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ECOLOGICAL DIFFERENTIATION AND ALTITUDINAL ZONATION OF SPECIES OF THE SUBGENUS *CAMPANULA* IN AZERBAIJAN

Asya Akbarova^{a*}, Rashad Salimov^b

^aInstitute of Botany of Ministry of Science and Education of the Republic of Azerbaijan, A.Abbaszada 99, Az1073, Baku, Azerbaijan

^bSumgait State University, Ministry of Science and Education of the Republic of Azerbaijan, 43rd mcr., Baku st. 1, AZ5008, Sumgait, Azerbaijan

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Abstract

Understanding the bioecological characteristics of plant species is essential for both systematics and conservation planning. Here we analyze the ecological responses of 16 species of the subgenus *Campanula* distributed in Azerbaijan and assess their differentiation along elevation gradients. Field surveys across multiple regions and elevation zones were combined with herbarium evidence and authoritative taxonomic databases to verify identifications. Species were classified into ecological groups by light, water, and substrate preferences, and their presence across altitudinal belts was summarized. Similarity in species composition among belts was quantified using the Sorensen–Czekanowski coefficient. Most species are shade-tolerant with mesophytic water requirements and petrophytic substrate affinities. The lower mountain belt harbors the highest share of species (62.5%), followed by the subalpine–alpine belts (56.25%), the middle mountain belt (25%), and the high mountain belt (18.75%). Pairwise similarity is highest between the lower mountain and subalpine–alpine belts ($S = 0.53$) and lowest between the middle and high mountain belts ($S = 0$). These patterns highlight ecological plasticity within *Campanula*, with several species spanning multiple light and moisture groups and occurring across two or more elevation zones.

Keywords: *Ecological gradients; Altitudinal belts; Heliophyte; Mesophyte; Xerophyte; Petrophyte; Sorensen–Czekanowski similarity*

1. Introduction

The genus *Campanula* L. (Campanulaceae) is one of the species-rich plant groups of the Northern Hemisphere, widely distributed across Europe, the Caucasus, the Mediterranean basin and parts of Western Asia. It occupies a broad ecological amplitude, ranging from lowland meadows to alpine grasslands. The genus comprises nearly 600 species worldwide and includes a substantial number of taxa endemic to the Caucasus, underscoring the floristic uniqueness of the region [1, 10]. In the Caucasus, including Azerbaijan, *Campanula* contributes significantly to regional biodiversity; however, the ecological characteristics and elevational distributions of many local taxa remain insufficiently synthesized.

Understanding how species partition environmental space across mountain belts, and how they respond to light, moisture, and substrate conditions, is essential for refining taxonomic concepts, informing conservation strategies, and anticipating ecological responses to environmental change.

This study compiles verified records for 16 species of the subgenus *Campanula* (*C. glomerata* L., *C. latifolia* L., *C. odontosepala* Boiss., *C. rapunculoides* L., *C. bononiensis* L., *C. sibirica* L., *C. alliariifolia* Willd., *C. sclerotricha* Boiss., *C. sarmatica* Ker – Gawl., *C. collina* Sims., *C. kolenatiana* C.A.Mey., *C.*

armena Stev., *C. zangezura* (Lipsky) Kolak et Serdyuk., *C. bayerniana* Rupr., *C. lezgina* (Alexeenko) Kolak et Serdyuk. and *C. coriacea* P.H.Davis.) occurring in Azerbaijan and evaluates: (i) ecological grouping by light availability, water relations, and substrate preference; (ii) species distribution across lower, middle, subalpine–alpine, and high mountain belts; and (iii) the compositional similarity among these belts [4, 11]. Field observations are supplemented by herbarium and database documentation.

2. Materials and Methods

Sixteen species of the subgenus *Campanula* occurring in Azerbaijan were examined. Taxonomic identities and nomenclature were verified using modern databases (Euro+Med, IPNI, WFO) and herbarium specimens from BAK, supplemented by virtual collections (GBIF, JSTOR, JACQ) [3, 5–8, 13].

Targeted fieldwork was conducted across multiple elevational zones, from lowlands to subalpine and alpine belts. For each species, habitat characteristics (e.g., rocky slopes, forest margins, subalpine tall- herb communities, shrublands, gardens, stony debris) were recorded. Species were assigned to ecological groups based on light (heliophyte, sciophyte, shade- tolerant), water relations (mesophyte, xerophyte, mesoxerophyte), and substrate preference (calciphyte, petrophyte, mesophilous, ruderal), using diagnostic traits, literature, herbarium specimens, and field observations.

Species occurrences were summarized for four mountain belts: lower mountain, middle mountain, subalpine–alpine, and high mountain. Compositional similarity between belts was quantified using the Sørensen–Czekanowski coefficient [2, 9, 12]:

$$S = 2C / (A + B)$$

where,

- C is the number of species shared by both belts,
- A is the total number of species count in the first mountain belt,
- B is the total number of species count in the second mountain belt.

Values of $S=1$ indicate complete similarity, $S=0$ indicates no similarity, and $0 < S < 1$ indicates partial similarity.

Figures illustrating ecological grouping and altitudinal patterns are also provided.

3. Results and Discussions

The ecological differentiation of the studied *Campanula* species reveals consistent patterns across light, water, substrate, and altitudinal gradients.

1) Light preferences. Heliophytes dominate the assemblage and include *C. collina*, *C. sarmatica*, *C. kolenatiana*, *C. bayerniana*, *C. armena*, *C. zangezura* and *C. lezgina*, whereas *C. odontosepala* is the only strictly sciophytic species. Shade- tolerant taxa are well represented by species such as *C. latifolia*, *C. rapunculoides*, *C. bononiensis*, *C. glomerata*, *C. sarmatica*, *C. kolenatiana*, *C. coriacea* and *C. alliariifolia*. The presence of *C. sarmatica* and *C. kolenatiana* in both heliophytic and shade- tolerant groups indicates notable plasticity along light gradients.

2) Water relations. Water- relation categories are similarly structured: most species are mesophytes, including *C. latifolia*, *C. rapunculoides*, *C. bononiensis*, *C. glomerata*, *C. kolenatiana*, *C. coriacea*, *C. alliariifolia*, *C. odontosepala*, and *C. collina*, while xerophytic taxa such as *C. lezgina*, *C. coriacea*, *C. bayerniana*, *C. armena* and *C. zangezura* are adapted to drier conditions. *C. sibirica* and *C. sarmatica* occupy an intermediate mesoxerophytic niche.

3) Substrate preferences. Substrate preferences further structure the flora: calciphytes (*C. coriacea*, *C. alliariifolia*, *C. bononiensis*, *C. glomerata*) are restricted to lime- rich soils; petrophytes including *C. sarmatica*, *C. rapunculoides*, *C. sclerotricha*, *C. kolenatiana*, *C. bayerniana*, *C. armena*, *C. zangezura*, and *C. lezgina* predominate on rocky substrates and in rock crevices; mesophilous species (*C. latifolia*, *C. odontosepala*, *C. collina*) occupy moderately moist, nutrient- balanced sites; and ruderal taxa (*C. rapunculoides*, *C. sibirica*) occur in disturbed habitats.

4) Altitudinal distributions. The altitudinal distribution of the studied *Campanula* species reveals clear ecological stratification across mountain belts. The lower mountain belt hosts the highest richness, comprising 62.5% of all species, including *C. sibirica*, *C. lezgina*, *C. odontosepala*, *C. latifolia*, *C. rapunculoides*, *C. bononiensis*, *C. glomerata*, *C. kolenatiana*, *C. sclerotricha*, *C. armena*. The middle mountain belt contains 25% of species, represented by *C. bayerniana*, *C. zangezura*, *C. coriacea*, *C. alliariifolia*. In contrast, 56.25% of species extend into the subalpine–alpine belts, including *C. latifolia*, *C. rapunculoides*, *C. glomerata*, *C. collina*, *C. sarmatica*, *C. bayerniana*, *C. zangezura*, *C. kolenatiana*, *C.*

armena. Only three species, *C. bononiensis*, *C. sarmatica*, *C. sibirica*, reach the high mountain belt, accounting for 18.75% of the total. These taxa collectively occupy a wide range of habitats, from clayey and stony slopes to rocky debris, forests, shrublands, subalpine meadows, tall- herb communities, and anthropogenic rocky sites.

The colored altitude chart (Fig. 1) summarizes ecological- group representation of *Campanula* species across belts. Counts were derived by matching species in each belt to all ecological groups they belong to, allowing multi- assigned species to be counted multiple times. The lower and subalpine belts exhibit the highest ecological complexity, while the high- mountain belt shows a reduced set of ecological attributes.

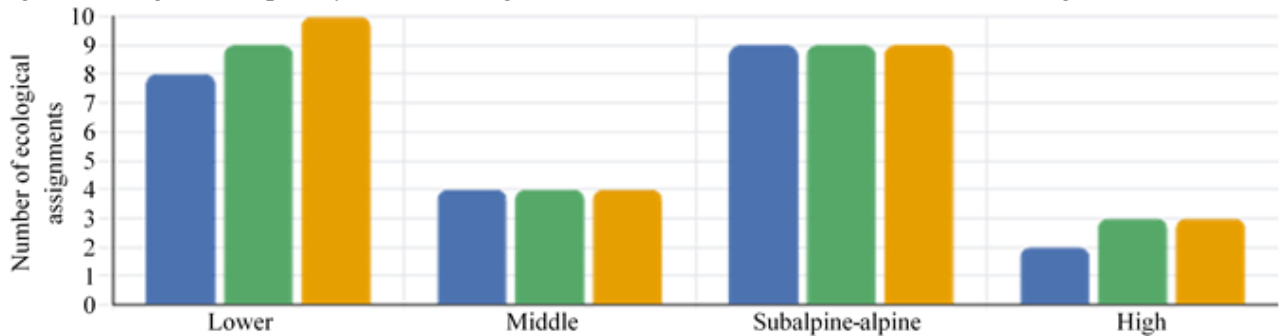


Fig 1. Distribution of ecological group assignments of *Campanula* species across mountain belts. The chart illustrates how light- preference (blue), water- relation (green), and substrate- preference (orange) characteristics accumulate within species inhabiting each altitudinal zone

5) Compositional similarity among belts. Similarity between belts is generally low. No species are shared between the lower vs. middle belts or the middle vs. high belts ($S = 0$). Moderate similarity occurs between the lower and subalpine–alpine belts ($S = 0.53$, five shared species). Partial similarity is observed for lower vs. high ($S = 0.31$, two shared species) and middle vs. subalpine–alpine ($S = 0.31$, two shared species). The subalpine–alpine and high belts share only one species ($S = 0.17$), emphasizing the distinctiveness of high- elevation assemblages and strong ecological filtering by altitude. Overall, similarity declines with increasing elevational distance (Fig. 2).

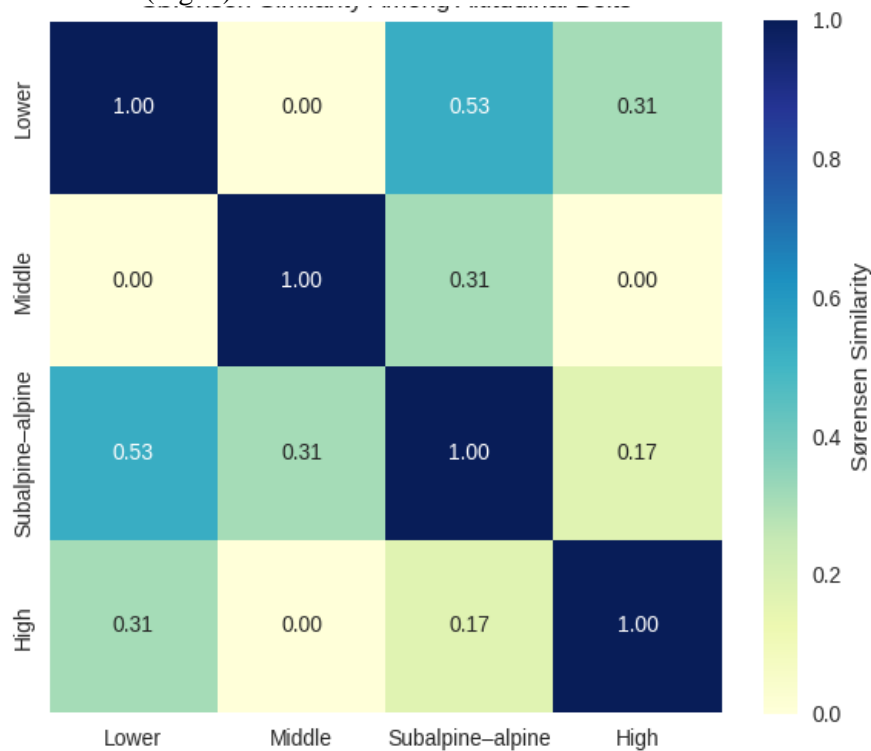


Fig 2. Sørensen–Czekanowski similarity heatmap illustrating floristic relationships among elevation belts. Warmer colors indicate stronger compositional similarity, while cooler colors highlight weak or absent species overlap. The visualization clearly depicts the contrasting degrees of species overlap among the lower, middle, subalpine–alpine, and high mountain zones, emphasizing both transitional links and the distinctiveness of high- elevation assemblages.

Ecological assignments and elevational distributions of *Campanula* species are summarized in Table 1, with belt-level percentages and similarity values.

Table 1. Ecological groups and altitudinal occurrence of *Campanula* species in Azerbaijan

Species	Light group	Water group	Substrate	Altitudinal belts
<i>C. glomerata</i>	shade- tolerant	mesophyte	calciphyte	lower; subalpine–alpine
<i>C. latifolia</i>	shade- tolerant	mesophyte	mesophilous	lower; subalpine–alpine
<i>C. odontosepala</i>	sciophyte	mesophyte	mesophilous	lower
<i>C. rapunculoides</i>	shade- tolerant	mesophyte	petrophyte; ruderal	lower; subalpine–alpine
<i>C. bononiensis</i>	shade- tolerant	mesophyte	calciphyte	lower; high
<i>C. sibirica</i>	heliophyte	mesoxerophyte	ruderal	lower; high
<i>C. alliariifolia</i>	shade-tolerant	mesophyte	calciphyte	middle
<i>C. sclerotricha</i>	shade-tolerant	mesophyte	petrophyte	lower
<i>C. sarmatica</i>	heliophyte; shade- tolerant	mesoxerophyte	petrophyte	subalpine–alpine; high
<i>C. collina</i>	heliophyte	mesophyte	mesophilous	subalpine–alpine
<i>C. kolenatiana</i>	heliophyte; shade- tolerant	mesophyte	petrophyte	lower; subalpine–alpine
<i>C. armena</i>	heliophyte	xerophyte	petrophyte	lower; subalpine–alpine
<i>C. zangezura</i>	heliophyte	xerophyte	petrophyte	middle; subalpine–alpine
<i>C. bayerniana</i>	heliophyte	xerophyte	petrophyte	middle; subalpine–alpine
<i>C. lezgina</i>	heliophyte	xerophyte	petrophyte	lower
<i>C. coriacea</i>	shade-tolerant	mesophyte; xerophyte	calciphyte	middle

These patterns show that *Campanula* species in Azerbaijan exhibit broad ecological amplitude. To further visualize the multidimensional ecological associations among the studied taxa, a species–environment bipartite network was constructed (Fig. 3). The network links each *Campanula* species to the ecological categories (light, water, and substrate groups) to which it belongs, offering a graphical representation of how species distribute across key environmental gradients. This approach highlights structural patterns of ecological connectivity that are not evident from unidimensional groupings alone.

The network reveals a strongly interconnected ecological core dominated by the petrophyte and mesophyte nodes, each showing the highest number of connections to species. This result is consistent with the dominance of rocky slopes, cliff systems, and moderately moist habitats in the mountainous landscapes of Azerbaijan. Species such as *C. sarmatica*, *C. kolenatiana*, and *C. coriacea* act as network hubs, each linked to multiple ecological classes, thereby demonstrating considerable ecological plasticity. For example, *C. sarmatica* connects simultaneously to heliophytic, shade- tolerant, petrophytic, and mesoxerophytic groups, while *C. coriacea* bridges mesophytic and xerophytic moisture regimes. These multi- linked species provide functional connectivity among ecological modules.

In contrast, species with limited ecological breadth occupy peripheral positions in the network. *C. odontosepala*, linked primarily to the sciophyte and mesophilous groups, appears as a specialist adapted to moist, shaded habitats. Similarly, *C. sibirica*, associated with mesoxerophytic and ruderal conditions, occupies a marginal ecological niche compared with the more widespread taxa.

The bipartite visualization also clarifies how light- preference groups cluster within the assemblage. Heliophytic and shade- tolerant categories show significant overlap through species such as *C. latifolia*, *C. rapunculoides*, and *C. kolenatiana*, supporting the interpretation that many taxa tolerate varying irradiance and microhabitat structures. This plasticity likely contributes to their distribution across multiple elevation zones.

Overall, the species–environment bipartite network highlights a clear contrast between generalist, highly connected species and specialists with narrow ecological affinities. The pattern reinforces the importance of petrophytic and mesophytic habitats in structuring *Campanula* diversity in Azerbaijan and reveals how certain taxa serve as ecological bridges across environmental gradients.

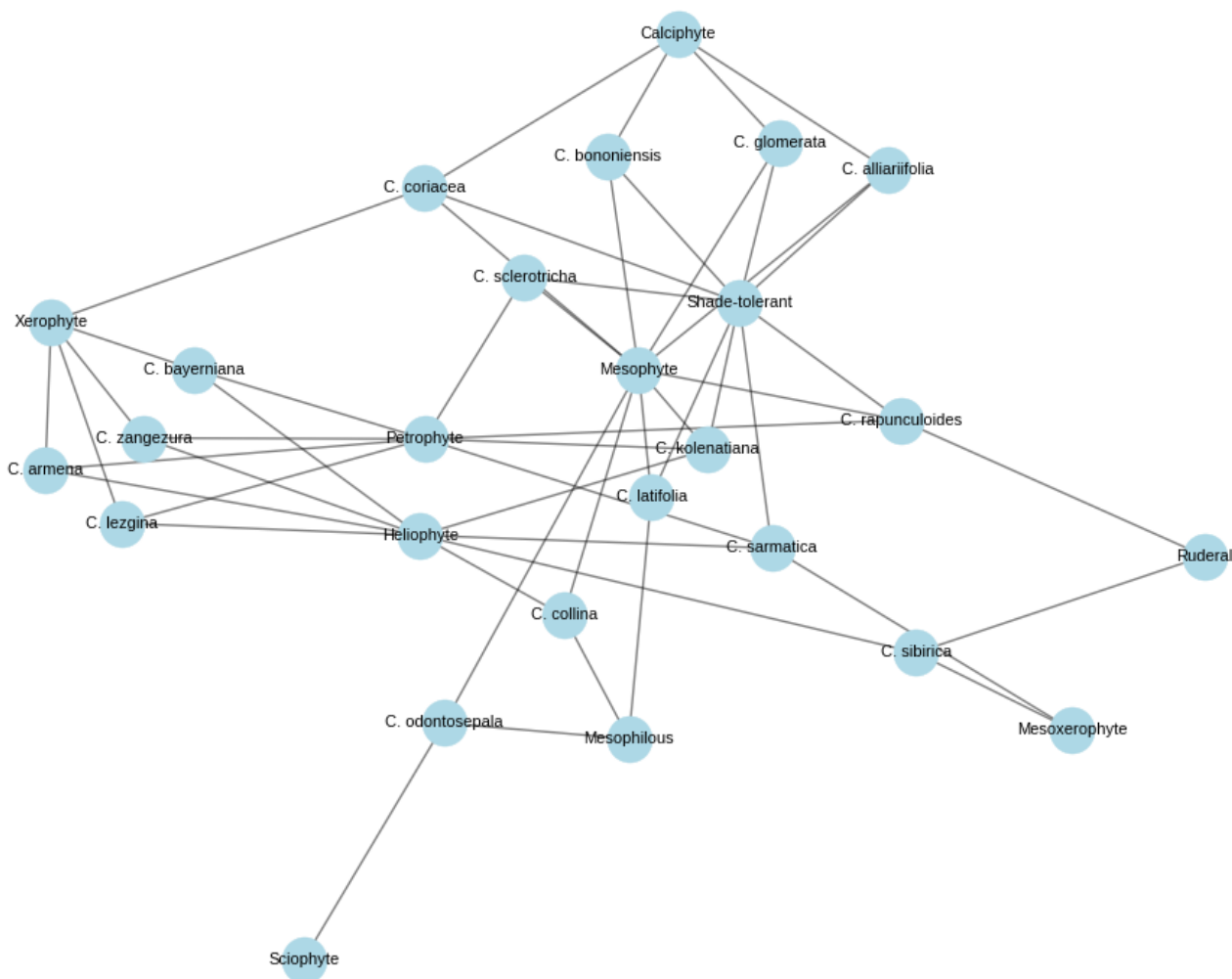


Fig 3. Species–environment bipartite network showing connections between *Campanula* species and their ecological categories (light, water, substrate). Node size is equal across categories; edge presence indicates ecological membership. Central nodes (e.g., petrophyte, mesophyte) represent dominant ecological conditions, while peripheral nodes highlight specialist species.

5. Conclusion

Species of the subgenus *Campanula* in Azerbaijan are predominantly shade-tolerant mesophytes with strong petrophytic affinities, though several taxa exhibit notable ecological plasticity. Species richness peaks in the lower mountain belt and declines toward higher elevations. Community similarity is highest between the lower and subalpine–alpine belts. These findings provide an ecological baseline useful for conservation planning, habitat management in mountain systems, and future studies on adaptation along elevational gradients.

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