

Distribution, ecology and variability of *Galanthus reginae-olgae* Orph. along the northern limit of its Balkan distribution (Croatia)

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Abstract – *Galanthus reginae-olgae* Orph. occurs in mainland Greece, the Ionian Islands, Corfu, Albania, Italy, Sicily, Montenegro, Bosnia and Herzegovina, and Croatia. This paper aims to extend the knowledge of the distribution and ecology of *G. reginae-olgae* in Croatia and the northwestern Balkans. A field study in 2023 revealed as many as 35 populations in southern Croatia, some of them counting up to 100,000 individuals. Most of the populations exhibit semi-sciophilic behaviour within transitional habitats (ecotones) from insolated grassland to shaded eu- and sub-Mediterranean thickets and forests, and are found in the altitudinal range from sea level to 664 m a.s.l., at an average distance of 5.44 km from the coastline. Analysis of the bioclimatic variables reveals that the populations studied find an optimum in Mediterranean conditions with a mean annual air temperature of 14.61 °C and mild winters. The annual precipitation is high, exceeding 1600 mm, although it is limited to the winter period. The analyses of the temperature data provided insight into the environmental conditions that might serve as triggers for the initiation and duration of anthesis. In view of the the observed leaf length and flowering time, the populations are designated *G. reginae-olgae* subsp. *vernalis* Kamari. Since the Croatian populations are sparsely scattered along the northern limit of the species' distribution on the Balkan Peninsula, future research should investigate the adaptability of this species to habitat and climate changes in the eastern Mediterranean region.

Keywords: bioclimatic variables, flowering period, *Galanthus reginae-olgae* subsp. *vernalis*, morphology, taxonomy, transitional habitats

Introduction

The genus *Galanthus* L. (Amaryllidaceae) comprises 23 species of bulbous, petaloid monocots native to Europe, Asia Minor, and the Near East (Davis 1999, 2001, Zubov and Davis 2012, Tan et al. 2014, Zubov et al. 2019, Timukhin and Tuniyev 2022). Centres of species diversity are found in Greece and regions adjacent to the Balkans, Turkey, and the Caucasus. Species of this genus commonly occur in woodland and forests, on fertile, base-rich soils, on limestone or other calcareous substrates, at altitudes up to 2700 m (Davis 1999, 2001). They rank among the finest garden plants and have long been used for pharmaceutical purposes due to their content of bioactive compounds (e.g., alkaloid galanthamine) (Jovanović et al. 2016, 2018). As a result of illegal collection, habitat destruction and climate change, *Galanthus* is threatened in the wild; all species have been listed in

Appendix II of CITES, and several of them are included in one of the threatened categories of the IUCN Red List (IUCN 2023).

Queen Olga's snowdrop (*G. reginae-olgae* Orph.) was first discovered in the Taigetos Mountains in southern Greece by the botanist T. G. Orphanides in 1876 (Boissier 1882). Closely related to the common snowdrop (*G. nivalis* L.), it was treated as its subspecies by many authors (e.g., Gottlieb-Tannenhain 1904, Stern 1956, Webb 1978). Both species have applanate veneration, narrow linear leaves and a single green mark at the apex of each inner perianth segment, but the leaves of *G. reginae-olgae* are typically absent at the onset of flowering, or only 1–3 cm long, with a conspicuous glaucous stripe running down the middle of the upper leaf surface. In addition, it is predominantly an autumn- to early winter-flowering species, whereas *G. nivalis* is characterized by its late winter- to early spring-flowering

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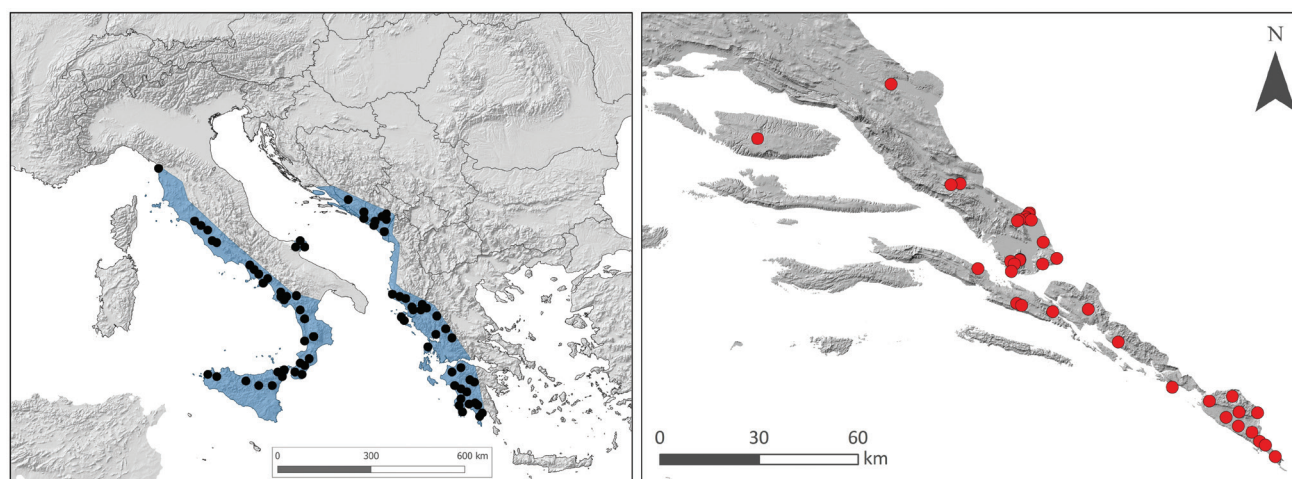


Fig. 1. The area of distribution of *Galanthus reginae-olgae* based on literature, herbaria, online databases and personal communications (left). Distribution of *G. reginae-olgae* in Croatia based on our research (right).

time (Davis 1999, 2001). To date, *G. reginae-olgae* has been found in mainland Greece (Delipawlow and Angeliew 1970, Davis 1999, 2001, Vladimirov et al. 2011), Corfu (Stern 1956, Delipawlow and Angeliew 1970, Davis 1999, 2001), the Ionian Islands (Trigas et al. 2021), Albania (Delipawlow and Angeliew 1970, Malo and Shuka 2008, Shuka et al. 2011, Mahmutaj et al. 2015, Barina, 2017), Montenegro (Davis 1999, 2001, Jovanović 2019), Bosnia and Herzegovina (Šilić 1996, Davis 2001, Tomović et al. 2023), Croatia (Davis 1999, 2001, Čičovački and Alegro 2013, Jovanović et al. 2013), mainland Italy (Davis 1999, 2001, Conti et al. 2005, Bartolucci et al. 2018, Rosati et al. 2020) and Sicily (Stern 1956, Gramuglio et al. 1978, Davis 1999, 2001, Conti et al. 2005, Di Marco et al. 2012, Bartolucci et al. 2018) (Fig. 1).

It is most common in or near woodlands, in damp, north-facing shady locations, among rocks or in narrow gorges, on moist, humus-rich and deep soils overlaying limestone, at a wide range of altitudes, but usually above 500 m (Davis 1999, 2001). Along with chorological and ecological research, this species has been the subject of numerous studies, including morphological and taxonomical (Kamari 1982, Davis 1999), karyological (Kamari 1981, Papanicolaou and Zacharof 1983), anatomical (Davis and Barnett 1997), phytochemical (Conforti et al. 2010), palynomorphological (Jovanović et al. 2022) and molecular investigations (Zonneveld et al. 2003, Lledó et al. 2004, Meerow et al. 2006, Larsen et al. 2010, Rønsted et al. 2013).

Based on flowering time and leaf length at the onset of flowering, *G. reginae-olgae* is divided into two subspecies. *Galanthus reginae-olgae* subsp. *reginae-olgae* flowers in autumn with leaves either absent or only 1–3 cm long, whereas *G. reginae-olgae* subsp. *vernalis* Kamari flowers in winter or early spring with leaves that are always present and usually several centimetres long (Davis 1999, 2001). However, as the degree of leaf development is not a fully reliable character (Shuka et al. 2011), and the flowering period varies greatly depending on the environmental conditions, the infraspecific differentiation of this species is considered difficult to ascertain (Trigas et al. 2021).

In Croatia, *G. reginae-olgae* was recorded by Davis (1999, 2001), then confirmed on Mt. Snježnica by Čičovački and Alegro (2013), and thus presented to the Croatian botanical community. In addition, several localities in southern Croatia (i.e., Konavle, Lokrum, Metković, Brač, and Donji Proložac) were recorded and published in the Flora Croatica on-line database (Nikolić et al. 2025). Due to the morphological similarities with *G. nivalis* and the challenging delimitation of its subspecies, the actual patterns of the diversity and distribution of *G. reginae-olgae* have remained uncertain. Hence, the present paper aims to extend the knowledge of the distribution and ecology of *G. reginae-olgae* in Croatia and the northwestern Balkans.

Material and methods

Field inspection was conducted regularly once a month from November 2022 to March 2023, in order to detect snowdrop populations and to monitor their flowering period. An extended field survey, performed in January and February 2023, included population size assessment, habitat type record and estimation of canopy coverage. Population size was estimated by counting the number of individuals in smaller populations (up to 1,000 individuals). The same was implemented in larger populations, however using five smaller 10 × 10 m subplots (managed by five botanists) and performing extrapolation on entire population area. The habitat types were described using dominant tree or shrub species, while canopy coverage (%) was assessed visually.

To determine parameters that define the ecological preferences of *G. reginae-olgae* along its northern limit of Balkan distribution, 14 bioclimatic variables from CHELSA climatological datasets (vers. 2.1) at spatial resolution 1 × 1 km were used (Karger et al. 2017, 2021). The variables were selected according to relevant literature data for *Galanthus* (Artjushenko 1963, Davis 1999, 2001, Cox 2013). Additionally, for each population, the distance from the coastline, altitude and inclination were obtained from the datasets of the European Environmental Agency – EEA Coastline

(EEA 2020) and EU-DEM (vers. 1.0) (CLMS 2020). Basic descriptive statistics of the climatic and geographic parameters were calculated and shown in the standard box-plot diagrams using Past software (vers. 4.15) (Hammer et al. 2001).

The populations discovered were identified according to the observed flowering time and leaf development, using the keys proposed by Davis (1999, 2001). The average leaf length was assessed during peak flowering using the following categories: 0–3 cm, 3–6 cm, 6–9 cm, and 9–12 cm. In addition, the variation in flower morphology and markings, and other possibly informative taxonomic features, were inspected in each studied population.

Results

A total of 35 populations of *G. reginae-olgae* were found or confirmed in southern Croatia (On-line Suppl. Tab. 1) over a range of more than 160 km (Fig. 1). The largest populations with an estimated number of up to 100,000 individuals were recorded in only six locations (Vidonje, Rosni Do North, Rosni Do South, Putnikovići, Mutni Do (Pelješac) and Kuna Konavoska), whereas 72% of the populations (25) had fewer than 10,000 individuals. Among the latter, almost half counted no more than 1,000 individuals (On-line Suppl. Tab. 1).

The populations of *G. reginae-olgae* in Croatia are mostly recorded in semi-shaded habitats (the average canopy coverage 60%; min 10%, max 100%) (Fig. 2). At higher altitu-

dinal positions, this species was found growing in semi-shade of deciduous forests and thickets of downy oak (*Quercus pubescens* Willd.), oriental hornbeam (*Carpinus orientalis* Mill.) and European hop-hornbeam (*Ostrya carpinifolia* Scop.). At lower altitudes (and closer to the sea), it occurs in the vegetation of transitional thickets and low forests of evergreen oak (*Q. ilex* L.) and other eu-Mediterranean shrubs. Some parts of particular populations (e.g. Pločice, Osobjava (Pelješac), Komarna) also spread to cultivated areas (e.g., olive groves). Most of the recorded populations grow on deep soils with sporadic surface rocks.

The investigated populations were found in an altitudinal range from sea level up to 664 m a.s.l., with an average altitude of 203.27 ± 29.44 m a.s.l. (Fig. 3, On-line Suppl. Tab. 2). Most of the populations recorded in Croatia occurred on flat or slightly sloping terrain ($5.86^\circ \pm 0.85^\circ$). The average distance from the coastline was $5.44 \text{ km} \pm 0.68 \text{ km}$ (min 0.06 km, max 16.42 km) (Fig. 3, On-line Suppl. Tab. 2).

Based on bioclimatic data, Croatian habitats of *G. reginae-olgae* are climatologically characterised by typical Mediterranean conditions with a mean annual air temperature of $14.61 \pm 0.18^\circ\text{C}$, and mild winters with the mean daily minimum air temperature of the coldest month (bio 6) ($2.31 \pm 0.34^\circ\text{C}$), of the coldest quarter (bio 11) ($6.66 \pm 0.21^\circ\text{C}$) and of the wettest quarter (bio 8) ($11.16 \pm 0.20^\circ\text{C}$) all above zero (Fig. 3, On-line Suppl. Tab. 2). According to the bioclimatic data, frost events in even the coldest month are very rare, occurring at only three population sites. The annual precipitation in the study area exceeds 1600 mm, most of the pre-

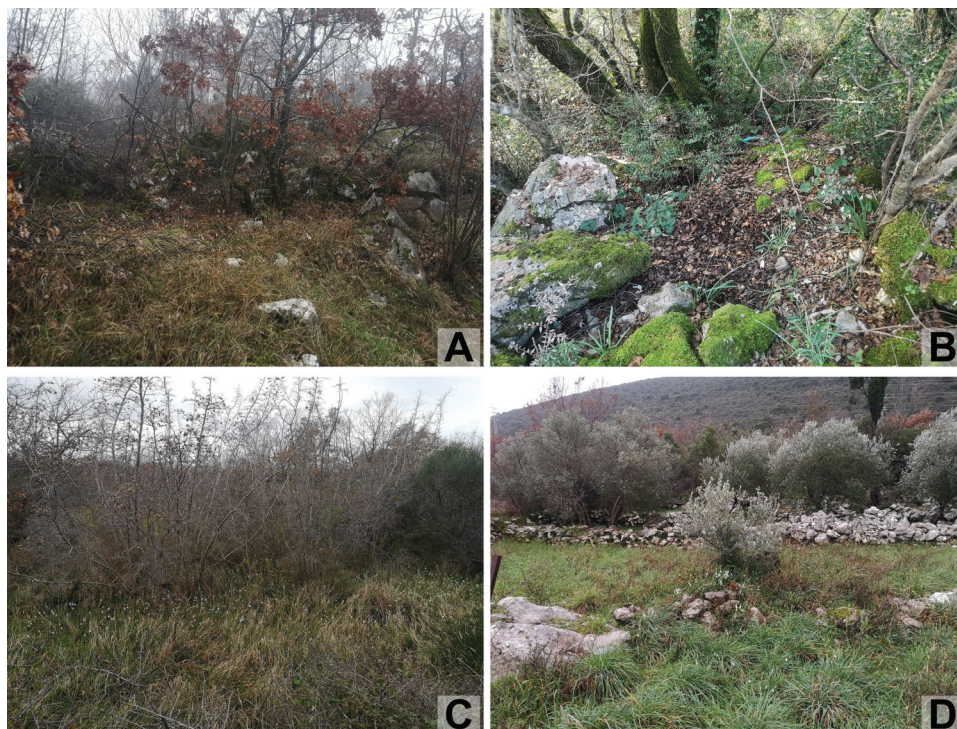


Fig. 2. Habitats of *Galanthus reginae-olgae* in Croatia: A – Mediterranean deciduous *Quercus pubescens* low forests and thickets (Kuna Konavoska, 663 m a.s.l.), B – Mediterranean evergreen *Q. ilex* low forests and thickets (Vratar North, 8 m a.s.l.), C – semi-shaded habitats on the edge of *Paliurus spina-christi* thickets (Majkovi, 391 m a.s.l.), D – semi-shaded habitats within cultivated land – olive groves (Pločice, 164 m a.s.l.).

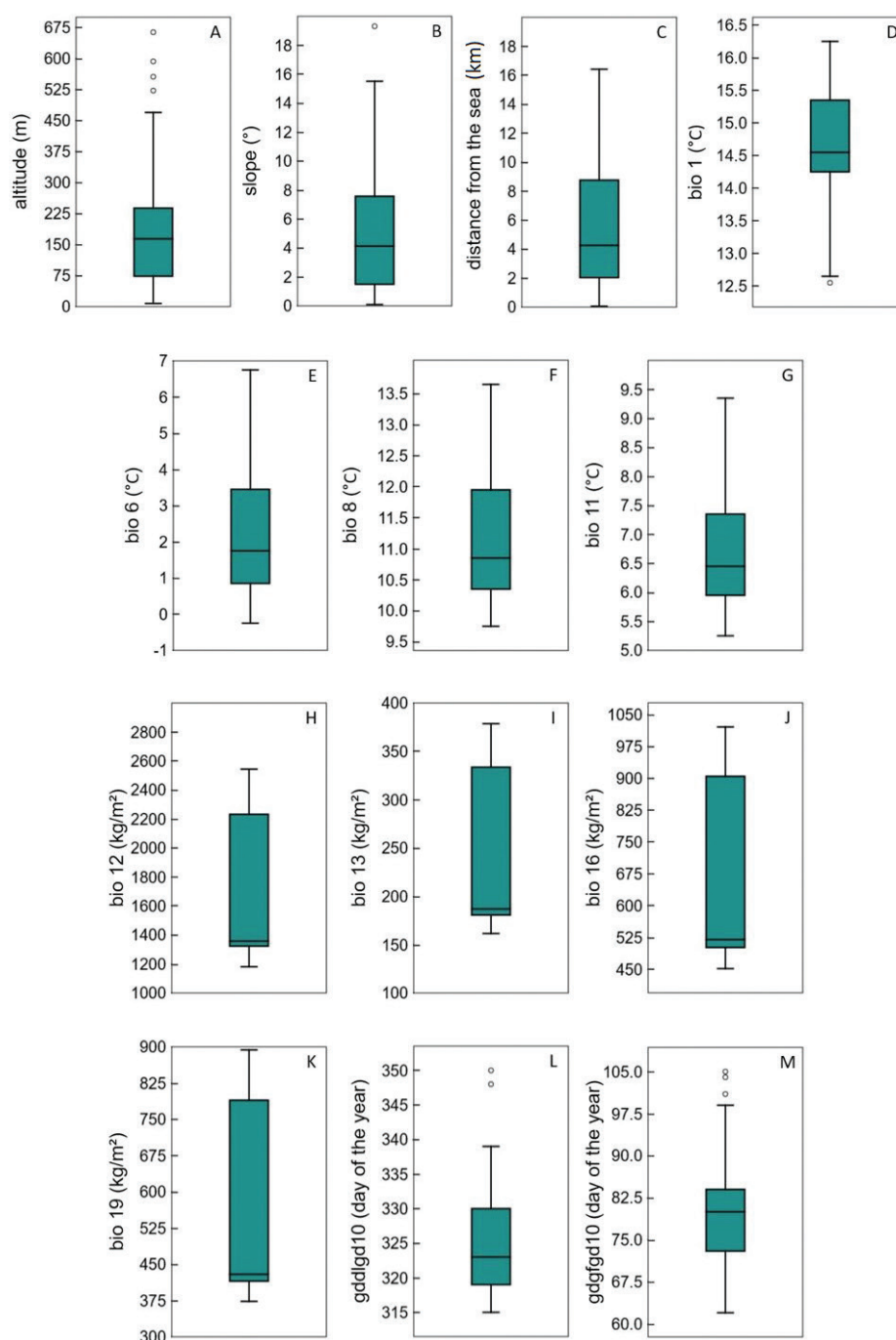


Fig. 3. The box-plot diagrams of geographical, terrain, temperature and precipitation parameters for populations of *Galanthus reginae-olgae* (N = 35) in Croatia. A – altitude (m), B – slope (°), C – distance from the sea (km), D – mean annual air temperature (Bio 1), E – mean daily minimum air temperature of the coldest month (bio 6), F – mean daily mean air temperatures of the wettest quarter (bio 8), G – mean daily mean air temperatures of the coldest quarter (bio 11), H – annual precipitation amount (bio 12), I – precipitation amount of the wettest quarter (bio 13), J – mean monthly precipitation amount of the wettest quarter (bio 16), K – mean monthly precipitation amount of the coldest quarter (bio 19), L – last day of the year above 10 °C (gddl, day of the year), M – first day of the year above 10 °C (gdgfgd, day of the year). The upper and lower box limits show upper and lower quartile values, while whiskers show minimum and maximum data values.

precipitation occurring only in the wettest and coldest quarter of the year (i.e., the winter period) (Fig. 3, On-line Suppl. Tab. 2).

The observation of the onset of anthesis revealed that some of the populations started to flower as early as the beginning of December, but the majority of them opened the flowers later on in December. On average, the flowering ter-

minated by the end of February, whereas some populations at higher altitudes flowered until the first half of March. Occasional observations of several Croatian populations in the growing season of 2021/2022 showed that the onset of anthesis was ten days later than in the season of 2022/2023. Based on bioclimatic data, the mean first day of the year with a temperature below 10 °C (e.g. the last day of the year



Fig. 4. *Galanthus reginae-olgae* subsp. *vernalis* in Croatia: A – flower, B – pale median stripe on the adaxial leaf surface, C – leaves, D – individuals growing in a dense population.

above 10 °C – gddlgd10) is November 20, whereas the mean last day of the year with the temperature below 10 °C (e.g. first day of the year above 10 °C – gdgfgd10) is March 20 (Fig. 3, On-line Suppl. Tab. 2). When this period was restricted to temperatures beneath 5 °C (gddlgd5, gdgfgd5), a narrower temporal frame was obtained – from January 3 to February 9, based, however only on seven (20%) population sites in which the winter temperature drops beneath 5 °C. According to these data and field observations, the flowering period in the investigated populations of *G. reginae-olgae* begins and continues when winter temperatures are beneath 10 °C.

During the peak flowering in our study, the average leaf length within all populations exceeded 3 cm. Nearly two-thirds of populations (60%) had an average leaf length from 3 cm to 6 cm, while more than one-third of the populations had longer leaves (6–9 cm). Based on the observed leaf length and flowering time, the populations are designated *G. reginae-olgae* subsp. *vernalis* (Fig. 4), with the possible presence of intermediate forms between the two subspecies.

Besides typical flower morphology (Fig. 5A), variation in individual specimens was observed, including the following atypical variants (on different sites):

- variant with a single apical abaxial green mark on each inner perianth segment, covering c. 2/3 of the segment (Lisac) (Fig. 5B);
- variant with slender perianth segments of equal length and width, i.e., a poculiform perigone (all segments in one circle, cup-shaped) (Vidonje) (Fig. 5C);
- variant with broadly ovate perianth segments of equal length and width, a poculiform perigone with a diffuse abaxial green mark near the apex (up to 1/3 of the segments) (Vidonje) (Fig. 5D);
- variant with an abaxial green mark consisting of parallel lines at the apex of outer perianth segments (Rosni Do, and Vidonje) (Fig. 5E, F);

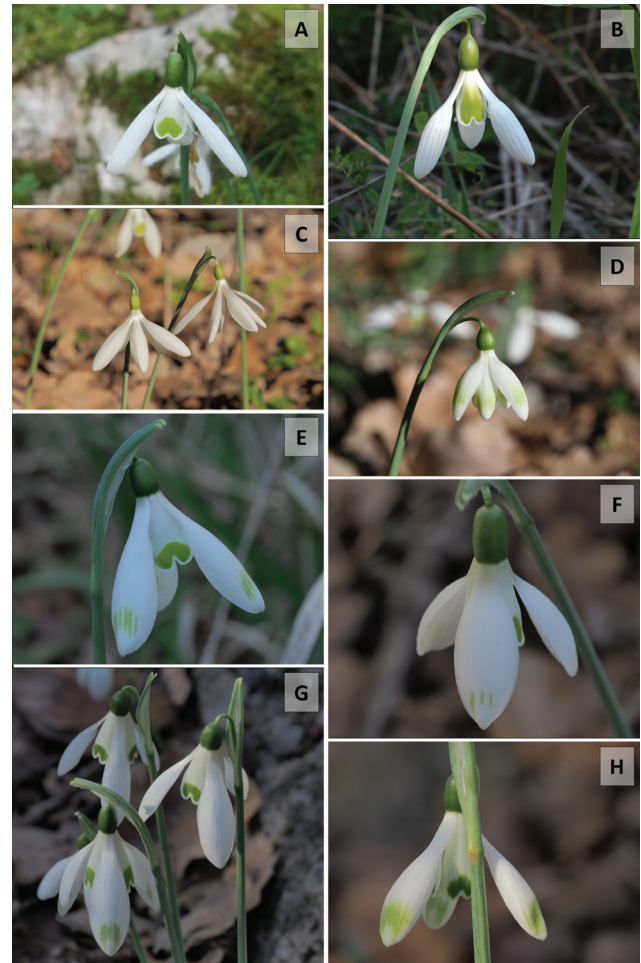


Fig. 5. Variation in flower morphology and markings of *Galanthus reginae-olgae* subsp. *vernalis* in Croatia: A – typical flower, B – a single apical abaxial green mark on inner perianth segments, covering c. 2/3 of the segment, C – slender perianth segments of equal length and width (poculiform perigone), D – broadly ovate perianth segments of equal length and width, a poculiform perigone with a diffuse abaxial green mark near the apex (up to 1/3 of the segments), E, F – an abaxial green mark consisting of parallel lines at the apex of outer perianth segments, G – an abaxial green mark consisting of discontinuous surfaces at the apex of outer perianth segments, H – an abaxial green mark at the apex of outer perianth segments (viridiapice).

- variant with an abaxial green mark consisting of discontinuous surfaces at the apex of outer perianth segments (Vidonje) (Fig. 5G);
- variant with an abaxial green mark at the apex of each outer perianth segment, i.e., viridiapice markings (Vidonje) (Fig. 5H).

Discussion

Galanthus reginae-olgae in Croatia is found in 35 populations, in a range of more than 160 km in the southern part of the country. Most of the recorded populations numbered fewer than 10.000 individuals. Considering that *G. reginae-olgae* was confirmed for Croatia in 2012 (Čičovački and Alegro 2013), the results represent a significant contribution

to the insufficient knowledge of the distribution of this species in Croatia and along its northern distributional limit on the Balkan Peninsula (Davis 1999, 2001). Given that the investigated populations are mostly in semi-shaded habitats, it can be stated that this species exhibits semi-sciophilic behaviour in Croatia. At higher altitudes, it was found growing in the semi-shade of deciduous forests and thickets of *Quercus pubescens*, *Carpinus orientalis* and *Ostrya carpinifolia*, confirming Čičovački and Alegro (2013). At lower altitudes (closer to the sea), it occurs in the vegetation of transitional thickets and low forests of *Q. ilex* and other eu-Mediterranean shrubs. Most of the recorded populations grow on deep soils with sporadic surface rocks. These habitats are similar to those in Bosnia and Herzegovina (Tomović et al. 2023), and Albania (Malo and Shuka 2008, Shuka et al. 2011). According to Davis (1999, 2001), *G. reginae-olgae* is mostly found in or near woodlands of oriental plane (*Platanus orientalis* L.), pine (*Pinus* spp.) and Greek fir (*Abies cephalonica* Loudon), growing in damp, north-facing shady places, among rocks or in narrow gorges, on moist, humus-rich, and deep soils overlaying limestone. *G. reginae-olgae* subsp. *vernalis* occurs in similar habitats, including deciduous woodlands of European beech (*Fagus sylvatica* L.), oak (*Quercus* spp.), hornbeam (*Carpinus* spp.) and other species, and occasionally in coniferous woodland (*Abies* spp.). The populations in Croatia occur in the altitudinal range from sea level to 664 m a.s.l., with an average altitude of 203.27 m a.s.l. On Mt. Sniježnica, the species occurs at altitudes from 650 m to 750 m a.s.l. (Čičovački and Alegro 2013). In Bosnia and Herzegovina, it was found at altitudes of 260–330 m a.s.l. (Tomović et al. 2023), and in Albania from 300 m to 1200 m a.s.l. (Malo and Shuka 2008, Shuka et al. 2011). In the overall area of distribution, *G. reginae-olgae* was recorded at an even wider range of altitudes, from near sea level to 1300 m a.s.l., but more commonly above 500 m a.s.l. (Davis 2001).

Considering the climatological characterization of Croatian habitats of *G. reginae-olgae* based on bioclimatic data, it is evident that this snowdrop prefers typical Mediterranean conditions, with a mean annual air temperature of 14.61 °C, and mild winters. Although the annual precipitation in the study area exceeds 1600 mm, seemingly unexpected for the Mediterranean region, the most of the rainfall comes in the winter period, providing favourable conditions for the growth and development of *G. reginae-olgae*. Depending on the altitudinal position, the populations in Croatia flower between early December and early March, but on average the flowering period begins in late December and terminates by the end of February, similar to the reports for other areas of the species' range (Davis 2001, Malo and Shuka 2008, Shuka et al. 2011, Vladimirov et al. 2011). According to literature, the flowering time of *Galanthus* species is genetically determined and influenced by air and soil temperature, and precipitation (Davis 1999). In addition, flower opening is not induced by light but by air temperature (Church 1908). The analysis of the temperature data could provide insights into the environmental circum-

stances that might serve as triggers for the onset and duration of anthesis. Based on temperature data and field observations in Croatia, and assuming that temperature is a key trigger for the onset of flowering in *Galanthus* (Davis 1999), it may be argued that the flowering period in the researched populations of *G. reginae-olgae* begins and continues when winter temperatures drop beneath 10 °C.

According to Davis (1999, 2001), *G. reginae-olgae* is divided into two subspecies based on flowering time and leaf length at the onset of flowering. Namely, *G. reginae-olgae* subsp. *reginae-olgae* is autumn-flowering (September to December) with leaves absent or 1–3 cm long, whereas *G. reginae-olgae* subsp. *vernalis* is characterized by winter-to spring-flowering time (December to March), and leaf length of 3–7 cm at the onset of flowering (Davis 1999, 2001). Based on the observed leaf length and flowering time, the populations in Croatia are designated *G. reginae-olgae* subsp. *vernalis*, but intermediate forms with subsp. *reginae-olgae* might also be present. The variability of these taxonomic characters, as stated by several authors (e.g., Shuka et al. 2011, Trigas et al. 2021, Tomović et al. 2023), suggests that the infraspecific division of *G. reginae-olgae* needs to be thoroughly reconsidered.

As previously shown, *G. reginae-olgae* in Croatia prefers semi-shaded habitats, inhabiting transitional habitats (ecotones) from insolated grassland to shaded thickets and forests. Being a eurivalent species in terms of light exposure, it is not particularly endangered, as are, for example, typical heliophilous species of grassland habitats. However, to maintain these transitional habitats, it is necessary to maintain both habitat types in which it occurs. Namely, it is important to conserve grasslands, preferably by traditional grazing, to prevent them from becoming overgrown. On the other hand, it is also important to preserve thickets and young forests, preventing them from being cleared and burned. Finally, although the species is well adapted to changes in both habitat types, sudden disturbances caused by logging, fire or grassland encroachment could have detrimental effects on populations. Although *G. reginae-olgae* subsp. *vernalis* is not protected under national legislation or by the EU Habitat Directive, it is strongly advised that a monitoring scheme for this taxon be developed and implemented. Considering that the Croatian populations are rare and scattered along the northern limit of the distribution on the Balkan Peninsula, the monitoring would provide insights into the adaptability of the species to habitat changes (fires and vegetation succession), as well as into the way the species adapts its phenology (proliferation, flowering, pollination, and fruiting) to the climate changes in the eastern Mediterranean region.

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Author contribution statement

V.Š., F.J. – conceptualization and methodology; V.Š., F.J., B.I., M.D., M.B. – data collection and sampling; V.Š., A.R. – data analysis; V.Š., F.J. – manuscript preparation. All authors have read and agreed to the published version of the manuscript.

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