https://doi.org/10.31298/sl.149.9-10.4

Izvorni znanstveni članci – Original scientific papers
Šumarski list, 9-10 (2025): 443-456

LEAF MORPHOLOGICAL VARIATION IN *Ribes alpinum* L. ACROSS ELEVATION GRADIENTS IN THE NORTH-WESTERN DINARIC ALPS: EVIDENCE OF PHENOTYPIC PLASTICITY AND HABITAT INFLUENCE

Igor POLJAK[1]*, Marijan VUKOVIĆ[1], Ana VUKOVIĆ[1], Matija MAGDIĆ[1], Antonio VIDAKOVIĆ[1], Ivana ZEGNAL[2], Doris MARJANOVIĆ[1], Irena ŠAPIĆ[1]

SUMMARY

Mountain ecosystems are shaped by steep environmental gradients that influence plant morphology and adaptation. *Ribes alpinum* L., a deciduous shrub with a wide European distribution, remains poorly studied in terms of its intraspecific variability. This study aimed to investigate leaf morphological variation across five natural populations from the Dinaric Alps, focusing on differences in leaf size and shape in relation to elevation and habitat conditions. Leaves were sampled from four populations and photographed *in situ* at a fifth site located within a strict nature reserve. Ten morphometric traits were measured – five related to leaf size (e.g., area, length, petiole length) and five describing leaf shape and lobe configuration. Statistical analyses revealed significant differences among populations in seven traits, with leaf size parameters showing the greatest divergence. Populations from contrasting elevations were consistently identified as morphologically distinct. The low-elevation population showed the greatest degree of within-population morphological diversity, likely reflecting the influence of heterogeneous terrain and fine-scale microhabitat variation. Multivariate analyses (PCA and clustering) confirmed population-level structuring, while Redundancy Analysis (RDA) showed that geographic coordinates had no significant influence on trait variation. Instead, elevation-related environmental gradients emerged as the dominant drivers of morphological differentiation. These findings suggest that leaf traits in *Ribes alpinum* are shaped primarily by local ecological pressures, reflecting phenotypic plasticity rather than broad spatial separation. The study highlights the adaptive flexibility of *Ribes alpinum* and underscores the ecological importance of the Dinaric Alps as a valuable setting for investigating plant responses to environmental heterogeneity.

KEY WORDS: Dinaric Alps, alpine shrub, leaf morphometry, elevation gradient, phenotypic plasticity, habitat heterogeneity, intraspecific variation, mountain flora adaptation

INTRODUCTION

Mountain ecosystems are among the most ecologically and biogeographically distinctive regions on Earth. Characterized by steep environmental gradients, fragmented landscapes, and pronounced spatiotemporal heterogeneity, they often function as isolated ecological islands (Körner 2003, Flantua et al. 2020). These environments support a high number of endemic and specialized species, particularly among plants adapted to narrow altitudinal niches (Lomolino 2001, Steinbauer et al. 2016, Perrigo et al. 2019). Yet, the same factors that foster diversification also make mountain flora especially vulnerable to environmental disturbances. Climate change and land-use pressures increasingly threaten alpine and subalpine plant populations (Steinbauer et al. 2018, Hanjalić Kurtović et al. 2025), many of which are confined to

---

[1] Assoc. Prof. Igor Poljak, PhD, Marijan Vuković, M.Eng., Ana Vuković, M.Eng., Matija Magdić, M.Eng., Antonio Vidaković, PhD, Doris Marjanović, Assist. Prof. Irena Šapić, PhD, University of Zagreb Faculty of Forestry and Wood Technology, Zagreb, Croatia

[2] Ivana Zegnal, M.Eng., Croatian Forest Research Institute, Jastrebarsko, Croatia

* Corresponding author: Igor Poljak, e-mail: ipoljak@sumfak.unizg.hr

rear-edge habitats with limited dispersal potential (Watts et al. 2022). Understanding the variability of mountain plants is therefore essential – not only for documenting their adaptive strategies, but also for guiding conservation efforts aimed at preserving evolutionary potential under accelerating global change.

The morphology of mountain plants is shaped by a complex interplay of abiotic stressors and microhabitat diversity. Alpine environments impose extreme conditions – low temperatures, high UV radiation, short growing seasons, and mechanical stress from wind and snow – that favour compact growth forms, reduced stature, and specialized leaf and root traits (Körner 2003). Morphological adaptations such as reduced plant height, dense leaf hairiness, cushion-like or rosette architecture, and robust root systems are common strategies that enhance thermal buffering, reduce water loss, and protect meristems from frost damage (Neuner 2014, Zhang et al. 2021, Rai et al. 2025). These traits are not merely passive responses but reflect evolutionary innovations that enable survival in topographically complex and climatically unstable habitats.

One of the most influential factors shaping leaf morphology in alpine plants is altitudinal variation. Elevation affects temperature regimes, atmospheric pressure, and solar radiation intensity, all of which directly influence leaf size, thickness, and anatomical structure (Körner et al. 1989, Körner 2003). Numerous studies have shown that leaf area tends to decrease with increasing elevation (Körner et al. 1986, Milla and Reich 2011, Poljak et al. 2018, Liu et al. 2020, Ke et al. 2022), while traits such as leaf hairiness and margin complexity often increase as adaptive responses to harsher conditions (Körner 2003, Moles et al. 2020, Wang et al. 2022). Additionally, topographic heterogeneity creates fine-scale habitat mosaics (Bruun et al. 2006, Ford et al. 2013, Bueno de Mesquita et al. 2018), where soil moisture, snow cover duration, and nutrient availability vary dramatically over short distances. These environmental pressures frequently lead to high intraspecific morphological variability (Körner 2003, Boucher et al. 2013, Opedal et al. 2015), especially in traits related to leaf size, shape, and architecture. Such variability may reflect both phenotypic plasticity and underlying genetic differentiation (Gonzalo-Turpin and Hazard 2009), making morphometric analyses a valuable tool for detecting population-level divergence and potential local adaptation.

Ribes alpinum L. – commonly known as mountain or alpine currant – is a deciduous shrub from the family Grossulariaceae, typically reaching up to 1.5 meters in height (Schütt 2011). It lacks spines and features small, palmately lobed leaves (up to 5 cm), with finely toothed margins and a variable number of lobes (usually three to five). The species is functionally dioecious, with male inflorescences forming upright racemes of 10–30 flowers, and female racemes bearing 2–10 flowers (Idžojtić 2019). The fruits are smooth, red berries with little taste, maturing in mid to late summer. Despite its wide distribution across Europe and southwestern Asia (Hegi 1961, Krüssmann 1962), *Ribes alpinum* remains poorly studied from a morphological and ecological perspective. Most available data are limited to floristic records and general habitat descriptions (Horvat 1937, Vukelić and Rauš 1998, Vukelić et al. 2011, Vukelić 2012, Dakskobler and Rozman 2021, Sirovica 2025), with no insights into its adaptive traits or population-level differentiation.

Ecologically, *Ribes alpinum* occupies a broad range of habitats – from lowland forests in northern Europe to montane and subalpine zones in the south (Weber 1995). In Central and Northern Europe, it grows from sea level up to approximately 2000 meters, with upper elevation limits reaching around 2020 meters in the Swiss Alps (Schütt 2011). However, in southern parts of its range – including the Dinaric Alps – the species is largely restricted to mountainous terrain. In the Dinarides, *Ribes alpinum* is typically found along forest edges and rocky slopes, but it also colonizes open high-altitude habitats such as dwarf pine (*Pinus mugo* Turra) shrublands (Horvat 1937, Vukelić 2012). It thrives in shady microhabitats with moderate soil moisture (Ellenberg 1979), often within mixed stands of beech (*Fagus sylvatica* L.), fir (*Abies alba* Mill.), spruce (*Picea abies* (L.) H.Karst.), and sycamore maple (*Acer pseudoplatanus* L.) (Vukelić et al. 2011). The Dinaric Alps are especially notable for their rich plant diversity and ecological complexity (Médail and Diadema 2009, Brus 2010, Médail et al. 2019, Liber et al. 2020), yet no prior research has examined how these conditions influence morphological variation in *Ribes alpinum*, making the region an ideal setting for studying adaptive responses in mountain flora.

This study investigates leaf morphology across five natural populations of *Ribes alpinum* in Croatia, sampled from sites differing in elevation, habitat structure, and microclimatic conditions. The populations span both shaded forest margins and open subalpine habitats, including dwarf pine shrublands. Through detailed morphometric analyses, we aim to quantify variation within and among populations and assess the extent to which this variation is shaped by geographic factors, as well as environmental conditions like elevation, light exposure, temperature, and precipitation. Importantly, we consider the role of phenotypic plasticity, recognizing that the observed morphological differences may reflect flexible responses to local conditions rather than fixed genetic divergence. We hypothesize that (1) leaf morphology will vary significantly with elevation and habitat openness, and (2) populations from higher altitudes and more exposed sites will exhibit traits associated with alpine adaptation, such as reduced leaf size. By disentangling the relative influence of geographic and environmental drivers, this research contributes to a deeper understanding of plant adaptation in mountain ecosystems and highlights the ecological significance of the Dinaric Alps as a natural laboratory for studying evolutionary processes.

MATERIALS AND METHODS

Sample collection

During the 2023 field season, fully developed and intact alpine currant leaves were sampled from five natural populations across the Dinaric Alps in Croatia: Snježnik (P1), Risnjak (P2), Bijele and Samarske stijene (P3), Zavižan (P4), and Zečjak (P5) (Table 1, Figure 1). From four populations (P1, P2, P4, and P5), leaf material was physically collected in the field and immediately stored in cardboard folders for transport to the Herbarium DEND (Faculty of Forestry and Wood Technology, University of Zagreb), where it was permanently deposited. At each site, 20 leaves were collected from as many individual shrubs as possible, usually between 7 and 12 shrubs per site. In the case of the P3 population, located within the strictly protected Bijele and Samarske stijene nature reserve, sampling was carried out through *in situ* photographic documentation with a visible scale, and subsequent morphometric analyses were performed using these images. All fieldwork in the protected areas was conducted under official permission granted by the Ministry of Economy and Sustainable Development (UP/I 612-07/21-33/57, UP/I-352-04/24-08/18).

Table 1 Populations, sampling sites, geographic coordinates, altitude, and bioclimatic variables (BIO1, BIO9, BIO17) used in redundancy analysis (RDA), along with multivariate diversity index (MDI) for five mountain currant (*Ribes alpinum* L.) populations. Bioclimatic variables: BIO1 (mean annual temperature), BIO9 (mean temperature of the driest quarter), and BIO17 (precipitation of the driest quarter).

Population ID	Population	Latitude	Longitude	Altitude	BIO1	BIO9	BIO17	MDI
P1	Snježnik	45.443076	14.577918	1391	4.48	-2.53	382	3.12
P2	Risnjak	45.427662	14.622818	1384	4.39	-2.60	384	2.18
P3	Bijele and Samarske stijene	45.225201	14.968227	1280	5.48	-1.58	356	4.60
P4	Zavižan	44.801167	14.972380	1608	4.00	11.85	358	3.43
P5	Zečjak	44.702748	14.992914	1600	4.08	11.97	345	2.84

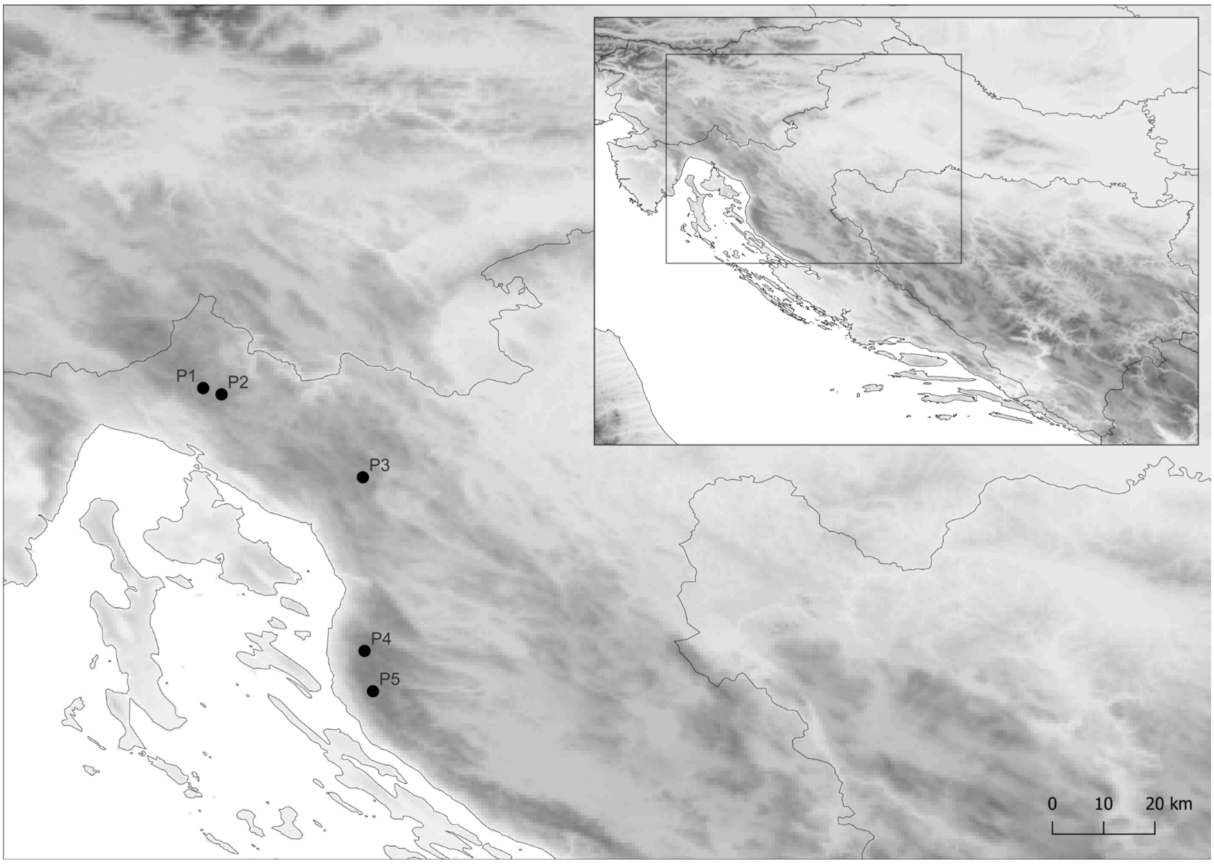

Figure 1 Geographic distribution of the five natural populations of mountain currant (*Ribes alpinum* L.) sampled in the Dinaric Alps. Populations are labelled as follows: P1 – Snježnik, P2 – Risnjak, P3 – Bijele and Samarske stijene, P4 – Zavižan, and P5 – Zečjak.

Morphometric analysis

Following field collection, all mountain currant leaves were immediately pressed between absorbent sheets to ensure flattening and desiccation, and subsequently herbarized. Dried leaves were scanned at 600 dpi using a MICROTEK ScanMaker 4800 and saved in TIFF format. Leaf outlines were analysed using WinFolia™ 2001 software, together with *in situ* photographs from the Bijele and Samarske stijene population (P3). A total of ten morphological parameters were measured (Table 2, Figure 2), including traits related to leaf size and shape. Measurements were performed using the "Leaf Morphology" and "Interactive Measurements" functions, focusing on overall dimensions, petiole length, base angles, and lobe geometry. Acronyms and detailed trait definitions are provided in Table 2.

Statistical analysis

Descriptive statistical analyses were carried out for all examined traits in accordance with the methodology outlined by Sokal and Rohlf (2012). The following parameters were calculated: arithmetic mean, median, minimum, maximum, lower quartile (Q1), upper quartile (Q3), standard deviation, and coefficient of variation (%). These statistics were computed collectively across all samples (45 shrubs) using the dplyr package (Wickham et al. 2025) in R Statistical Software (v4.4.0, R Core Team 2025).

Table 2 Leaf morphometric traits included in this research.

Trait acronym	Trait
LA	Leaf area (cm^2)
LL	Leaf length (cm)
MLW	Maximal leaf width (cm)
PMLW	Distance from the leaf base to the point of maximal leaf width (cm)
PL	Petiole length (cm)
LBA1	Angle closed by the main leaf vein and the line defined by the leaf blade base and a point on the leaf margin at 10% of leaf blade length (°)
LBA2	Angle closed by the main leaf vein and the line defined by the leaf blade base and a point on the leaf margin at 25% of leaf blade length (°)
ALA	Angle between the vectors drawn from the leaf base to the tips of the left and right lobes (°)
SAC	Angle enclosed between the sinuses of the left and right lobes and the apex of the central lobe (°)
LTA	Angle formed by the apex of the left lateral lobe, the apex of the central lobe, and the point at the sinus separating them (°)

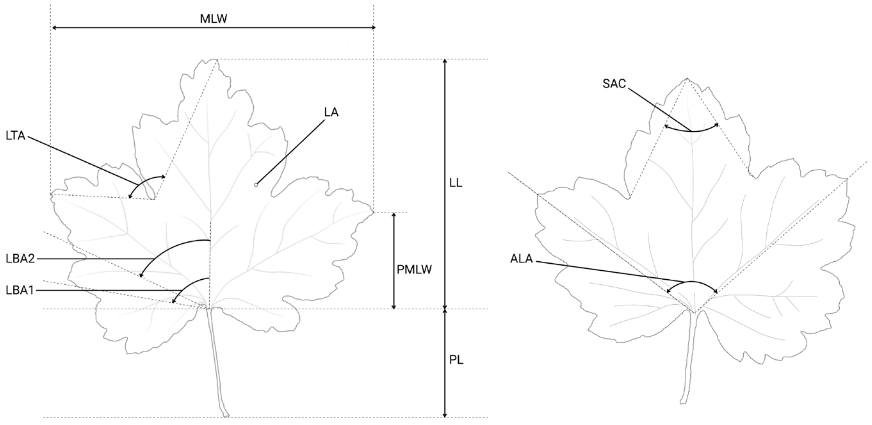

Figure 2 Measured leaf morphological traits of *Ribes alpinum* L. (for description see Table 2). Illustration created by Anamarija Zegnal.

To assess differences among populations, a one-way analysis of variance (ANOVA) was performed for each trait using the aov() function, followed by Tukey's Honest Significant Difference (HSD) test via the TukeyHSD() function. Homogeneous groups were identified with the aid of the multcompView package (Graves et al. 2024), and labelled using letter annotations (e.g., "a", "ab", "b", "bc", "c") to indicate statistically non-significant differences.

Box plots were generated for each trait using ggplot2 package in R (Wickham 2016) to visualize trait distributions across populations. Each box plot displays the first quartile (Q1), third quartile (Q3), and the interquartile range (IQR = Q3 − Q1). The whiskers extend to the smallest and largest values within 1.5 × IQR from the lower and upper quartiles, respectively. Outliers beyond this range are shown as individual points. The median, representing the central tendency of the data, is depicted as a horizontal line within the box. Letter groupings derived from Tukey's HSD tests were displayed above each box to indicate statistically homogeneous groups.

Principal component analysis (PCA) was conducted to examine patterns of variation among individuals and populations based on morphometric traits. The analysis was performed in R using the FactoMineR (Lê et al. 2018), factoextra (Kassambara and Mundt 2020), and ggplot2 (Wickham 2016) packages. Prior to PCA, input variables were standardized, and trait columns were filtered to retain only numerical data. Eigenvalues, explained variance, and loadings were extracted to assess component significance and trait contributions. Visualization outputs included scree plots and variable contribution diagrams, providing insights into trait influence on principal components. A biplot was constructed using the first two principal components, allowing simultaneous interpretation of both individual clustering and variable orientations. Contributions ($\cos^2$ values and percentage influence) of individual traits and samples were calculated and graphically represented to identify patterns of association and structural differentiation among populations.

Euclidean distances were calculated between all pairs of individuals based on their scores from the first two principal components, considering a total of 10 leaf morphological parameters. The mean Euclidean distance within each population was used to derive a multivariate diversity index (MDI) as described by Poljak et al. (2024).

The clustering tendency of the dataset was assessed using the Hopkins statistic, implemented via the hopkins() function from the clustertend package in R (Wright et al. 2023). This test was used to determine the appropriateness of applying cluster-based algorithms. To identify the optimal number of clusters, several validity indices – including silhouette width and within-cluster sum of squares – were examined across multiple k-values. Based on these evaluations, k-values of 3 and 4 were selected for further analysis. K-means clustering was performed using standardized leaf trait variables through the kmeans() function in R. The resulting cluster memberships were visualized using scatter plots generated with the factoextra (Kassambara and Mundt 2020) and ggplot2 (Wickham 2016) packages, providing a graphical overview of the sample distribution across clusters.

To explore the influence of geographic and environmental factors on leaf morphology in *Ribes alpinum*, we performed Redundancy Analysis (RDA) using the vegan package (v2.6-4, Oksanen et al. 2022) within R Statistical Software (v4.4.0, R Core Team 2025). Leaf morphological traits showing lower intercorrelation ($r < 0.85$) and significant population-level differentiation were selected as response variables. Prior to ordination, these traits were Hellinger-transformed to reduce scale dependency and conform to assumptions of constrained ordination. Predictor variables were categorized into two sets: geographic predictors, which included latitude and longitude, and environmental predictors, comprising altitude and bioclimatic variables. Altitude data were obtained independently using GPS measurements, while bioclimatic data were retrieved from WorldClim v2.1 (Fick and Hijmans 2017) at 30 arc-second resolution. Initial environmental dataset included 19 bioclimatic layers; multicollinearity among them was addressed using the vifstep procedure from the usdm package (Naimi et al. 2014), retaining BIO1 (mean annual temperature), BIO9 (mean temperature of the driest quarter), and BIO17 (precipitation of the driest quarter) as final climatic predictors. All predictors were standardized (z-transformed) prior to the analysis. To partition variation attributable to climate and geography, three RDA models were constructed: (1) a full RDA model including both environmental and geographic predictors; (2) a partial RDA where environmental effects were conditioned on geography (environment | geography); and (3) a partial RDA where geographic effects were conditioned on environment (geography | environment). Significance of the models was assessed using permutation tests (999 iterations), and adjusted R^2 was used to evaluate explanatory power. Ordination scores for sites, traits, and predictors were visualized in biplots using ggplot2 (Wickham 2016), with enhancements via ggrepel (Slowikowski 2024) and ggsci palettes (Xiao 2024).

RESULTS

Descriptive statistics for each trait across all 45 shrubs in the overall sample are presented in Table 3. On average, leaves of *Ribes alpinum* measured 1.98 cm in length and 2.21 cm in width, with petioles averaging 1.57 cm. Among all measured traits, the least variable were the leaf base angles (LBA1 and LBA2), with coefficient of variation (CV) values of 3.27% and 3.76%, respectively. Angles obtained through interactive measurements also exhibited low variability, with CVs ranging from 7.81%

Table 3 Descriptive statistics of morphological variability in mountain currant (*Ribes alpinum* L.) across five populations in the Dinaric Alps, Croatia. Trait acronyms as in Table 2.

Trait	Descriptive parameters							
	Mean	Median	Minimum value	Maximum value	1st quartile	3rd quartile	Standard deviation	Coefficient of variation (%)
LA (cm^2)	3.16	2.94	0.96	9.69	2.05	3.42	1.76	55.8
LL (cm)	1.98	1.94	1.21	3.57	1.70	2.06	0.49	24.6
MLW (cm)	2.21	2.05	1.19	3.91	1.90	2.46	0.57	25.7
PMLW (cm)	0.85	0.80	0.47	1.60	0.72	0.93	0.24	27.8
PL (cm)	1.57	1.46	0.71	3.31	1.25	1.83	0.54	34.6
LBA1 (°)	74.8	75.2	65.8	79.0	73.8	76.1	2.44	3.27
LBA2 (°)	61.9	61.8	56.4	67.2	60.5	63.3	2.33	3.76
ALA (°)	111	111	90.1	130	107	117	8.67	7.81
SAC (°)	54.9	54.9	39.0	68.6	50.0	58.5	6.74	12.3
LTA (°)	85.4	84.9	69.2	108	79.5	90.5	7.91	9.25

to 12.3%. In contrast, LA was by far the most variable trait, with a CV of 55.8%, followed by petiole length (PL) at 34.6%. Other traits related to leaf dimensions showed medium to high variability across the sample. Leaf length (LL) had a CV of 24.6%, maximum leaf width (MLW) of 25.7%, and the position of maximum width (PMLW) of 27.8%. Although these values were lower than those for leaf area and petiole length, they still reflected a substantial degree of morphological variation.

Descriptive statistics and results of the Tukey's HSD test are presented in Figure 3. The analysis revealed clear distinctions among populations based on leaf morphology, with statistically significant differences observed in seven out of ten traits: LA, LL, MLW, PMLW, PL, ALA and SAC. Population P3 consistently formed a separate homogeneous group, showing significantly higher values for leaf area (LA), leaf length (LL), maximal leaf width (MLW), petiole length (PL), and the distance to maximal leaf width (PMLW). In contrast, populations P1, P2, and P4, frequently grouped together, showed similar trait values, while P5 displayed intermediate values and occasionally overlapped with other groups. Population P4, within this broader cluster, consistently displayed the lowest median values for LA, LL, MLW, and PMLW. For LL and MLW in particular, P4 formed a distinct homogeneous group, underscoring its tendency toward reduced leaf size compared to all other populations. When examining traits related to leaf base and apex geometry (LBA1, LBA2, and LTA), all populations fell into a single homogeneous group, indicating high uniformity in these structural parameters. Meanwhile, traits associated with lobe configuration – namely ALA and SAC – showed moderate differentiation. For ALA, P4 was grouped with P2 and P3, forming a subset with higher values, whereas P1 and P5 fell into a group with lower trait expression. Regarding SAC, P4 was classified into group "a", while P5 formed a distinct group "b"; the remaining populations (P1, P2, and P3) occupied overlapping groupings ("ab"), indicating intermediate positioning. These patterns suggest that although P4 did not always form an entirely separate group, it consistently tended toward elevated values in lobe angle traits.

The first three principal components had eigenvalues above 1, and explained 92.3% of total variability. The first principal component, which explained 52.7% of total variability, was in a high positive correlation with LA, LL, MLW, PMLW and PL, i.e. all of the morphometric parameters referring to the leaf size. The second principal component explained additional 28.4% of total variability, and was highly positively correlated with LBA1, LBA2 and LTA (Figure 4). Additional 11.2% of total variability was explained by the third principal component, which was positively correlated with SAC. The biplot of the principal component analysis based on 10 morphological parameters is shown in Figure 4. Although most of the samples were highly intermixed, a clear separation of populations Zavižan (P4) and Bijele and Samarske stijene (P3) along the first PC axis is visible. Namely, individuals within population Zavižan (P4) were grouped on the left side of the diagram, and characterized by the smallest leaves, while individuals within population Bijele and Samarske stijene (P3) were grouped on the right side of the diagram and characterized by the largest leaves.

To evaluate morphological variability within populations, a multivariate diversity index (MDI) was calculated for each of the five studied populations based on the mean Euclidean distance between individuals, derived from their scores along the first two principal components encompassing ten leaf morphological traits (Table 1). The highest intra-population diversity was observed in the Bijele and Samarske stijene population (P3, MDI = 4.60), followed by Zavižan (P4, MDI = 3.43), Snježnik (P1, MDI = 3.12), and Zečjak (P5, MDI = 2.84), while the lowest diversity was recorded in Risnjak (P2, MDI = 2.18). These values reveal notable variation in leaf morphology among individuals across populations.

Clustering tendency was confirmed by a high Hopkins statistic (0.9988), indicating a strong underlying structure suitable for clustering. Based on silhouette analysis and other validation indices, both three-cluster (k = 3) and four-cluster (k = 4) solutions were identified as optimal.

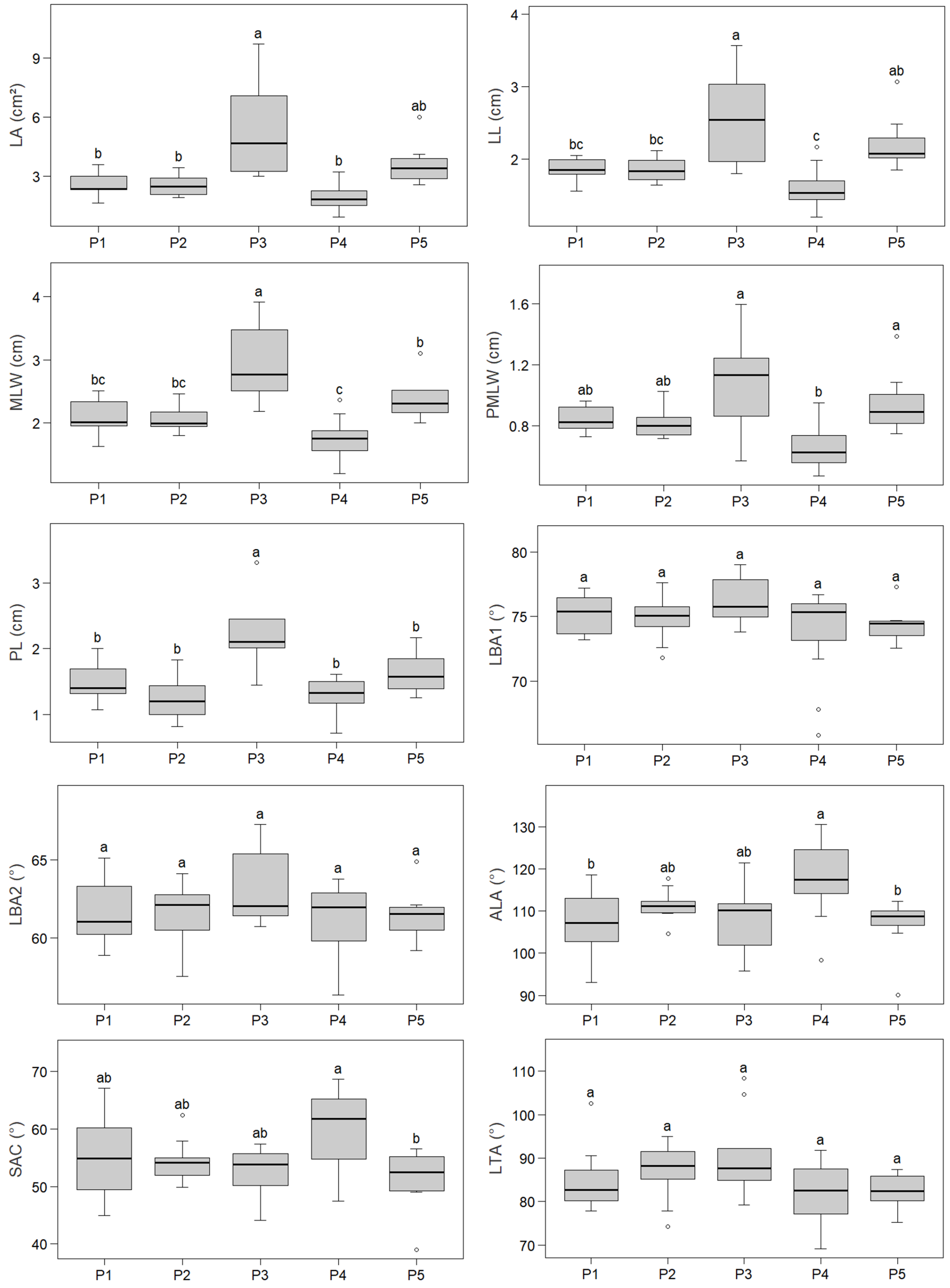

Figure 3 Variation in leaf morphological traits across five natural populations of mountain currant (*Ribes alpinum* L.) in the Dinaric Alps illustrated by box plots showing the first and third quartiles, interquartile range, and median values, with whiskers extending 1.5 times the interquartile range, outliers depicted as individual points, and statistically homogeneous groups identified by letter annotations based on Tukey's HSD tests following one-way ANOVA. Populations labelled as in Table 1 and trait acronyms as in Table 2.

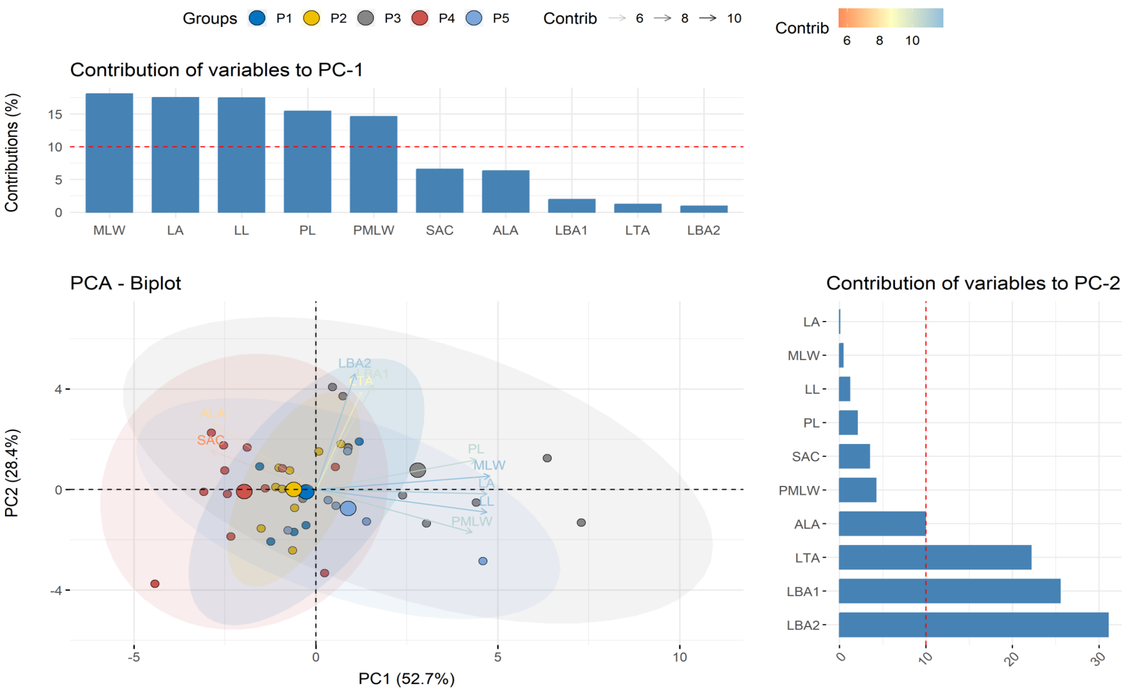

Figure 4 Principal Component Analysis (PCA) of leaf morphological traits in mountain currant (*Ribes alpinum* L.) individuals across five natural populations in the Dinaric Alps. Biplot displays individuals as coloured points based on population affiliation (as in Table 1), with ellipses outlining clustering patterns. Overlaid arrows represent direction and magnitude of morphological traits, with colour shading indicating trait contributions. Accompanying plots (above and to the right) display variable contributions to the PC variance. A red dashed reference line indicates the 10% threshold used to highlight variables with notable contribution. Trait acronyms follow definitions in Table 2.

In the k = 3 configuration (Figure 5), samples from population P3 were predominantly assigned to Cluster 1, forming a distinct group, while most individuals from P1, P2, P4, and P5 appeared in Cluster 2, with scattered assignments to Cluster 3. The k=4 solution provided finer separation (Figure 6), with P3 samples mainly grouped into Cluster 3 and P5 samples frequently into Cluster 1. Populations P1 and P2 showed dominant membership in Cluster 1 but with consistent representation in Cluster 2 as well. Notably, population P4 showed a dominant affiliation with Cluster 4, with 67% of its individuals grouped therein. Although individuals from P4 appeared across all clusters, this concentration in Cluster 4 suggests the emergence of a distinct morphological subset within the population.

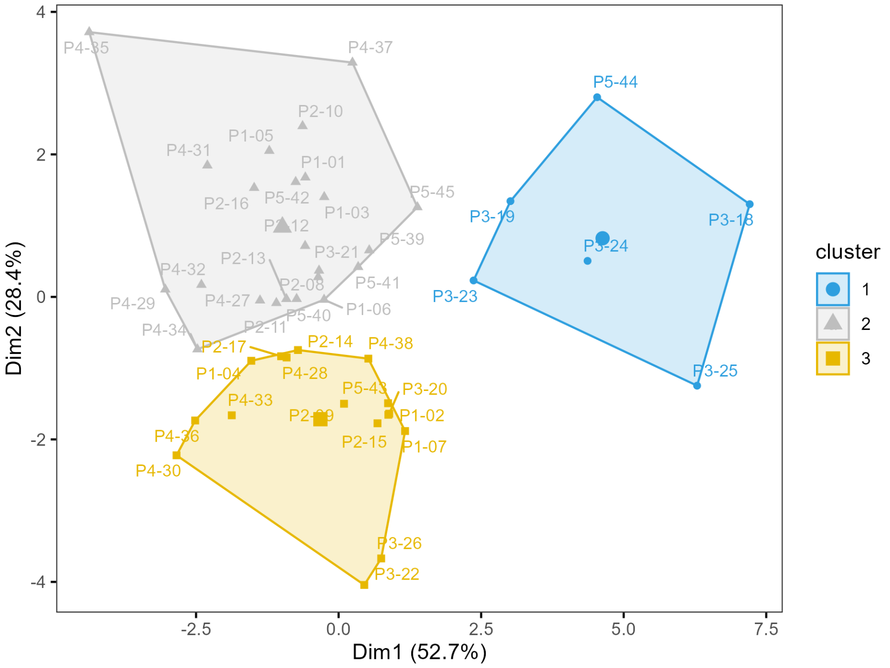

Figure 5 Factor map showing mountain currant (*Ribes alpinum* L.) individuals grouped into three clusters (k = 3) based on leaf morphological traits. Individuals are plotted as smaller symbols coloured by cluster affiliation, with larger symbols representing cluster centroids. Population labels are as in Table 1.

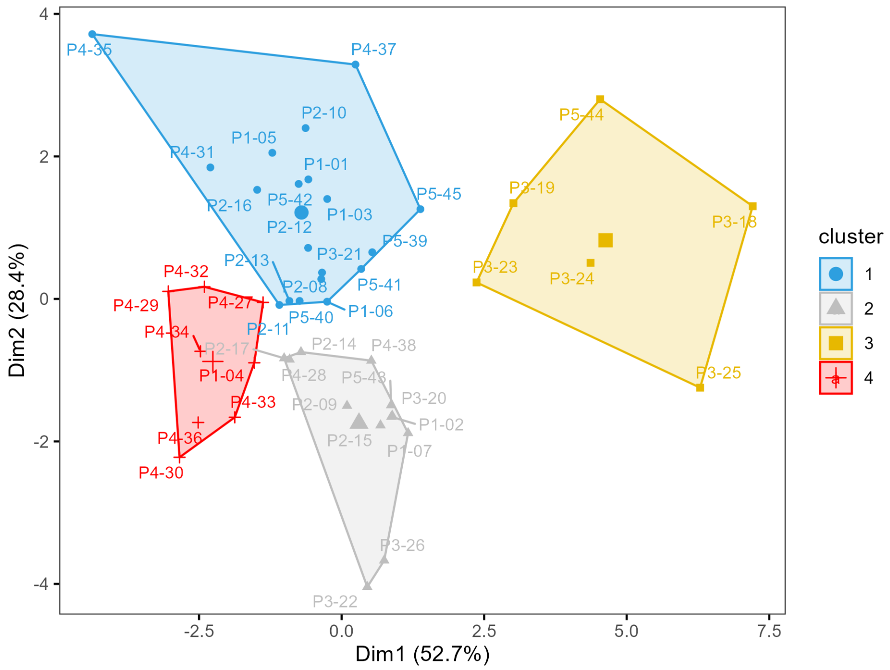

Figure 6 Factor map showing mountain currant (*Ribes alpinum* L.) individuals grouped into four clusters (k = 4) based on leaf morphological traits. Individuals are plotted as smaller symbols coloured by cluster affiliation, with larger symbols representing cluster centroids. Population labels are as in Table 1.

Redundancy analysis (RDA) revealed that environmental factors, including altitude and bioclimatic variables, were the primary drivers of leaf morphological variation in *Ribes alpinum* (Table 4). The full RDA model, which incorporated both environmental and geographic predictors, explained 45.5% of the total variation (adjusted $R^2 = 0.369$) and was statistically significant (F = 5.2966, p = 0.001). After accounting for geographic effects, the pure environmental component remained significant, explaining 19.7% of the variation (adjusted $R^2 = 0.147$, F = 3.4439, p = 0.001). In contrast, the pure geographic effect explained only 1.1% of the variation and was not statistically significant (adjusted $R^2 = -0.019$, F = 0.3904, p = 0.797). These results emphasize the predominant role of local environmental conditions – particularly temperature and elevation – in shaping leaf morphology across populations, whereas spatial position alone did not exhibit a detectable effect once environmental differences were controlled for.

Table 4 Performance metrics for full and partial RDA models assessing the effects of environmental and geographic predictors on leaf morphological variation in mountain currant (*Ribes alpinum* L.). Adjusted R², F-values, and p-values are based on permutation tests with 999 iterations.

Model	Predictors/effect	R^2	R^2_{adj}	F-value	p-value
RDA_{full}	Environment + Geography	0.455	0.369	5.2966	0.001
$pRDA_{env}$	Environment | Geography	0.197	0.147	3.4439	0.001
$pRDA_{geo}$	Geography | Environment	0.011	-0.019	0.3904	0.797

The RDA ordination plot (Figure 7) provides a visual representation of the relationship between leaf morphological traits and the underlying environmental and geographic gradients. The strongest contributors to the first RDA axis (RDA1), which explains the majority of constrained variation, were BIO1 (annual mean temperature) and altitude. These variables showed high loadings on RDA1 (BIO1 = 0.798; altitude = –0.721) and were highly correlated with leaf morphology ($r^2 = 0.372$ and 0.305, respectively; p = 0.001), indicating that temperature and elevation are the primary environmental drivers of trait divergence in *Ribes alpinum*. Conversely, BIO9 (mean temperature of the driest quarter), BIO17 (precipitation of the driest quarter), and geographic coordinates (latitude and longitude) had low r^2 values and were not statistically significant ($p > 0.1$), suggesting minor or negligible influence on morphological variation. Loadings on RDA2 were generally lower, and none of the predictors showed strong contribution to this axis, implying that most variation is captured along RDA1.

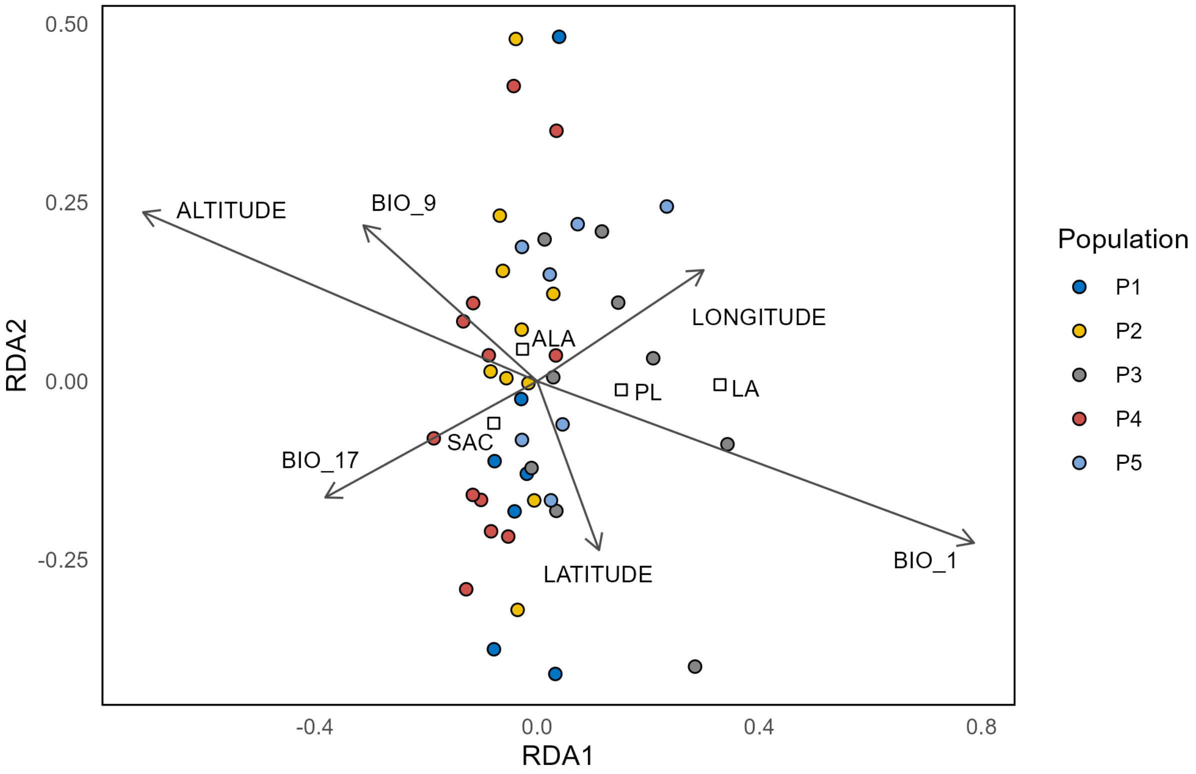

Figure 7 RDA ordination plot visualizing population–level variation in leaf morphological traits of mountain currant (*Ribes alpinum* L.) in relation to environmental and geographical gradients across five natural populations. Individuals are shown as coloured circles grouped by population (labels as in Table 1), morphological traits are displayed as square markers (acronyms as in Table 2), and environmental/geographic predictors are represented by vectors indicating direction and magnitude of association. The ordination highlights spatial and ecological structuring of trait variation.

DISCUSSION

The morphological data obtained from five natural populations of *Ribes alpinum* across the Dinaric Alps of Croatia reveal pronounced variation in leaf size and shape, underscoring the complexity of phenotypic expression within the species. This variation reflects differing degrees of developmental stability and plasticity across measured traits. Leaf dimension traits – such as length, width, and petiole length – showed moderate to high variability, suggesting that these parameters are particularly sensitive to microenvironmental influences. Notably, petiole length and total leaf area were especially variable, potentially indicating functional adjustments linked to photosynthetic optimization or mechanical support (Takenaka 1994, Filartiga et al. 2022). In contrast, shape-related traits – especially those quantifying leaf geometry – remained remarkably consistent across individuals and populations, implying structural conservatism and reduced environmental responsiveness. This contrast between size-related plasticity and geometric stability highlights the multifactorial architecture of leaf morphology, where certain traits exhibit dynamic shifts, while others are under tighter developmental or genetic control.

The analysis of morphological variability revealed significant differences among populations in seven out of ten measured traits, with leaf size parameters showing the greatest divergence. This suggests that populations of *Ribes alpinum* differ more in the overall dimensions of their leaves than in their geometric shape, pointing to a stronger influence of phenotypic plasticity in size-related traits. Among all populations, P3 (Bijele and Samarske stijene) exhibited the highest within-population variability (MDI = 4.60), likely reflecting the exceptional habitat heterogeneity of this site (Vucelić 1987, Sirovica 2025). The landscape is characterized by rocky outcrops, shallow soil pockets, and transition zones along fir–spruce forest edges. Many shrubs were found growing in these marginal microhabitats, where soil depth and moisture availability change drastically over short distances. Such spatial heterogeneity may foster plastic responses in leaf morphology, enabling individual plants to modulate their traits in response to localized environmental conditions (Körner 2003, Boucher et al. 2013, Opedal et al. 2015).

Multivariate analyses revealed clear morphological structuring among populations of *Ribes alpinum*, with PCA and k-means clustering consistently distinguishing P3 (Bijele and Samarske stijene) and P4 (Zavižan) as the most divergent groups. Although PCA showed partial overlap among individuals, the first principal component – strongly associated with leaf size traits – separated P3 and P4 along a clear gradient. P3, sampled from the lowest elevation site (1280 m), was characterized by larger leaves and formed a coherent cluster in both k = 3 and k = 4 solutions. In contrast, P4, from the highest elevation site (1608 m), exhibited markedly smaller leaves and showed dominant affiliation with Cluster 4 in the k = 4 configuration, suggesting the emergence of a distinct high-altitude morphotype. These patterns align with broader ecological findings that leaf size tends to decrease with increasing altitude due to lower temperatures, increased solar radiation, and reduced atmospheric pressure, which collectively constrain leaf expansion and favour compact morphologies for thermal and hydraulic efficiency (Körner et al. 1986, Körner 2003, Milla and Reich 2011). Whether these morphological differences stem primarily from phenotypic plasticity – flexible trait expression under environmental influence – or represent true local adaptation driven by selective pressures, remains uncertain. Phenotypic plasticity likely enables populations to modulate trait expression in response to environmental variability (Crispo 2008). However, when such plastic responses are consistently favoured across generations, they may become developmentally canalized and ultimately contribute to adaptive divergence. In reality, both mechanisms often act in tandem (Nicotra et al. 2010, Nonaka et al. 2015), and their relative contribution may vary across traits, environments, and populations.

Recent studies further suggest that phenotypic plasticity may be mediated by epigenetic mechanisms, particularly DNA methylation, which has been shown to increase in variance under stressful conditions such as elevated radiation (Nicotra et al. 2015). These epigenetic modifications can influence ecologically relevant traits without altering the underlying genetic code, providing a rapid and reversible source of phenotypic variation (Rapp and Wendel 2005, Bossdorf et al. 2008). Although direct evidence remains limited, such mechanisms may contribute to the observed morphological shifts in alpine plant populations, including *Ribes alpinum*, and enhance their capacity to persist under changing climatic conditions.

Redundancy Analysis (RDA) revealed that geographic coordinates – specifically latitude and longitude – did not significantly contribute to the observed morphological variation among populations of *Ribes alpinum*. This suggests that horizontal spatial positioning across the Dinaric Alps has limited explanatory power for leaf trait variability (Vidaković et al. 2025). In contrast, elevation-related environmental gradients – such as temperature, solar radiation, and habitat structure – emerged as the dominant factors influencing morphological differentiation. These vertical gradients shape microclimatic conditions more directly and consistently than geographic location (Körner et al. 1986, Körner 2003, 2007), especially in mountainous terrain where ecological transitions occur over short distances. The lack of correlation with geographic coordinates reinforces the idea that local environmental pressures, rather than broad spatial separation, are the main drivers of trait variation in *Ribes alpinum* across the Croatian Dinarides. Comparable findings were reported for *Dianthus sylvestris* Wulfen in the Balkan Peninsula, where environmental factors were shown to play a potentially more important role than geography in shaping morphological variability (Terlević et al. 2023).

Although our study revealed a clear elevational signal in leaf morphology, particularly in leaf size traits, it is important to note that elevation does not uniformly shape plant traits across species or even within species (de Villemereuil et al. 2018, Lampei et al. 2019, Liu et al. 2023, Vidaković et al 2025). Notably, phenotypic responses are often population-specific (Pfennigwerth et al. 2017), as illustrated in our dataset by population P5, which occupies a relatively high elevation, slightly lower than P4, yet displayed intermediate leaf sizes compared to both lower (P3) and higher (P4) elevation populations. This unexpected pattern may reflect microhabitat complexity within the sampling area: individuals from P5 occurred along a transitional ecotone between subalpine dwarf pine stands and the upper belt of beech-dominated montane forests, potentially experiencing moderate light, soil, and temperature conditions. Such ecotonal zones can buffer plants from extreme alpine stressors or lowland competition, resulting in intermediate trait expression. Similar population-specific responses have been documented in other woody taxa. For instance, Pfennigwerth et al. (2017) found that trait variation in *Rhododendron maximum* L. across elevation gradients in the Appalachian Mountains was largely driven by phenotypic plasticity, with trait–environment associations differing significantly across sites. This suggests that morphological differentiation along elevational gradients arises through a spectrum of plastic and genetic mechanisms, whose relative contributions vary among taxa, traits, and ecological settings.

Additional observations from cultivated specimens of *Ribes alpinum* grown in Croatian arboreta and botanical gardens – typically located at low elevations, slightly above 100 m a.s.l. – provide compelling evidence of the species' morphological responsiveness to environmental variation. In these lowland settings, leaves were consistently larger than those recorded in natural montane populations, often exceeding the upper range documented in our study. Moreover, cultivated plants exhibited a near-complete absence of trichomes, which are otherwise prominent on leaves from high-altitude habitats. These differences suggest that phenotypic plasticity in *Ribes alpinum* extends beyond leaf size to include surface traits, highlighting the species' capacity to modulate its morphology in response to habitat structure and elevation. These observations are further supported by data from dendrological literature, which typically reports leaf sizes ranging from 3 to 5 cm (Hegi 1961, Krüssmann 1962, Schütt 2011), in contrast to the average dimensions of approximately 2 cm recorded in our montane samples. This discrepancy likely reflects the limited ecological scope of earlier descriptions, probably based on herbarium specimens of lowland populations from the northern parts of the species' natural range, where *Ribes alpinum* is known to occur in lowland habitats (Weber 1995, Schütt 2011). In contrast, our findings, derived from *in situ* sampling across diverse high-elevation sites in the Dinaric Alps, underscore the importance of ecological context in morphological assessments and highlight the need for geographically and environmentally inclusive trait documentation.

Taken together, these results emphasize the practical significance of integrating field-based measurements with broader ecological and biogeographical perspectives. By capturing both inter- and intra-population variability, such studies not only refine species-level trait descriptions but also contribute to a deeper understanding of how environmental gradients shape plant morphology. This has implications for conservation, habitat management, and predictive modelling under changing climatic conditions, in which trait plasticity may play a key role in species resilience and adaptive potential.

CONCLUSIONS

The morphometric analysis of *Ribes alpinum* populations in the Dinaric Alps revealed substantial variation in leaf traits, primarily driven by elevation-related environmental gradients rather than geographic positioning. Leaf size traits exhibited greater variability than shape-related parameters, suggesting a strong role of phenotypic plasticity in response to local microclimatic conditions. Populations from contrasting altitudes – particularly P3 and P4 – showed clear morphological differentiation, with P3 also displaying the highest within-population diversity, likely due to its heterogeneous habitat. RDA confirmed that latitude and longitude had no significant influence on trait variation, reinforcing the importance of vertical ecological gradients in shaping plant morphology in mountainous landscapes. These findings highlight the adaptive flexibility of *Ribes alpinum* and underscore the ecological value of the Dinaric Alps as a natural setting for studying intraspecific variation and environmental adaptation.

ACKNOWLEDGMENT

This research was supported by funding from the University of Zagreb. The authors thank the staff of North Velebit National Park and Risnjak National Park for their kind assistance during fieldwork. All field activities were conducted in accordance with institutional, national, and international regulations concerning biodiversity research and sample collection. Permission to collect plant material was granted by the Ministry of Economy and Sustainable Development of the Republic of Croatia (Permit Nos. UP/I 612-07/21-33/57 and UP/I-352-04/24-08/18).

REFERENCES

- Bossdorf, O., C.L. Richards, M. Pigliucci, 2008: Epigenetics for ecologists. Ecology Letters 11 (2): 106–115. https://doi.org/10.1111/j.1461-0248.2007.01130.x
- Boucher, F.C., W. Thuiller, C. Arnoldi, C.H. Albert, S. Lavergne, 2013: Unravelling the architecture of functional variability in wild populations of *Polygonum viviparum* L. Functional Ecology 27 (2): 382–392. https://doi.org/10.1111/1365-2435.12034
- Brus, R., 2010: Growing evidence for the existence of glacial refugia of European beech (*Fagus sylvatica* L.) in the south-eastern Alps and north-western Dinaric Alps. Periodicum biologorum 112 (3): 239–246. https://hrcak.srce.hr/58182
- Bruun, H.H., J. Moen, R. Virtanen, J.-A. Grytnes, L. Oksanen, A. Angerbjörn, 2006: Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science 17 (1): 37–46. https://doi.org/10.1111/j.1654-1103.2006.tb02421.x
- Bueno de Mesquita, C.P., L.S. Tillmann, C.D. Bernard, K.C. Rosemond, N.P. Molotch, K.N. Suding, 2018: Topographic heterogeneity explains patterns of vegetation response to climate change (1972–2008) across a mountain landscape, Niwot Ridge, Colorado. Arctic, Antarctic, and Alpine Research 50 (1): e1504492. https://doi.org/10.1080/15230430.2018.1504492
- Crispo, E., 2008: Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. Journal of Evolutionary Biology 21 (6): 1460–1469. https://doi.org/10.1111/j.1420-9101.2008.01592.x.
- Dakskobler, I., A. Rozman, 2021: Vegetation analysis of the subalpine beech forest on the upper forest line in the Julian Alps (NW Slovenia and NW Italy) and in the northern Dinaric Alps. Hacquetia 20: 373–564. https://doi.org/10.2478/hacq-2021-0013
- Ellenberg, H., 1979: Zeigerwerte der Gefäßpflanzen Mitteleuropas. Verlag E. Goltze, Göttingen.
- Fick, S.E., R.J. Hijmans, 2017: WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302–4315. https://doi.org/10.1002/joc.5086
- Filartiga, A.L., A. Klimeš, J. Altman, M.P. Nobis, A. Crivellaro, F. Schweingruber, J. Doležal, 2022: Comparative anatomy of leaf petioles in temperate trees and shrubs: the role of plant size, environment and phylogeny. Annals of Botany 129 (5): 567–582. https://doi.org/10.1093/aob/mcac014
- Flantua, S.G.A., D. Payne, M.K. Borregaard, C. Beierkuhnlein, M.J. Steinbauer, S. Dullinger, F. Essl, S.D.H. Irl, D. Kienle, H. Kreft, B. Lenzner, S.J. Norder, K.F. Rijsdijk, S.B. Rumpf, P. Weigelt, R. Field, 2020: Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. Global Ecology and Biogeography 29 (7): 1193–1208. https://doi.org/10.1111/geb.13155

- Ford, K.R., A.K. Ettinger, J.D. Lundquist, M.S. Raleigh, J. Hille Ris Lambers, 2013: Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape. PLoS ONE 8 (6): e65008. https://doi.org/10.1371/journal.pone.0065008
- Gonzalo-Turpin, H., L. Hazard, 2009: Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. Journal of Ecology 97: 742–751. https://doi.org/10.1111/j.1365-2745.2009.01509.x
- Graves, S., H. Piepho, S. Dorai-Raj, 2024: multcompView: Visualizations of Paired Comparisons. R package version 0.1-10. https://CRAN.R-project.org/package=multcompView
- Hanjalić Kurtović, J., B. Kalamujić Stroil, S. Siljak-Yakovlev, N. Pojskić, A. Durmić-Pašić, A. Hajrudinović-Bogunić, L. Lasić, L. Ušanović, F. Bogunić, 2025: Spatial distribution of genetic, ploidy, and morphological variation of the edaphic steno-endemic *Alyssum moellendorfianum* (Brassicaceae) from the Western Balkans. Plants 14: 146. https://doi.org/10.3390/plants14020146.
- Hegi, G., 1961: Illustrierte Flora von Mitteleuropa. Band IV, Teil 2A, Verlag Paul Parey, Berlin, Hamburg.
- Horvat, I., 1937: Pregled šumske vegetacije u Hrvatskoj. Šumarski list 61 (7–8): 337–344.
- Idžojtić, M., 2019: Dendrology: Cones, flowers, fruits and seeds. Elsevier-Academic Press, London, San Diego, Cambridge, Oxford.
- Kassambara, A., F. Mundt, 2020: factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7.999. https://github.com/kassambara/factoextra
- Ke, X., H. Kang, Y. Tang, 2022: Reduction in leaf size at higher altitudes across 39 broad-leaved herbaceous species on the northeastern Qinghai-Tibetan Plateau. Journal of Plant Ecology 15: 1227–1240. https://doi.org/10.1093/jpe/rtac051
- Körner, C., 2003: Alpine plant life: Functional plant ecology of high mountain ecosystems. Springer, Berlin, Heidelberg.
- Körner, C., 2007: The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22 (11): 569–574. https://doi.org/10.1016/j.tree.2007.09.006
- Körner, C., M. Neumayer, S. Menendez-Riedl, A. Smeets-Scheel, 1989: Functional morphology of mountain plants. Flora 182: 353–383. https://doi.org/10.1016/S0367-2530(17)30426-7
- Körner, C., P. Bannister, A.F. Mark, 1986: Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. Oecologia 69: 577–588. https://doi.org/10.1007/BF00410366
- Krüssmann, G., 1962: Handbuch der Laubgehölze. Paul Parkey Verlag, Berlin.
- Lampei, C., J.-W. Wunder, T. Wilhalm, K.J. Schmid, 2019: Microclimate predicts frost hardiness of alpine *Arabidopsis thaliana* populations better than elevation. Ecology and Evolution 9 (20): 11471–11481. https://doi.org/10.1002/ece3.5659
- Lê, S., J. Josse, F. Husson, 2008: FactoMineR: A Package for Multivariate Analysis. Journal of Statistical Software 25 (1): 1–18. https://doi.org/10.18637/jss.v025.i01
- Liber, Z., B. Surina, T. Nikolić, D. Škrtić, Z. Šatović, 2020: Spatial distribution, niche ecology and conservation genetics of *Degenia velebitica* (Brassicaceae), a narrow endemic species of the northwestern Dinaric Alps. Plant Systematics and Evolution 306: 64. https://doi.org/10.1007/s00606-020-01695-3
- Liu, J.M., J.M. de Vos, C. Körner, Y. Yang, 2023: Phylogeny and phenotypic adjustments drive functional traits in *Rhododendron* across elevations in its diversity hot-spot in W-China. Alpine Botany 133: 69–84. https://doi.org/10.1007/s00035-023-00294-5
- Liu, W., L. Zheng, D. Qi, 2020: Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. Ecology and Evolution 10 (15): 8166–8175. https://doi.org/10.1002/ece3.6519
- Lomolino, M.V., 2001: Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10 (1): 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x
- Médail, F., A.C. Monnet, D. Pavon, T. Nikolić, P. Dimopoulos, G. Bacchetta, J. Arroyo, Z. Barina, M.C. Albassatneh, G. Domina, B. Fady, V. Matevski, S. Mifsud, A. Leriche, 2019: What is a tree in the Mediterranean Basin hotspot? A critical analysis. Forest Ecosystems 6: 17. https://doi.org/10.1186/s40663-019-0170-6
- Médail, F., K. Diadema, 2009: Glacial refugia influence plant diversity patterns in the Mediterranean Basin. Journal of Biogeography 36: 1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x
- Milla, R., P.B. Reich, 2011: Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing altitude. Annals of Botany 107: 455–465. https://doi.org/10.1093/aob/mcq261
- Moles, A.T., S.W. Laffan, M. Keighery, R.L. Dalrymple, M.L. Tindall, S.-C. Chen, 2020: A hairy situation: Plant species in warm, sunny places are more likely to have pubescent leaves. Journal of Biogeography 47 (9): 1934–1944. https://doi.org/10.1111/jbi.13870
- Naimi, B., N.A.S. Hamm, T.A. Groen, A.K. Skidmore, A.G. Toxopeus, 2014: Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2): 191–203. https://doi.org/10.1111/ecog.00571
- Neuner, G., 2014: Frost resistance in alpine woody plants. Frontiers in Plant Science 5: 654. https://doi.org/10.3389/fpls.2014.00654
- Nicotra, A.B., O.K. Atkin, S.P. Bonser, A.M. Davidson, E.J. Finnegan, U. Mathesius, P. Poot, M.D. Purugganan, C.L. Richards, F. Valladares, M. van Kleunen, 2010: Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15: 684–692. https://doi.org/10.1016/j.tplants.2010.09.008
- Nicotra, A.B., D.L. Segal, G.L. Hoyle, A.W. Schrey, K.J.F. Verhoeven, C.L. Richards, 2015: Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant. Ecology and Evolution 5 (3): 634–647. https://doi.org/10.1002/ece3.1329
- Nonaka, E., R. Svanbäck, X. Thibert-Plante, G. Englund, Å. Brännström, 2015: Mechanisms by which phenotypic plasticity affects adaptive divergence and ecological speciation. The American Naturalist 186 (5): 126–143. https://doi.org/10.1086/683231.
- Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, H. Wagner, 2022: vegan: Community Ecology Package. R package version 2.6-4. https://CRAN.R-project.org/package=vegan
- Opedal, Ø.H., W.S. Armbruster, B.J. Graae, 2015: Linking small-scale topography with microclimate, plant species diversity and intraspecific trait variation in an alpine landscape. Plant Ecology and Diversity 8 (3): 305–315. https://doi.org/10.1080/17550874.2014.98733
- Perrigo, A., C. Hoorn, A. Antonelli, 2019: Why mountains matter for biodiversity. Journal of Biogeography 46 (10): 2105–2114. https://doi.org/10.1111/jbi.13731
- Poljak, I., M. Idžojtić, I. Šapić, P. Korijan, J. Vukelić, 2018: Diversity and structure of Croatian continental and Alpine-Dinaric populations of grey alder (*Alnus incana* [L.] Moench subsp. *incana*): isolation by distance and environment explains phenotypic divergence. Šumarski list 142 (1–2): 19–31. https://doi.org/10.31298/sl.142.1-2.2

- Poljak, I., Z. Šatović, A. Vidaković, K. Tumpa, M. Idžojtić, 2024: Population variability of rosemary willow (*Salix eleagnos* Scop.) based on the leaf morphometry: Evidence of small and large-leaf morphotypes. Šumarski list 148 (5–6): 219–235. https://doi.org/10.31298/sl.148.5-6.1
- R Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
- Rai, S., N. Breme, V. Jandova, V. Lanta, J. Altman, A.T. Ruka, C. Rixen, J. Dolezal, 2025: Growth dynamics and climate sensitivities in alpine cushion plants: insights from *Silene acaulis* in the Swiss Alps. Alpine Botany 135: 79–89. https://doi.org/10.1007/s00035-024-00318-8
- Rapp, R.A., J.F. Wendel, 2005: Epigenetics and plant evolution. New Phytologist 168: 81–91. https://doi.org/10.1111/j.1469-8137.2005.01491.x
- Schütt, P., 2011: *Ribes alpinum*. In (Roloff, A., H. Weisberger, U.M. Lang, B. Stimm, P. Schütt, eds.): Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie. Wiley-VCH, Weinheim.
- Sirovica, I., 2025: Florističke i vegetacijske značajke Strogoga rezervata Bijele i Samarske stijene. PhD Thesis, University of Zagreb Faculty of Forestry and Wood Technology, Zagreb, Croatia.
- Slowikowski, K., 2024: ggrepel: Automatically Position Non-Overlapping Text Labels with 'ggplot2'. R package version 0.9.6. https://CRAN.R-project.org/package=ggrepel
- Sokal, R.R., F.J. Rohlf, 2012: Biometry: The principles and practice of statistics in biological research. W.H. Freeman and Co., New York.
- Steinbauer, M.J., J.-A. Grytnes, G. Jurasinski, A. Kulonen, J. Lenoir, H. Pauli, C. Rixen, M. Winkler, M. Bardy-Durchhalter, E. Barni, A.D. Bjorkman, F.T. Breiner, S. Burg, P. Czortek, M.A. Dawes, A. Delimat, S. Dullinger, B. Erschbamer, V.A. Felde, O. Fernández-Arberas, K.F. Fossheim, D. Gómez-García, D. Georges, E.T. Grindrud, S. Wipf, 2018: Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556: 231–234. https://doi.org/10.1038/s41586-018-0005-6
- Steinbauer, M.J., R. Field, J.-A. Grytnes, P. Trigas, C. Ah-Peng, F. Attorre, H.J.B. Birks, P.A.V. Borges, P. Cardoso, C.-H. Chou, M. De Sanctis, M.M. de Sequeira, M.C. Duarte, R.B. Elias, J.M. Fernández-Palacios, R. Gabriel, R.E. Gereau, R.G. Gillespie, J. Greimler, D.E.V. Harter, T.-J. Huang, S.D.H. Irl, D. Jeanmonod, A. Jentsch, A.S. Jump, C. Kueffer, S. Nogué, R. Otto, J. Price, M.M. Romeiras, D. Strasberg, T. Stuessy, J.-C. Svenning, O.R. Vetaas, C. Beierkuhnlein, 2016: Topography-driven isolation, speciation and a global increase of endemism with elevation. Global Ecology and Biogeography 29 (7): 1193–1208. https://doi.org/10.1111/geb.12469
- Takenaka, A., 1994: Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. Ecological Research 9 (2): 109–114. https://doi.org/10.1007/BF02347485
- Terlević, A., M. Temunović, S. Bogdanović, M. Grgurev, I. Ljubičić, I. Rešetnik, 2023: Morphological and environmental variability of *Dianthus sylvestris* (Caryophyllaceae) in the Balkan Peninsula. Botanical Journal of the Linnean Society 201 (3): 377389. Https://doi.org/10.1093/botlinnean/boac045
- Vidaković, A., M. Vuković, A. Vuković, M. Magdić, V. Gašparović, I. Poljak, 2025: Evaluation of fruit and leaf morphological variability in bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) Dinaric Alps populations. Šumarski list 149 (7–8): 353–363. https://doi.org/10.31298/sl.149.7-8.4
- Vucelić, N., 1987: Tipološka istraživanja i ekološko-gospodarski tipovi šuma. Šumarski list 111 (7–9): 414–422.
- Vukelić, J., 2012: Šumska vegetacija Hrvatske. Sveučilište u Zagrebu, Fakultet šumarstva i drvne tehnologije, Zagreb.
- Vukelić, J., A. Alegro, D. Baričević, V. Šegota, I. Šapić, 2011: Fitocenoze obične smreke (*Picea abies* (L.) Karsten) u altimontanskom i subalpinskom pojasu Hrvatske. Glasnik za šumske pokuse 44: 29–46.
- Vukelić, J., Đ. Rauš, 1998: Šumarska fitocenologija i šumske zajednice u Hrvatskoj. Sveučilište u Zagrebu, Zagreb.
- Wang, H., R. Wang, S.P. Harrison, I.C. Prentice, 2022: Leaf morphological traits as adaptations to multiple climate gradients. Journal of Ecology 110 (6): 1344–1355. https://doi.org/10.1111/1365-2745.13873
- Watts, S.H., D.K. Mardon, C. Mercer, D. Watson, H. Cole, R.F. Shaw, A.S. Jump, 2022: Riding the elevator to extinction: Disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. Biological Conservation 272: 109620. https://doi.org/10.1016/j.biocon.2022.109620
- Weber, H.E., 1995: *Ribes alpinum*. In (Conert H.J., J.J. Jäger, J.W. Kadereit, W. Schulze-Motel, G. Wagenitz, H.E. Weber, eds.): Illustrierte Flora von Mitteleuropa, Band IV. Teil 2A, Blackwell Wissenschaft, Berlin.
- Wickham, H., 2016: ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York. https://ggplot2.tidyverse.org
- Wickham, H., R. François, L. Henry, K. Müller, D. Daughan, 2025: dplyr: A grammar of data manipulation. R package version 1.1.4, https://dplyr.tidyverse.org.
- WinFoliaTM, 2001: version PRO 2005b. Regent Instruments Inc., Quebec City.
- Wright, K., Y. Luo, R. Zeng, 2023: clustertend: Check the Clustering Tendency. R package version 1.7. https://CRAN.R-project.org/package=clustertend
- Xiao, N., 2024: ggsci: Scientific Journal and Sci-Fi Themed Color Palettes for 'ggplot2'. R package version 3.2.0. https://CRAN.R-project.org/package=ggsci
- Zhang, Y., J. Chen, H. Sun, 2021: Alpine speciation and morphological innovations: revelations from a species-rich genus in the northern hemisphere. AoB Plants 13 (3): plab018. https://doi.org/10.1093/aobpla/plab018