

Article

Horticultural Potential of the Flora from Karstic Dolines in the Northern Dinarides

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Abstract

Karstic dolines are unique geomorphological and ecological features of limestone landscapes, characterised by strong microclimatic and edaphic gradients. These concave landforms form natural microrefugia that harbour a variety of plant species. In this study, dolines in the northern Dinarides on the Kras Plateau were investigated to assess the horticultural potential of their flora. Vegetation surveys along edge-to-bottom transects revealed a pronounced species turnover and differentiation of functional traits. Shade-tolerant geophytes and early-flowering perennials dominate the bottoms of the dolines, while the edges harbour drought-tolerant aromatic herbs. Not only do dolines serve biodiversity conservation by acting as microrefugia, but they also preserve cultural heritage through ethnobotanical species and provide a species pool for the selection of plants with horticultural potential. We selected horticultural important plants (HPs) and analysed them within the dolines. Depending on their morphology and seasonal occurrence, they can be divided into woody species, early and late spring flowering species, orchids, and structural species. By linking biodiversity conservation with applied horticulture, this study emphasises the multifunctional role of dolines as small natural features of disproportionate ecological and horticultural importance. We suggest that integrating doline species into horticultural utilisation could improve sustainability, diversify plantings, and strengthen climate adaptation strategies.

Keywords: chorotypes; climate resilience; doline; functional strategy; horticultural potential; karst; life forms; microrefugium; plant traits; vegetation



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1. Introduction

Karstic dolines, also known as sinkholes, are among the most striking features of limestone landscapes [1]. Their concave topography creates steep microclimatic and edaphic gradients, resulting in unique ecological conditions and important refugia for plant species [2]. The steep ecological gradient from the bottom of the doline to the top (karstic plateau) allows species with different ecological requirements to coexist in close proximity. This ecological heterogeneity supports high local biodiversity and provides opportunities to explore the high horticultural potential of native flora of dolines, especially in the context of climate change [3,4].

Recent studies have emphasised the role of dolines as microrefugia that protect cold-adapted and moisture-demanding species from regional warming trends [5]. At the same time, these small-scale refugia can prolong the flowering period and extend the growing season, which is also important for the other biota [6,7]. The existence of horticulturally important plants (HPs) in dolines could provide new resources for sustainable horticulture and food security [8]. At the same time, cultural knowledge about edible and medicinal plants remains relevant for modern horticultural use [9]. For example, many wild plant species have increased tolerance to drought and other stressors, high nutritional or medicinal value, and ethnobotanical importance, making them candidates for new horticultural crops in a changing climate [8]. The cultivation of wild species not only expands the number of crops available to farmers but also helps preserve botanical heritage and genetic diversity. In particular, several species characteristic of the Dinaric dolines (e.g., *Galanthus nivalis*, *Helleborus* spp., *Paeonia officinalis*, *Primula vulgaris*, *Dictamnus albus*) are already valued ornamental or herbal plants. Nevertheless, their occurrence in these natural refugia has rarely been studied from a horticultural perspective [10–16].

However, the potential horticultural value of karstic dolines has not been well studied. So far, research in dolines has mainly focused on ecology and nature conservation [17,18], while the link between doline ecology, HPs, and climate change has not been well elaborated. Studies in urban horticulture show that plant selection based on traits such as drought tolerance, phenology, and ecosystem services can improve the resilience of green spaces in changing environments [19]. In karst landscapes, similar ecological problems (e.g., water scarcity, temperature extremes) occur, and dolines, with their ecological plasticity, support a buffering capacity and provide a safe haven for biodiversity. Although dolines are recognised as biodiversity hotspots and climate refugia [5], their potential to serve as a species pool for HPs has been largely neglected. This study aims to highlight the potential importance of dolines for horticulture.

The aims of this study are as follows: (1) sampling the floristic composition of dolines and elaboration of HPs appearing along the ecological (microclimatic and edaphic) gradient in dolines; (2) identification and elaboration of plant traits of HPs along doline slopes (from bottom to top); (3) assessment of the potential of HPs for sustainable horticultural use; and (4) demonstration of the potential of dolines for linking biodiversity conservation and horticultural use. Our study aims to bridge the gap between ecological research on biodiversity in dolines and the importance of plant species for practical horticultural utilisation.

2. Materials and Methods

2.1. Area of Research

This study took place on the Kras Plateau (350 km²), a limestone karstic plateau located above the Bay of Trieste in the northernmost part of the Adriatic Sea, at an altitude of 300–500 m. It is an elevated and slightly levelled corrosive plain in the NW part of the Dinarides. The climate is transitional between Mediterranean and continental (i.e., sub-Mediterranean), with rainy, cool winters and hot summers. Annual rainfall is around 1400 mm, and the average annual temperature is 12 °C. The Kras Plateau consists of karstified Mesozoic limestone, which is mainly covered by rendzinas and cambisols. The zonal forests in the area are dominated by hop hornbeam (*Ostrya carpinifolia*), pubescent oak (*Quercus pubescens*), and manna ash (*Fraxinus ornus*) [20–22].

The object of the research was dolines. They are natural, closed depressions created by the dissolution of carbonate rock. They have diameters ranging from a few metres to several hundred metres and are gently sloping to vertical at the sides. Their depth ranges from a few metres to several dozen metres. Microrefugia occur in dolines because

the ecological (microclimatic and edaphic) conditions change due to the concavity of the terrain [23,24].

To exclude the effects of disturbance (logging, cattle grazing, and agriculture), only dolines in forests were selected. We selected forests that are very similar to the potential natural vegetation, where differences in floristic composition in dolines should result only from the climatic and edaphic conditions [17,25].

2.2. Fieldwork

The transect method was used to sample and analyse the vegetation in the dolines. We sampled 10 dolines with different depths (Figure 1; Table 1). The sampled dolines were selected in the same area to ensure the same macroclimatic conditions. We sampled continuous line transects with 2 m × 2 m plots from the northern edge of the doline to the southern edge, spanning the bottom. The length of the transects varied depending on the size of the dolines. All vascular plants in the ground layer were recorded, and their cover was visually estimated according to the standard Central European 7-degree scale [26]. Sampling took place in May/June 2020. At the same time, we estimated the percentage of bare rock and total plant cover in each plot. We obtained a matrix of 286 plots and 124 species (Table S1).

Table 1. Selected dolines. They vary in depth; the length of the transect from the centre to the northern and southern edges of the dolines is indicated.

Doline	Depth (m)	Transect Length (m) North	Transect Length (m) South
A1	2.41	10	22
A2	5.98	14	20
A3	7.51	14	24
A4	8.17	18	34
A5	8.71	22	18
A6	13.38	32	36
A7	13.55	30	30
A8	15.4	40	34
A9	18.84	34	54
A0	21.74	38	48

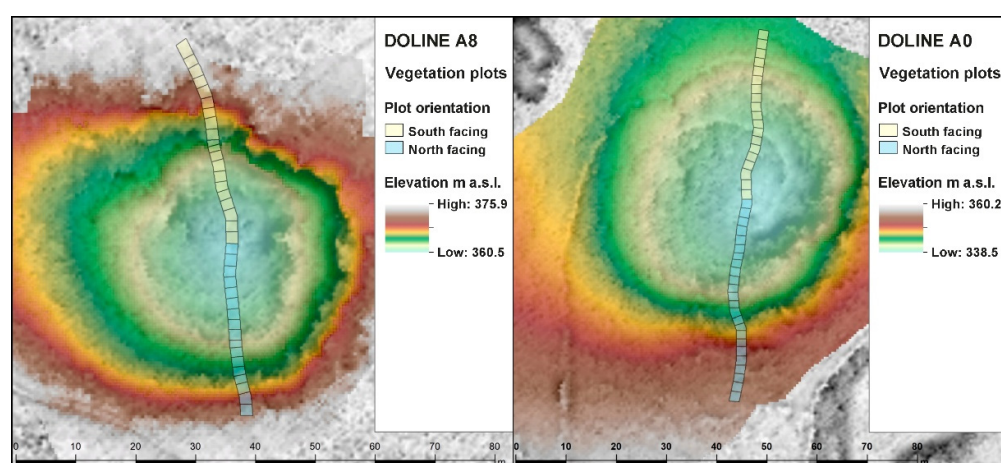


Figure 1. Sampling design with the transect method, by which the plant composition was sampled from the doline's bottom to the top. Dolines A8 and A0 are presented as examples of bigger dolines to visualise the ratio between doline depth and length of transects (after [4]).

2.3. Data Elaboration

We consulted several literature sources [14–16] and identified plant species with high potential for horticulture (HPs). We removed species with low horticultural potential from the dataset, as well as one plot that had no HPs. In this way, we obtained 285 plots and 68 plant species. This matrix served as a starting point for the analysis (Table S1).

We carried out the cluster analysis using the TWINSpan programme [27]. The cover values of the plant species were converted into percentages [26]. We defined the cut levels as 0, 5, and 25% [28], and the accepted split at the second level resulted in 4 clusters representing the main groups of HPs. We tried to characterise these four groups in further elaboration. We presented the depth of vegetation plots and the percentage of bare rock on the surface by violin plots. We linked the main groups of HPs to the TWINSpan groups, which represent the position of the plots within the dolines, as previously noted [24] by a Sankey diagram. The violin plots and Sankey diagram were created using the ggSankey package in the R environment [29,30].

We used the JUICE programme for the manipulation and analysis of data; it is a specialised software designed for the editing and analysis of vegetation data. It supports various classification techniques (TWINSpan; DCA) and diagnostic species identification; calculates bioindicator (Ellenberg) values; and facilitates the creation of synoptic tables [31]. We created a synoptic table and sorted out the diagnostic species of four groups by calculating the fidelity of each species to each group using the ϕ -coefficient as a measure of fidelity [31,32], where species with a phi value above 0.10 were considered diagnostic. The phi coefficient was calculated for equal cluster sizes. HP, for which its concentration of occurrence in the vegetation plots of a given group (cluster) was not significant at $p < 0.05$ (Fisher's exact test), was excluded from the group of diagnostic species [33]. The other species were sorted according to decreasing occurrence.

We performed a Detrended Correspondence Analysis (DCA) within the matrix of vegetation plots [34]. The ordination reduced the complexity of the data and visualised the relationship between vegetation plots, and we could identify the gradient within the data [35]. The cover values of the plant species were converted into percentages and subjected to a logarithmic transformation. By this procedure, we transformed the original Central European 7-degree scale into an ordinal scale and gave an adjusted weight to the species covers [36]. We present the diagram of vegetation plots and the diagram of plant species. On the diagram of vegetation plots, we also passively plotted the depth of the plots, the total cover, the bare rock cover on the surface and the unweighted values of the bioindicator (Ellenberg) values. The bioindicator values were calculated using the JUICE programme [31]. We used all species presented in the plots only for the calculation of the bioindicator values. Calculations were performed using the mass module of the vegan programme package [37] in the R environment [30]. We calculated chorotypes, functional strategies, life forms, and the beginning and duration of flowering, as well as the proportion of flower colour, using the community weighted mean (CWM) of each trait in the CANOCO programme [35]. We binarised the presence of plants in the vegetation plots. The results were visualised by their passive projection onto the DCA ordination planes. We categorised the plants into chorotypes according to the classification proposed by Pignatti [38], grouping steno- and euri-Mediterranean species into Mediterranean species. The chorotypes express the origin of the plant species [39]. We also calculated functional strategies, for which we used Grime's CSR model [40], as competitors (c), stress tolerants (s), ruderals (r), and their combinations (csr, sr, and cs). The strategies express the response of species to disturbance and stress conditions. The data were provided by the BiolFlor database [41]. We determined the life forms of the plants using the morphological characteristics of the plants based on the life forms of Raunkiaer [42]. Raunkiaer's system is based on the

location of the buds during seasons with unfavourable conditions (cold or dry seasons). Pignatti proposed the extended classification [43], in which the existing life forms, such as phanerophytes, nanophanerophytes, hemicryptophytes, therophytes, and geophytes, are subdivided according to growth forms, including caespitose, rosette, scapose, suffruticose, creeping, and rhizomatous types, to name only the most important ones. The information on the beginning of flowering (month), the duration of flowering (in months), and the colour of the flowers for each plant species was taken from the local flora [44].

We decided to apply the functional traits provided by species lists and databases [38,41,43,44]. The measurement of traits in the site would be time-consuming and, in some cases, not possible [45]. The same procedure is used even for the analysis on the global scale [46], although some variation could be expected [47].

3. Results

The numerical analysis divided the vegetation plots into four groups (Table 2). Group 1 is characterised by *Campanula pyramidalis*, *Frangula rupestris*, *Juniperus communis*, *Moehringia muscosa*, *Polygonatum odoratum*, and *Prunus mahaleb*; Group 2 by *Anthericum ramosum*, *Asparagus tenuifolius*, *Betonica officinalis* var. *serotina*, *Carex humilis*, *Carex montana*, *Cotinus coggygria*, *Dictamnus albus*, *Genista tinctoria*, *Ostrya carpinifolia*, *Rosa canina*, *Sesleria autumnalis*, *Silene nutans*, *Teucrium chamaedrys*, and *Vincetoxicum hirundinaria*; Group 3 by *Aristolochia lutea*, *Asarum europaeum*, *Campanula trachelium*, *Galanthus nivalis*, *Lamium galeobdolon* subsp. *montanum*, *Hepatica nobilis*, *Mercurialis ovata*, *Mercurialis perennis*, *Paeonia officinalis*, *Primula vulgaris*, and *Veratrum nigrum*; Group 4 by *Carex digitata*, *Fragaria moschata*, *Melica nutans*, *Polygonatum multiflorum*, *Serratula tinctoria*, and *Tilia cordata*. *Cardamine enneaphyllos* and *Helleborus multifidus* subsp. *istriacus* simultaneously characterise the third and fourth groups. The position of the plant species in the DCA diagram confirms the results of the cluster analysis (Table 2; Figure 2).

Figures 3 and 4 show that Group 1 occurs on the upper slope near the edge of the dolines, where the sites are stony and rocky. Group 2 occurs on the karstic plateau and partly near the edge of the doline, where the sites are grassy and have little bare rock on the surface. Group 3 occurs on the lower slope and partly in the bottom, where there is a lot of bare rock on the surface. Group 4 occurs at the bottom, where there is a deep soil layer and a little bare rock on the surface.

Detrended Correspondence Analysis (DCA) (Figure 5: Ecology) with passively projected measured variables and bioindicator values reveals the ecological conditions in the dolines. The most humid and most nutrient-rich sites are located at the bottom of the doline (Groups 3 and 4). The warmest and lightest sites are located at the top and the upper slope (Group 1 and Group 2). Bare rock cover is the highest on the rocky upper and lower slopes (Groups 1 and 3), while the highest cover of plant species is found at the bottom over a deep soil layer and at the top (Groups 2 and 4).

As far as the chorotypes are concerned (Figure 5: Chorotypes), most Eurasian species are found at the bottom over deep soil (Group 4); the lower rocky slope (Group 3) is characterised by circumboreal species; the upper slope (Group 1) is characterised by Mediterranean-montane species and species from the mountains of southeastern Europe, and the top (Group 2) is characterised by Mediterranean species.

Figure 5: Strategies show that there are more species with the csr (competitor, stress-tolerant, and ruderal) and sr (stress-tolerant, ruderal) strategies at the bottom (Group 4), the s (stress-tolerant) strategy is more represented on the rocky upper slope, and the c (competitor) strategy is represented at the grassy upper slope and top.

Table 2. Synoptic table of vegetation plots by groups. Species are represented by percentage presence (first column) and fidelity of species to the given group multiplied by 100 in superscript (second column). Diagnostic species are framed. Legend for the groups: 1—rocky upper slope; 2—top and grassy upper slope; 3—lower slope and rocky bottom; 4—bottom with deep soil layer.

Group Number of Plots	1 27	2 125	3 112	4 21
<i>Moehringia muscosa</i> L.	70 69	1 ---	14 ---	. ---
<i>Frangula rupestris</i> (Scop.) Schur	52 55.3	13 ---	1 ---	. ---
<i>Campanula pyramidalis</i> L.	33 51.3	1 ---	. ---	. ---
<i>Polygonatum odoratum</i> (Mill.) Druce	44 46	16 ---	2 ---	. ---
<i>Prunus mahaleb</i> L.	30 42.3	5 ---	1 ---	. ---
<i>Juniperus communis</i> L.	19 31.2	4 ---	1 ---	. ---
<i>Vincetoxicum hirundinaria</i> Medik.	22 ---	59 51.5	7 ---	. ---
<i>Cotinus coggygria</i> Scop.	11 ---	29 34.7	2 ---	. ---
<i>Sesleria autumnalis</i> (Scop.) F.W.Schultz	85 ---	99 32.2	92 ---	24 ---
<i>Carex humilis</i> Leyss.	. ---	13 31.5	. ---	. ---
<i>Asparagus tenuifolius</i> Lam.	. ---	18 26.1	4 ---	5 ---
<i>Ostrya carpinifolia</i> Scop.	7 ---	19 25.5	4 ---	. ---
<i>Betonica officinalis</i> var. <i>serotina</i> (Host) Nyman	. ---	7 23.4	. ---	. ---
<i>Anthericum ramosum</i> L.	. ---	8 22.6	1 ---	. ---
<i>Teucrium chamaedrys</i> L.	4 ---	10 20.2	. ---	. ---
<i>Silene nutans</i> L.	. ---	5 19.1	. ---	. ---
<i>Rosa canina</i> L.	. ---	6 17.8	2 ---	. ---
<i>Genista tinctoria</i> L.	. ---	4 17.4	. ---	. ---
<i>Dictamnus albus</i> L.	22 ---	18 13.5	4 ---	. ---
<i>Carex montana</i> L.	. ---	12 12.6	. ---	14 ---
<i>Hepatica nobilis</i> Schreb.	7 ---	7 ---	50 49.8	5 ---
<i>Asarum europaeum</i> L.	7 ---	2 ---	36 44.9	. ---
<i>Campanula trachelium</i> L.	. ---	3 ---	31 41.6	5 ---
<i>Galanthus nivalis</i> L.	. ---	. ---	20 39.4	. ---
<i>Lamium galeobdolon</i> ssp. <i>montanum</i> (Pers.) Hayek	19 ---	4 ---	44 36.5	10 ---
<i>Aristolochia lutea</i> Desf.	. ---	. ---	6 21.8	. ---
<i>Mercurialis perennis</i> L.	11 ---	10 ---	37 20.9	29 ---
<i>Primula vulgaris</i> Huds.	. ---	1 ---	15 20.8	10 ---
<i>Paeonia officinalis</i> L.	22 ---	18 ---	29 18.5	. ---
<i>Mercurialis ovata</i> Strenb. & Hoppe	4 ---	18 ---	24 17.4	10 ---
<i>Veratrum nigrum</i> L.	. ---	. ---	4 16.4	. ---
<i>Tilia cordata</i> Mill.	. ---	5 ---	35 5.9	81 63.9
<i>Fragaria moschata</i> Duchesne ex Weston	. ---	. ---	. ---	29 48
<i>Polygonatum multiflorum</i> (L.) All.	. ---	2 ---	2 ---	33 47.4
<i>Carex digitata</i> L.	19 ---	8 ---	38 7.5	62 37.8
<i>Melica nutans</i> L.	. ---	6 ---	4 ---	29 37.8
<i>Serratula tinctoria</i> L.	. ---	1 ---	5 ---	14 24.1
<i>Cardamine enneaphyllos</i> (L.) Crantz	. ---	5 ---	64 27.2	95 63.6
<i>Helleborus multifidus</i> subsp. <i>istriacus</i> (Schiffn.) Merxm.&Podlech	7 ---	46 ---	68 20.1	81 35.2
<i>Fraxinus ornus</i> L.	85 ---	70 ---	75 ---	90 ---
<i>Prunus spinosa</i> L.	11 ---	10 8.3	1 ---	5 ---
<i>Aria edulis</i> (Willd.) M.Roem.	11 ---	2 ---	2 ---	10 ---
<i>Melittis melissophyllum</i> L.	33 ---	39 ---	38 ---	. ---
<i>Cornus mas</i> L.	. ---	7 ---	6 ---	14 ---
<i>Crataegus monogyna</i> Jacq.	. ---	4 ---	4 ---	14 ---
<i>Dactylorhiza maculata</i> (L.) Soó	6 4	. ---	2 ---	. ---

Table 2. Cont.

Group	1	2	3	4
Number of Plots	27	125	112	21
<i>Iris graminea</i> L.	. ---	6 ---	8 ---	. ---
<i>Campanula persicifolia</i> L.	. ---	2 ---	2 ---	. ---
<i>Cornus domestica</i> L.	. ---	1 ---	1 ---	. ---
<i>Cephalanthera longifolia</i> (L.) Fritsch	. ---	4 ---	. ---	5 ---
<i>Origanum vulgare</i> L.	4 ---	. ---	. ---	. ---
<i>Filipendula vulgaris</i> Moench	. ---	2 ---	. ---	. ---
<i>Leucanthemum platylepis</i> Borbás	. ---	2 ---	. ---	. ---
<i>Rhamnus cathartica</i> L.	. ---	2 ---	. ---	. ---
<i>Thalictrum minus</i> L.	. ---	2 ---	. ---	. ---
<i>Melica uniflora</i> Retz.	. ---	2 ---	. ---	. ---
<i>Allium sphaerocephalon</i> L.	. ---	2 ---	. ---	. ---
<i>Eryngium amethystinum</i> L.	. ---	1 ---	. ---	. ---
<i>Genista sagittalis</i> L.	. ---	1 ---	. ---	. ---
<i>Genista sylvestris</i> Scop.	. ---	1 ---	. ---	. ---
<i>Epipactis helleborine</i> (L.) Crantz	. ---	1 ---	. ---	. ---
<i>Ornithogalum orthophyllum</i> ssp. <i>kochii</i> (Parl.) Zahar.	. ---	1 ---	. ---	. ---
<i>Ulmus minor</i> Mill.	. ---	1 ---	. ---	. ---
<i>Melica ciliata</i> L.	. ---	1 ---	. ---	. ---
<i>Lilium bulbiferum</i> L.	. ---	1 ---	. ---	. ---
<i>Serapias vomeracea</i> (Burm.f.) Briq.	. ---	1 ---	. ---	. ---
<i>Campanula rapunculoides</i> L.	. ---	. ---	1 ---	. ---
<i>Maianthemum bifolium</i> (L.) F.W.Schmidt	. ---	. ---	. ---	5 ---
<i>Veronica chamaedrys</i> L.	. ---	. ---	. ---	5 ---

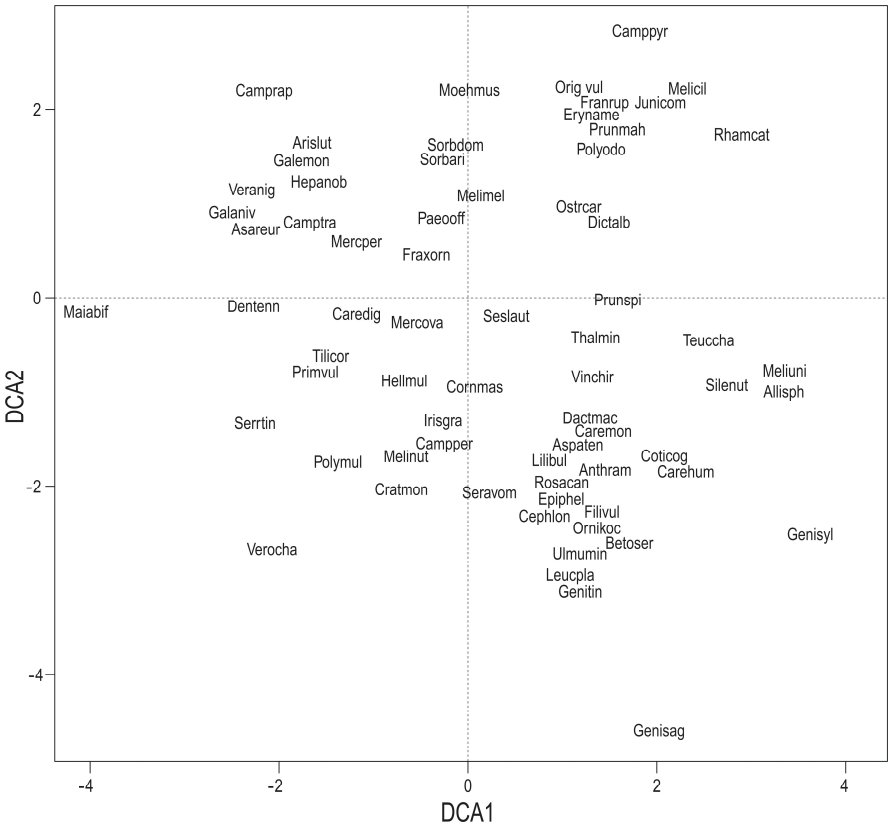


Figure 2. Diagram of the Detrended Correspondence Analysis (DCA) with all HPs. The eigenvalues are 0.4560 and 0.25090. Legend: Allisph-*Allium sphaerocephalon*; Anthram-*Anthericum ramosum*;

Arislut-Aristolochia lutea; Asareur-Asarum europaeum; Aspaten-Asparagus tenuifolius; Betoser-Betonica officinalis var. serotina; Campper-Campanula persicifolia; Campper-Campanula pyramidalis; Camprap-Campanula rapunculoides; Camptra-Campanula trachelium; Caredig-Carex digitata; Carehum-Carex humilis; Caremon-Carex montana; Cephlon-Cephalanthera longifolia; Cornmas-Cornus mas; Coticog-Cotinus coggygria; Cratmon-Crataegus monogyna; Dactmac-Dactylorhiza maculata agg.; Dentenn-Cardamine enneaphyllos; Dictalb-Dictamnus albus; Epiphel-Epipactis helleborine; Eryname-Eryngium amethystinum; Filivul-Filipendula vulgaris; Fragmos-Fragaria moschata; Franrup-Frangula rupestris; Fraxorn-Fraxinus ornus; Galaniv-Galanthus nivalis; Galemon-Lamium galeobdolon ssp. montanum; Genisag-Genista sagittalis; Genisyl-Genista sylvestris; Genitin-Genista tinctoria; Hellmul-Helleborus multifidus subsp. istriacus; Hepanob-Hepatica nobilis; Irisgra-Iris graminea; Junicom-Juniperus communis; Leucpla-Leucanthemum platylepis; Lilibul-Lilium bulbiferum; Maiabif-Maianthemum bifolium; Melicil-Melica ciliata; Melinut-Melica nutans; Meliuni-Melica uniflora; Melimel-Melittis melissophyllum; Mercova-Mercurialis ovata; Mercper-Mercurialis perennis; Moehmus-Moehringia muscosa; Origvul-Origanum vulgare; Ornikoc-Ornithogalum orthophyllum subsp. kochii; Ostrycar-Ostrya carpinifolia; Paeoff-Paonia officinalis; Polymul-Polygonatum multiflorum; Polyodo-Polygonatum odoratum; Primvul-Primula vulgaris; Prunmah-Prunus mahaleb; Prunspi-Prunus spinosa; Rhamcat-Rhamnus cathartica; Rosacan-Rosa canina; Seravom-Serapias vomeracea; Serrtin-Serratula tinctoria; Seslaut-Sesleria autumnalis; Silenut-Silene nutans; Sorbari-Aria edulis; Sorbdom-Cormus domestica; Teuccha-Teucrium chamaedrys; Thalmin-Thalictrum minus; Tilicor-Tilia cordata; Ulmumin-Ulmus minor; Veranig-Veratrum nigrum; Verocha-Veronica chamaedrys; Vinchir-Vincetoxicum hirundinaria.

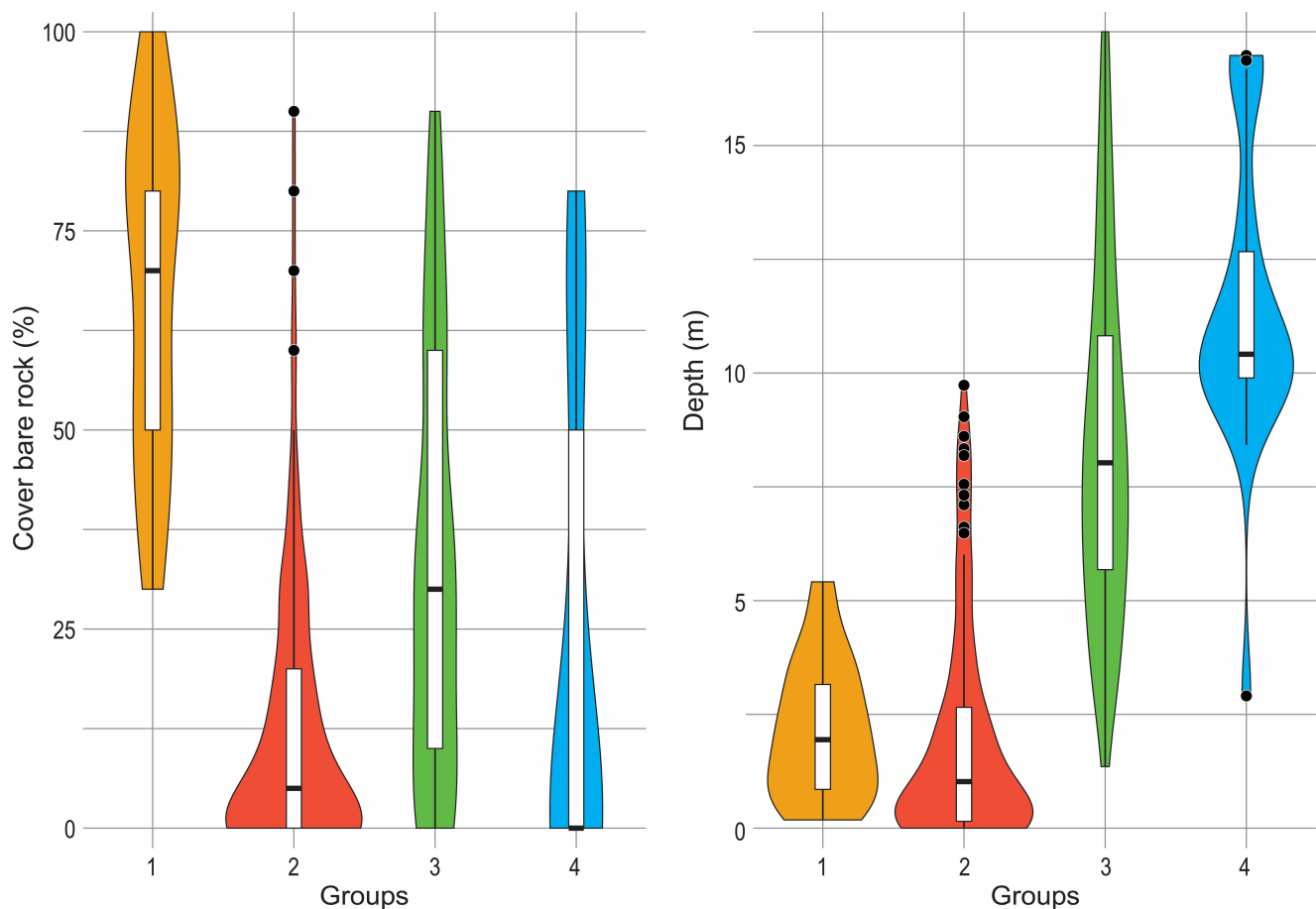


Figure 3. Violin plots of the bare rock cover on the surface (left) and the depth of the vegetation plots (from the top of the dolines) (right). Legend: 1—rocky upper slope; 2—top and grassy upper slope; 3—lower slope and rocky bottom; 4—bottom with deep soil layer.

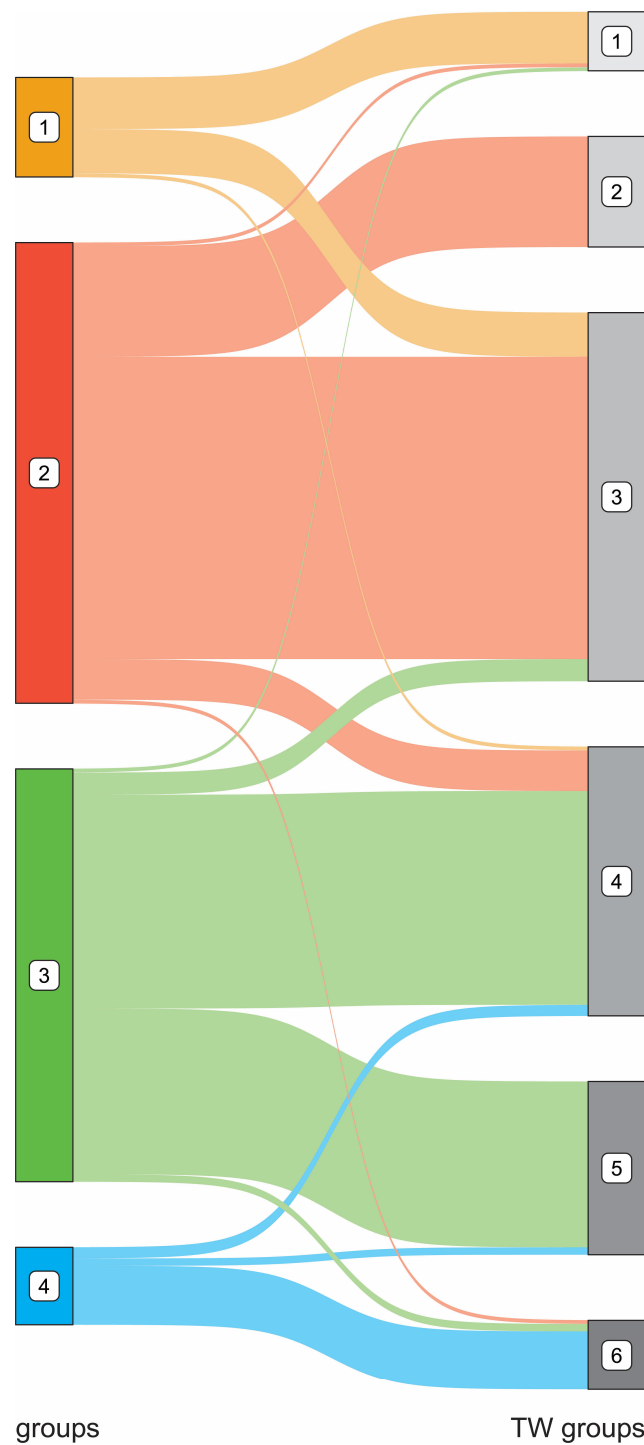


Figure 4. Sankey diagram linking the HP groups (left) as vegetation on the rocky upper slope (Group 1), vegetation on the top and grassy upper slope (Group 2), vegetation on the lower slope and rocky bottom (Group 3), and vegetation at the bottom over deep soil layer (Group 4) with the TWINSpan groups (right) based on the overall floristic composition of the dolines and integrated into their position along the slope: 1—rocky upper slope; 2—top; 3—grassy upper slopes; 4—lower slope; 5—rocky bottom; 6—bottom over deep soil layer (after [24]).

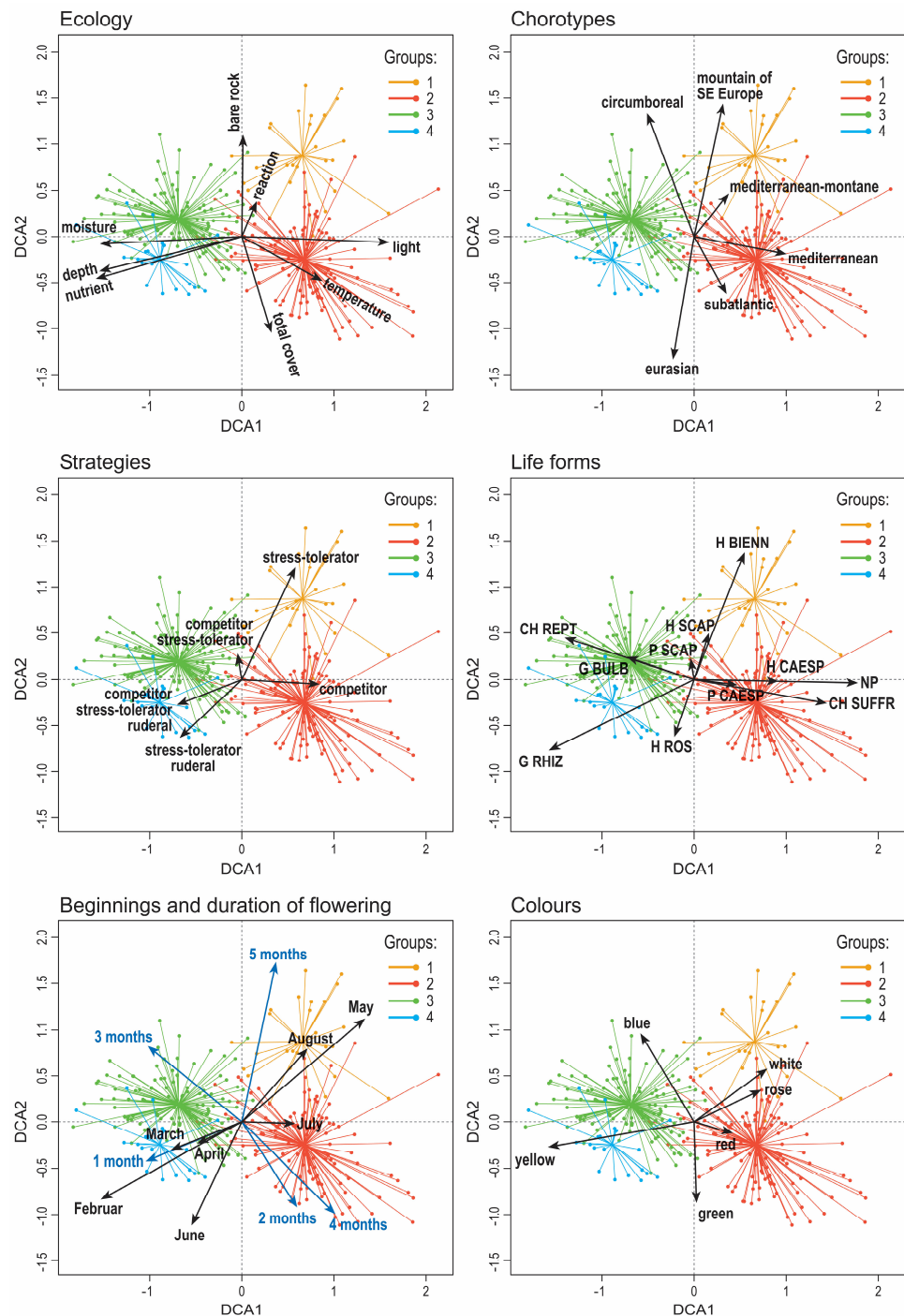


Figure 5. Detrended Correspondence Analysis (DCA) diagram visualising the four groups of HPs. All variables are passively projected onto the ordination plane: Ecology shows the measured variables (depth, bare rock cover, and total vegetation cover) and the bioindicator values (light, temperature, moisture, nutrients, and soil reaction). Chorotypes show the origin of the plants; Strategies show responses of plants to stress and disturbance. Life forms show the adaptation of plant forms to different site conditions. Beginning and duration of flowering and Colours show the beginning and duration of flowering and colours of flowers. Legend: 1-rocky upper slope; 2-top and grassy upper slope; 3-lower slope and rocky bottom; 4-bottom with deep soil layer. The figures are self-explanatory, with the exception of Life forms, which are represented by abbreviations: CH REPT-creeping chamaephytes; CH SUFFR-suffrutescent chamaephytes; G BULB-bulbous geophytes; G RHIZ-rhizomatous geophytes; H BIENN-biennial hemicryptophytes; H CAESP-caespitose hemicryptophytes; H ROS-rosette-shaped hemicryptophytes; H SCAP-scapose hemicryptophytes; NP-nanophanerophytes; P CAESP-caespitose phanerophytes; P SCAP-scapose phanerophytes.

The life forms (Figure 5: Life forms) show that at the bottom (Group 4), we find rhizomatous geophytes (e.g., *Polygonatum multiflorum*) and rosette-shaped hemicryptophytes (*Primula vulgaris* and *Silene nutans*); the lower slope (Group 2) is characterised by creeping hemicryptophytes (*Asarum europaeum*) and bulbous geophytes (*Galanthus nivalis*); the upper rocky slope (Group 1) is characterised by scapose hemicryptophytes (*Origanum vulgare*) and scapose phanerophytes (*Fraxinus ornus*), as well as biennial hemicryptophytes (*Campanula pyramidalis*); the top (Group 2) is characterised by suffrutescent chamaephytes (*Genista sylvestris*), caespitose hemicryptophytes (*Sesleria autumnalis*), and caespitose phanerophytes (*Tilia cordata*), as well as nanophanerophytes (*Cotinus coggygria*).

We find the early flowering plant species (February to April) at the bottom of the dolines (Groups 4 and 3). The rocky upper slope is characterised by the beginning of flowering in May and August (Group 1). The beginning of flowering in July is characteristic of the top (Group 2). The beginning of flowering in June is characteristic for the bottom over deep soil (Group 4). The duration of flowering is the shortest at the bottom (Group 4) and longer on the lower slope (Group 3) and at the top (Group 2). It is the longest in plants on the rocky upper slope (Group 1) (Figure 5: Beginning and duration of flowering).

The colour of the flowers (Figure 5: Colours) is mainly yellow at the bottom (Group 4), green on sites with high vegetation cover (Group 2 and Group 4), and blue on the lower slope and rocky upper slope (Group 1 and Group 3), while the flowers on the upper rocky slope and at the top (Group 1 and 2) are white and pink. Some HPs are presented in Figure 6.

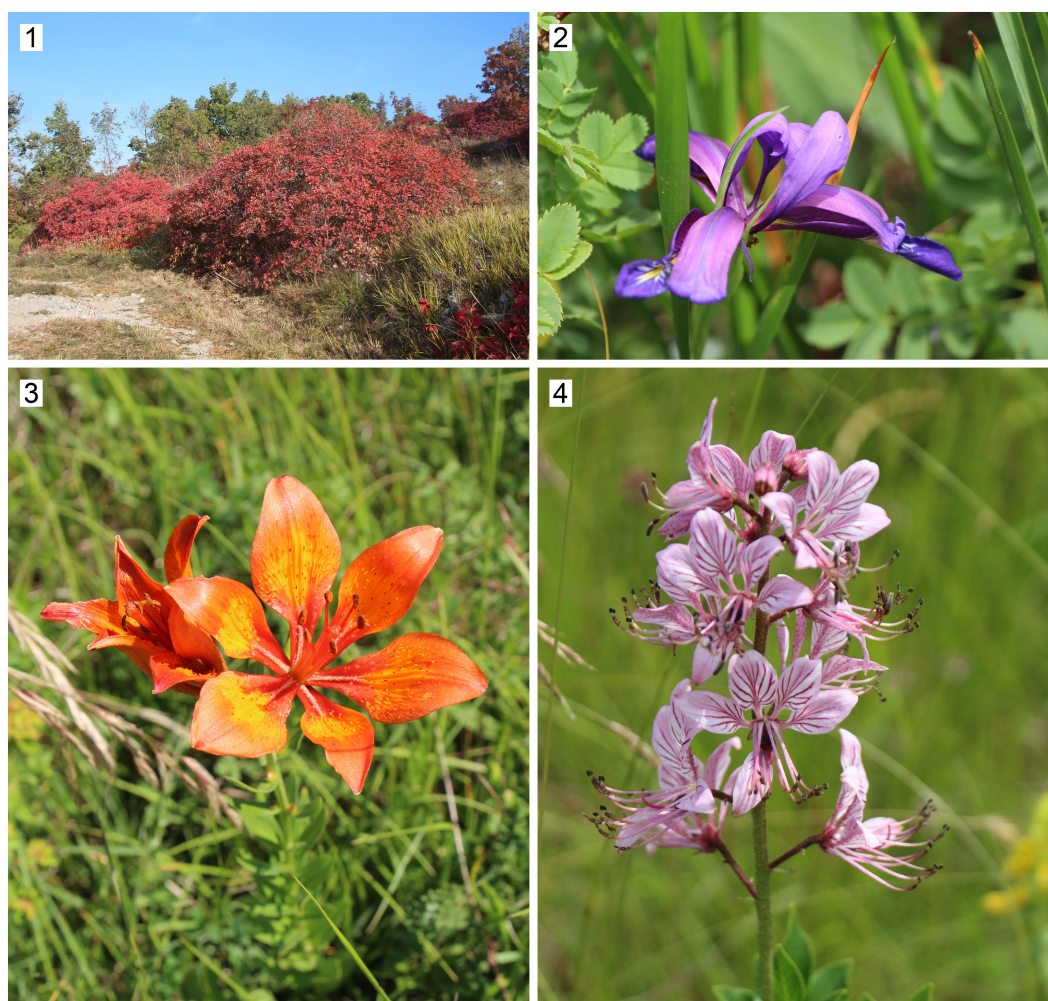


Figure 6. Cont.

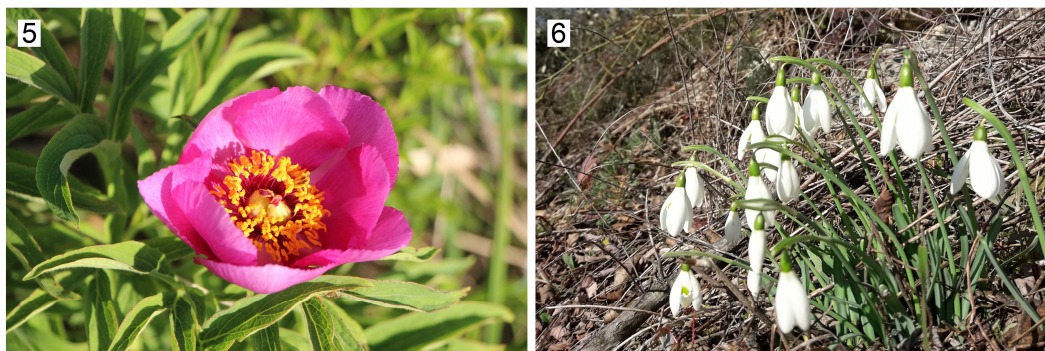


Figure 6. Some plants of horticultural importance. Legend: (1)—*Cotinus coggygia*; (2)—*Iris graminea*; (3)—*Lilium bulbiferum*; (4)—*Dictamnus albus*; (5)—*Paeonia officinalis*; (6)—*Galanthus nivalis*.

4. Discussion

4.1. Ecological Characteristics of HPs in Dolines

In accordance with the literature [48], we found that the dolines have a pronounced ecological gradient from the bottom to the top, which is clearly reflected in our results. The concave topography retains cold air and moisture, and it creates microhabitats that are distinctly different from the surrounding landscape [49]. Such contrasts favour high species richness and functional differentiation and confirm previous studies on doline microclimates as microrefugia for both thermophilic and cold-adapted species [4,6]. Our results confirm that this also applies to HPs. We have formed four groups of HPs that occupy different ecological niches and have different plant traits.

We can find early flowering species at the bottom that benefit from the high availability of nutrients and moisture [20]. As the soils in these locations are deep, we can find many geophytes [50], taking advantage of the high light availability before the leaves emerge in spring [51]. There are many wild boars in the region which actively dig and search for food [52]; this supports the ruderal functional strategy. Due to the relatively cool and moist site conditions, many Eurasian species appear to be present. These sites are dominated by oak-hornbeam forests [20].

The lower slope and the partially rocky bottom of the doline are sites of ravine forests [53]. The unstable substrate with moving stones creates special ecological conditions that favour plant species that are adapted to it, such as creeping species [4]. As there is still sufficient moisture, we find many species with bulbils. Due to the cool and moist site conditions and harsh environmental conditions, the circumboreal chorotype is well represented. These sites are dominated by maple and lime forests [24,54].

The rocky upper slope is exposed to harsh conditions, and the vegetation of the rock crevices appears on the stony sites. These sites are exposed to the sun, are dry, and are subject to strong temperature fluctuations. Here, we find the Mediterranean-montane species and species from the mountains of southeastern Europe. These conditions favour the stress-tolerant functional strategy and scapose or biennial species. The plants start flowering late, and the flowering period is long [55–57].

The last group of plants grows at the top and on the grassy upper slope. They represent the potential vegetation of the region—pubescent oak-hop hornbeam forests. This is considered the potential natural vegetation of the region, where the competitor functional strategy is well developed. The predominant chorotype is the Mediterranean element. We find many species with a caespitose life form, as well as nanophanerophytes and suffrutescent chamaephytes. This group belongs to thermophilic deciduous forests [20,54,58].

4.2. Identification of Species with Horticultural Potential

During the inventory of dolines, we recorded plant species that are either already horticulturally interesting or may become horticulturally useful due to their aesthetic value and adaptability to the karstic environment. Depending on their morphology and seasonal occurrence, they can be divided into **woody species** (*Aria edulis*, *Cornus mas*, *Cotinus coggygia*, *Crataegus monogyna*, *Fraxinus ornus*, *Prunus mahaleb*, and *Prunus spinosa*), **early and late spring flowering species** (*Galanthus nivalis*, *Helleborus multifidus*, *Hepatica nobilis*, *Iris graminea*, and *Primula vulgaris*), **orchids** (*Cephalanthera longifolia*, *Dactylorhiza maculata*, and *Serapias vomeracea*), and **structural species** (*Campanula persicifolia*, *Campanula pyramidalis*, *Dictamnus albus*, *Eryngium amethystinum*, *Lilium bulbiferum*, *Paeonia officinalis*, and *Veratrum nigrum*), which can also be used for arranging edges in gardens [59].

Most of the mentioned species thrive in temperature zones 9 to 8 [60], which in Slovenia includes the sub-Mediterranean area [61]. However, these species can also occur further inland in warmer microenvironments. Due to increasingly hot summers and mild winters, they already thrive very well in temperature zone 7, which covers most of Slovenia. Because of their adaptability to sub-Mediterranean conditions, they are more resilient in warm and dry environments than other species, especially in urban environments, which are increasingly becoming heat islands [62].

4.2.1. Woody Species

Woody species found in dolines are highly resistant to drought, strong solar UVB radiation, high temperatures and poor soil nutrient levels. These are mostly species that can withstand winter conditions, especially *Fraxinus ornus*, *Prunus mahaleb*, and *Crataegus monogyna*. They even have low salt tolerance [63]. Therefore, the species are very useful for planting in cities. As an example of good practice, we should mention the planting of the species *Fraxinus ornus* in an avenue along the main street of the city of Ljubljana, where the conditions for tree growth are very harsh, but the mentioned species has been growing very well there for more than ten years [64,65]. *Fraxinus ornus* is also a disease-resistant species and a honey-producing species [66,67]. It is also the wild relative of certain varieties, such as *Fraxinus ornus* 'Mecsek', which originates from Hungary [68] and is particularly recommended for planting in very arid areas. The shrub species present in the dolines are very resistant to drought and are therefore suitable for planting in various types of hedges. In particular, *Cornus mas*, which blooms very early, has great horticultural value as a hedge. It does not need to be pruned often; the hedge is dense, and at the same time, it always bears fruit. The fruits then provide food for birds. *Cotinus coggygia*, as a native species, is extremely suitable for planting on roadside hedges as it also tolerates intensive mechanical pruning to a low height. In Ljubljana, *C. coggygia* is planted in many places and has proven to be an extremely hardy species that turns beautiful in autumn [69].

Woody species are also important in ethnobotany. *Prunus mahaleb* was once used as a rootstock for cherry grafting. In the Kras region, cherry trees have a water problem because their roots grow superficially. *P. mahaleb*, however, has deep roots and can draw water from lower horizons during droughts [70]. Beekeepers extract honey produced from nectar from *P. mahaleb*, which has a distinctive taste [67]. *Prunus spinosa* fruits are useful as an addition to teas and are collected for the preparation of brandy [71]. *Crataegus monogyna* is a medicinal plant; the flowers were used for medicine, the fruits are a source of vitamin C, and the plant was also used as a low rootstock for grafting fruit species [70,71]. *Cornus mas* has hard wood; its fruits are used for marmalade, and the wood is used for the teeth of wooden rakes [72]. *Ostrya carpinifolia* also has extremely hard wood [70] and was used for cart wheel tracks and rifle hooves [70]. The same is valid for *Fraxinus ornus*, which was used to make tool handles for hay baskets in the past [73].

4.2.2. Early and Late Spring Flowering Species

Spring species, such as *Galanthus nivalis*, *Helleborus multifidus*, *Primula vulgaris*, *Hepatica nobilis*, and *Iris graminea*, are all highly sought-after horticultural species that are almost always present in garden plantings. The species *G. nivalis* has been an interesting horticultural species for centuries [74], from which numerous varieties have been bred. Its characteristic feature is the extremely high intraspecific variability, which can be manifested in the shape of the flowers, the presence of green colour in the flowers, and the multiplication of or reduction in floral parts [75,76]. Deviations from the average morphological form of the species are more common in extreme environments. For this reason, populations in karstic environments can be the source of new varieties. By 2002, over 80 different species of the genus *Galanthus* had been described [75], with over 500 varieties [76]. Over 80 varieties have also been described from the territory of present-day Slovenia based on findings in natural populations [77]. As a horticulturally interesting species, it began to be sold in Slovenia after 1871 [74]. The environmental conditions of the dolines also affect *Primula vulgaris* in a similar way, in which the white version occurs only in dolines and in the warmer coastal areas of Slovenia. This was already reported by Pospichal [78]. In other parts of Slovenia, however, the colour of the flowers of the mentioned species is yellow. Unlike Slovenia, in Sicily, the exclusively white variety prevails, which has a greater horticultural value than the yellow one [79]. The species *Helleborus multifidus* [80] is also extremely valued in horticulture. It can, for example, cross with other species of hellebore [81], which means the possibility of breeding new varieties, with genetic adaptability to the environment of the original species. Due to the species' presence in warmer parts of Slovenia and its adaptability to the environment, it is very suitable for planting in urban environments. Another frequently desired species is *Hepatica nobilis*, which is represented in horticulture by many varieties. Its intraspecific diversity is reflected in the colour of the flowers, which can vary from white, pink, to dark blue, or in the multiplication of petals [78,82,83]. The mentioned natural genetic diversity indicates that the species is suitable for breeding cultivars. At the same time, the use of natural forms that are different from each other can introduce variety into horticultural plantings.

4.2.3. Orchids

Orchids appearing in dolines (*Cephalanthera longifolia*, *Dactylorhiza maculata*, *Epipactis helleborine*, and *Serapias vomeracea*) have limited horticultural application but provide insight into orchid–mycorrhiza relationships, orchid–pollinator interactions, and plant nutritional strategies that could give information about sustainable cultivation practices for other species [84–86]. Orchids are difficult to cultivate, but nevertheless, they occur spontaneously in alternative habitats in urban environments. They can also serve as a good example for introducing species into alternative habitats, such as the creation of dry meadows on green roofs [87].

4.2.4. Structural Species

Aesthetic value is given to horticultural arrangements by structural species, many of which are also characteristic of dolines. These species inhabit the edges of dolines or specific areas with them. They have been used in horticulture for a long time [59]. For example, *Veratrum nigrum* has been present in horticulture since 1773. Darwin used it in his garden around 1840. It is often found in European and Asian gardens because its distinctive black flowers remain attractive even in the fruiting stage [88]. The species *Paeonia officinalis*, *Dictamnus albus*, and *Lilium bulbiferum* also have great aesthetic value, mainly due to their colourful flowers. All of the above are also drought-tolerant species. Given that *Lilium bulbiferum* is a protected species in Slovenia [89], plants should be propagated

from their genetic material and used in public plantings, thereby protecting the species *ex situ*. Aesthetically attractive native species are easier to protect by presenting them to the wider public through plantings. In addition to its aesthetic value, *Dictamnus albus* is also known in ethnobotany. All parts of the plant have been used in traditional medicine. The species is said to have antiseptic, antispasmodic, diuretic, and many other effects [90]. Recent research has also shown that the ethanol extract of *Dictamnus albus* has antioxidant properties and could be used in the treatment of diseases related to oxidative stress [91]. Its roots are an aromatic additive for vermouth [71]. Specimens from sites where plants are exposed to stress contain higher amounts of secondary metabolites.

Campanula pyramidalis, *C. persicifolia*, and *Eryngium amethystinum* are also often planted as structural plants, as they are easy to grow and are drought-resistant. Due to their production of large quantities of seeds, they spread effectively and may be suitable for the restoration of large areas [59].

4.3. Role of Dolines as a Natural Hub Linking Biodiversity and Horticulture

Apart from their floristic and ecological importance, dolines serve as a natural hub where several functions come together. They support biodiversity conservation by acting as microrefugia, preserve cultural heritage through ethnobotanical species, and provide a species pool for the selection of plants with horticultural potential. The native plants were found to be better in all respects (public preferences, conservation strategies, and plant performance) than the non-natives. This multifunctionality reflects the wider recognition of small natural features as disproportionately important for ecosystem services [92,93]. From a horticultural perspective, dolines can initiate new planting strategies that mimic their natural gradient. By incorporating bottom–slope–top zoning into the garden design, one can create plant combinations that maximise seasonal flowering, minimise watering requirements, and support pollinators throughout the year. For example, combining spring geophytes with summer-flowering aromatic herbs could replicate the sequential flowering patterns observed in dolines, providing both decorative interest and ecological function.

In small geomorphological features such as dolines, narrow endemic species can hardly occur (e.g., *Horstrissea dolinicola* [94]). However, the diverse microclimate allows species from various vegetation zones to establish, increasing the regional species pool and contributing to resilience against climate change. As dolines are numerous in the region and are situated close together (470,000 in Slovenia), they may enable greater connectivity for populations within them [4,24,95]. Some species found in the research area are protected in the country, such as *Cephalanthera longifolia*, *Dactylorhiza maculata*, *Epipactis helleborine*, *Galanthus nivalis*, *Helleborus multifidus*, *Iris graminea*, *Lilium bulbiferum*, *Paeonia officinalis*, and *Serapias vomeracea* [89]. Care must be taken when collecting these and other species from the wild.

We have demonstrated for the first time that the horticultural potential of dolines is very high, primarily due to the microtopography of the depressions and their abundance in the karstic landscape [96]. There are 14,000 dolines on the Kras Plateau, most of which are now covered with forest, and not all are relevant for conservation [1]. Further research will need to focus in more detail on analysing the impact of the geodiversity of individual dolines from a horticultural value perspective, as not all dolines are equally important. A question to which we currently have no answer is which dolines in the landscape are horticultural hotspots (areas of high horticultural potential) so that we can produce accurate maps of these dolines to support their protection and conservation value. Climatic refugia on the Kras Plateau are, for example, dolines that are deeper than 13 m [24]. Dolines that are important from a horticultural point of view seem to have a greater range of geodiversity as they host a wide variety of plant species, as demonstrated with the present analysis.

5. Conclusions

The ecological heterogeneity within dolines can be seen as a natural analogue of the controlled environment in botanical gardens, where deliberate gradients of shade, moisture, and soil conditions are created to maximise plant diversity. Our results emphasise that dolines are not only hotspots of biodiversity but also a potential model for species turnover under climate change.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/horticulturae11111355/s1>. Table S1: Table of vegetation plots with their details.

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Nomenclature

The nomenclature of plant species follows the Plants of the World Online, Royal Botanic Gardens Kew [Available online: <https://powo.science.kew.org/>, accessed 5 October 2025].

Abbreviation

HP Plant of horticultural importance

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