranspiration was reduced. In contrast, the other trees grow on sites with varying aspect, on the ridge of two different watersheds, and in higher altitudes. Increasing altitude under such conditions may be a disadvantage for the beech [53], especially for trees located on the upper margins of the perpendicular expansion of the species in Mt. Paggeo, where stressful conditions are common, such as higher solar radiation, more intense winds (and thus higher evapotranspiration), and cooler temperatures (thus the shortest growing season) [52].

In our study, habitat types appeared to have influenced the altitudinal trend of the leaf morphology differently. Trees in lower altitudes (800–1100 m als) grow on gneiss–schist and belong to the thermophytic type, while the trees growing in intermediate altitudes (1100–1300 m als) have the same substrate but belong to the acidophytic type. Finally, the trees growing in higher altitudes (1400–1760 m als) are characterized by marble substrate and the basiphytic plant community. While the substrate was not found to cause any significant interactions with the altitude to influence leaf morphology, the habitat type did, perhaps because the substrate is a major defining factor and its effects on leaf morphology are already included in the ones observed at the habitat type factor. The effect of the habitat type on the altitudinal trend in leaf size was significant in the shade leaves only. Specifically, the shade leaves became larger with altitude in the thermophytic type, while this trend was quite the opposite in the basiphytic habitat type, on the higher part of the mountain (e.g., Figure 6). Thus, these two opposite trends in the change of leaf size with altitude may be rooted in differences in the ecological conditions that exist in the different habitat types, besides—or along with—the differences in the environmental conditions that exist in the different altitudes.

Traits expressing leaf shape showed a similar pattern for both the light and shade leaves. The response towards altitude was weaker. The leaves of trees growing on high altitudes were generally rounder and more ovate, but so were the leaves of trees growing on the lowest altitude. The leaf shape followed a pattern where the two altitudinal extremes were almost similar, however this pattern was smoother and more complex. This complex pattern cannot be described as a reflection of the altitudinal differences among the trees, but it could be under a climatic effect at a local or a wider scale [54,55]. Regarding the leaf index (LI), studies report that this trait is relatively stable within plant species since it can be regulated by numerous genetic factors and also has an adaptive importance for photosynthesis optimization and drought resistance [55,56]. For beech, the LI has been used to differentiate beech species [57] or different postglacial lineages within the same species [30]. An interaction between the habitat type and altitude on the change of leaf shape traits was also observed. As was the case with leaf size, trees growing in the thermophytic habitat type showed a reverse altitudinal trend for all leaf shape traits, in comparison with trees growing in the acidophytic and basiphytic types. In the thermophytic type, at lower altitudes, the LI, MWI, and ROUNDNESS increased with the altitude and the leaves became more elongated and reverse ovate. The opposite trend was observed at intermediate and higher altitudes, in both the acidophytic and basiphytic types, where these leaf shape traits decreased their values with increasing altitude and the beech leaves became rounder. This interaction was observed in both the light and shade leaves and indicates that several environmental factors may have influenced the leaf shape in a different way, by different altitudes and habitat type combinations [58–61].

4.2. Total Phenotypic Variation of Leaf Traits

In our study, the results of the comparison between the light and shade leaves indicate that exposure to light strongly influences leaf morphology within the canopies of the individual trees. This is a well-documented phenotypic pattern in beech [7,24,62–64] and other broadleaved tree species, such as *Quercus* sp. [65,66], *Castanea sativa* Mill. [67,68], *Sorbus torminalis* (L.) Crantz [69] and *Fraxinus angustifolia* Vahl [70]. Plasticity in leaf traits, especially leaf size and shape, is frequently explained by a specific light-harvesting strategy,

aiming for the maximum absorption of light in the shaded part of the plant canopy [71]. This happens especially in shade tolerant trees, such as beech and oak, that keep their interior foliage under low irradiation through a closed canopy [72–76]. Studies of leaf morphology in beech, along a precipitation gradient, indicate that the shade leaves tend to become larger in populations growing under drier conditions, due to a more open canopy [52]. This seems to explain that the leaf size plasticity was more intense in those parts of Mt. Paggeo, where the environmental conditions were more adverse. Plasticity due to irradiation in leaf size has been reported to interact significantly with the altitude in *Nothofagus cunninghamii* (Hook.) Oerst., while there was no effect of the altitude in leaf shape [77]. PETIOLE and PI were the traits that showed the largest differences between the light and shade conditions, following a reverse trend in comparison to leaf size, since the shade leaves had larger laminas and smaller petioles than the light leaves of the same tree. This trend was described as a general pattern in beech populations in Greece [24,30] and Europe [78,79].

The results of this study indicate that leaf traits were influenced in a combined way by altitude and habitat type, with the altitude being the prevailing factor. Similar differentiation patterns in leaf morphology due to a combined influence of different environmental parameters has been reported, not only for beech [80,81] and other species of the Fagaceae family such as *Quercus robur* L. [18] and *N. cunninghamii* [13], but also in other species [6]. However, considering all leaf morphological traits, the RDA showed differences between the light leaves and shade leaves. These distinctions demonstrate the different strategies used by the light and shade leaves since the light leaves (the outer canopy part) aim to minimize carboxylation limitations while the shade leaves aim to increase light interception. In the shade leaves, trees seemed to be more differentiated in their morphology which could be related to the crown density or architecture [7,52]. The traits expressing leaf shape in the shade leaves were more related to the altitude, while the leaf size appeared to be more influenced by the habitat type and substrate. Similar differences between the light and shade leaves were described in deciduous broadleaved species [1], conifers [82] and evergreen trees [6,56]. The shade leaves utilize diffuse light and we therefore expect their size and shape to be less influenced by light irradiation at each site. For this reason, the shade leaf clusters observed in our study may stronger reflect the different ecological site factors besides light conditions, i.e., air temperature and humidity [83] or ontogenetic factors [84].

North Greece demonstrates a high diversity in beech morphotypes [24,29,30,79,85]. The beech forests on Mt. Paggeo are no different. The morphological patterns of leaf traits among individual trees growing on different altitudes, at a small geographical scale, suggest that a set of different environmental factors caused a strong phenotypic response related mainly to the altitude, but also to the habitat type and substrate. While these observations were probably the result of the direct environmental influence on the tree phenotypes, the diversity among the individuals may also reflect the diversity in adaptive traits (see review [59]). Thus, the altitudinal trend in leaf size and shape may be different or even reversed under different habitat types.

Furthermore, our results indicate that trees develop a total adaptation strategy that involves the plasticity between the light and shade leaves within the same tree genotype. Beech morphotypes seem to regulate the differences between shade and light leaves that facilitate the optimal light-harvesting strategy under specific environmental conditions that may differ with the altitude and substrate or habitat type [6]. This variability in morphological traits indicates a high potential for adaptation to extreme environmental changes that are expected under scenarios of climate change [86–88]. Studies involving the common environmental trials on functional beech traits, growing in mountains with broad beech forests such as Mt. Paggeo, may provide more valuable information in order to design a management and conservation strategy for the beech towards climate change.

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