PREPRINT

Author-formatted, not peer-reviewed document posted on 27/11/2025

DOI: https://doi.org/10.3897/arphapreprints.e180472

Picea omorika (Pinaceae): an endangered endemic species from Serbia and Bosnia-Herzegovina, naturalised in the Brembana Valley (Orobic Alps, Italy)

LUCA GIUPPONI, Alex Alberto, Stefano Sala, Annamaria Giorgi

Picea omorika (Pinaceae): an endangered endemic species from Serbia and Bosnia-Herzegovina, naturalised in the Brembana Valley (Orobic Alps, Italy)

Luca Giupponi[1,2], Alex Alberto[1], Stefano Sala[1,2], Annamaria Giorgi[1,2]

[1]Centre of Applied Studies for the Sustainable Management and Protection of Mountain Areas-C.R.C. Ge.S.Di.Mont., University of Milan, Via Morino 8, 25048 Edolo, Italy
[2]Department of Agricultural and Environmental Sciences - Production, Landscape and Agroenergy, University of Milan, Via Celoria 2, 20133 Milan, Italy

Corresponding author: Luca Giupponi (luca.giupponi@unimi.it)

Abstract
Picea omorika (Pančić) Purk. is an endangered conifer endemic to Serbia and Bosnia-Herzegovina. This research reports the first case of its naturalisation in Italy, specifically in the upper Brembana Valley (Orobic Alps, Lombardy), where an uneven-aged population of approximately 50-60 individuals grows within a wood pasture at 1760-1790 m a.s.l., inside the Orobie Bergamasche Regional Park. Dendrochronological analysis indicates that this population likely originated from a single tree planted for ornamental purposes near a mountain hut in the 1960s. Over the past 30 years, the species has propagated in the study area under cold, suboceanic climatic conditions and on moderately moist, nutrient-poor, slightly acidic soils, as inferred from climatic data and Ellenberg ecological indicator values. Grime's competitor-stress-tolerator-ruderal (CSR) functional strategy analysis classified *P. omorika* as a strictly stress-tolerant species (C = 0.0%, S = 100.0%, R = 0.0%) with low invasive potential. Phytosociological analysis indicates that the *P. omorika* community is part of a secondary succession that is progressing from pastures of *Nardion strictae* towards high-montane coniferous forests of *Piceion excelsae*. The results of this research suggest that the upper Brembana Valley may serve as a suitable site for the conservation/translocation of *P. omorika*.

Keywords
Serbian spruce, exotic species, naturalisation, Southern Alps, Ellenberg indicator values, CSR functional strategy

Introduction
Picea omorika (Pančić) Purk., commonly known as the Serbian spruce, is a conifer endemic to a restricted mountain area along the middle course of the Drina River, between western Serbia and eastern Bosnia and Herzegovina, within an area of approximately 10.000 km^2 (Mataruga et al. 2020; Vacek and Vacek 2023). In its natural range, it grows on steep slopes and on soils with diverse physico-chemical properties (Savill et al. 2017), at elevations between 800 and 1,700 m a.s.l., forming mixed forests of *Erico carneae-Piceion omorikae* Mucina et Čarni 2016 phytosociological alliance (Mucina et al. 2016), characterized by exclusive species such as *Epipogium aphyllum* Sw., *Equisetum hyemale* L., *Euphorbia glareosa* Pall. ex M.Bieb., *Anthoxanthum australe* (Schrad.) Veldkamp, *Petasites kablikianus* Tausch ex Bercht., and *Saxifraga tridactylites* L. (Ilić et al. 2022).
Over the past decades, several studies have investigated the genetic, morpho-anatomical and phytochemical variability of *P. omorika* populations from Serbia and Bosnia-Herzegovina, highlighting differences between Serbian and Bosnian populations in terms of needle morphology, leaf anatomy and phytochemical composition (Nikolić et al. 2023, 2024, 2025). Recently, Tichý et al. (2023) provided Ellenberg ecological indicator values for *P. omorika*,

contributing to filling a gap in the ecological characterisation of the species; nonetheless, its position within the competitor-stress-tolerator-ruderal (CSR) framework proposed by Grime (2001) has not yet been determined.

Palynological and palaeobotanical evidence indicates that during the Tertiary period, a species of the *Picea* genus (*P. omorikoides*), sharing similar traits with *P. omorika*, was widespread across large areas of Central and Southern Europe, including the Alps (Ravazzi 2002). However, climatic oscillations during the glacial and post-glacial periods led to its disappearance from the Alps, probably as a consequence of the reduction of suitable habitats and increased competition with more adaptable conifer species (Ravazzi 2002).

The current fragmentation of the distribution range and the low connectivity among *P. omorika* populations have raised concerns regarding the species' genetic diversity and natural regeneration capacity in Serbia and Bosnia-Herzegovina (EUFORGEN 2024). Furthermore, due to its extremely restricted distribution, competition with other forest species (particularly broadleaf trees) (Savill et al. 2017) and high vulnerability to climate change, *P. omorika* has been classified as "Endangered" on the IUCN Red List (Aleksić et al. 2017). The conservation of this species is therefore considered a priority, owing to both its ecological value and its phylogenetic significance as a glacial relict. Consequently, *P. omorika* is legally protected in both Serbia and Bosnia-Herzegovina. In Serbia, all individuals of *P. omorika* are protected, with the main populations included within Tara National Park, whereas in Bosnia-Herzegovina the species is listed among those whose felling, uprooting, or damaging is prohibited under forestry and protected-area legislation (Mataruga et al. 2020).

In modern times, *P. omorika* has been widely cultivated for ornamental purposes, owing to its slender columnar habit, the silvery sheen of the needle undersides, and its tolerance of a broad range of edaphic and climatic conditions (Savill et al. 2017; Vacek and Vacek 2023). Although planted in numerous gardens and parks across Europe, no stable cases of naturalisation have been documented outside its native range so far (Vacek and Vacek 2023; EUFORGEN 2024). This suggests that the species depends on highly specific ecological conditions to complete its full life cycle, thereby rendering its long-term conservation in (semi-)natural habitats challenging.

This research aims to report the first case of *P. omorika* naturalisation in Italy (Brembana Valley, Orobic Alps). In addition, it seeks to elucidate the potential causes of its introduction, assess its CSR functional strategy, and analyse the ecological and phytosociological features of the plant community in which it occurs, thereby enhancing current knowledge of the environmental conditions suitable for the establishment/conservation of this species.

Occurrence and study area

The *P. omorika* stand is located within the municipality of Carona (Province of Bergamo, Lombardy Region), in the upper Brembana Valley (latitude: 46° 01' 41'' N; longitude: 9° 51' 38'' E), at an elevation between 1760 and 1790 m a.s.l. (Fig. 1). The site lies within the boundaries of the Orobie Bergamasche Regional Park and is characterised by a suboceanic pre-Alpine climate, with abundant annual precipitation (>1700 mm) mainly distributed during the equinoctial periods and summer months (Fig. 2).

The soil in the study area is a podzol developed on acidic rocks belonging to the Collio geological formation (Lower Permian) (Provincia di Bergamo 2002). From a geobotanical perspective, the area falls within the South-Orobic District (Andreis 2002), which is characterised by a high number of endemic species (Martini et al. 2012), including some acidophilous species typical of the montane and subalpine vegetation belts such as *Sanguisorba dodecandra* Moretti and *Viola comollia* Massara (Bertolli 2024). The current potential vegetation is the Norway spruce forest of the *Vaccinio-Abietenion* Oberd. 1962 suballiance (alliance: *Piceion excelsae* Pawłowski et al. 1928), which is widespread in Lombardy in the high montane and subalpine belts of the mesalpic region, including the Orobic Alps (Del Favero 2002; Andreis et al. 2009). The secondary succession leading to this forest type (*Luzulo niveae-Piceo excelsae sigmetum*) generally starts from *Nardion strictae* Br.-Bl. 1926 pastures (Verde et al. 2010).

P. omorika was identified using the dichotomous keys of Tutin et al. (1968) and the morphological descriptions reported in the literature (Ballian et al. 2016; Savill et al. 2017; Vacek and Vacek 2023; Nikolić et al. 2025) (Fig. 3).

Within the study area, approximately 50-60 Serbian spruces of various sizes occur, distributed across a wood pasture of about 1 ha. At the margin of this wood pasture, along the right bank of the Brembo stream, stands the Armentarga hut (Fig. 1), a small building constructed in 1950 to host workers involved in building the artificial dam of Fregabolgia Lake for hydroelectric power production. In 1952, the hut was acquired, renovated, and has since been managed as a private alpine refuge by the “Penne Nere” Alpine Group of Bergamo.

A single Serbian spruce grows in proximity to the Armentarga hut (Fig. 4), while all others are located at least 10 m away, in what was a pasture in the 1950s and has since evolved into a wood pasture (Fig. 1 and Fig. 3a) due to the gradual abandonment of pastoral activities. This land-use change, widespread throughout the Alpine chain since the second half of the 20th century, has favoured forest expansion (Cislaghi et al. 2019).

No forest plantations or reforestation activities involving *P. omorika* have been carried out in the study area over the past century, as confirmed by data from the technical-environmental offices of the “Comunità Montana Valle Brembana” (Protocol No. 6062/11/2/AG/mb) and the Municipality of Carona (personal communication).

Figure 1. Distribution of *P. omorika* in Europe (data source: GBIF database) and location of the new occurrence in Italy. The study area (wood pasture with *P. omorika*) is highlighted in green.

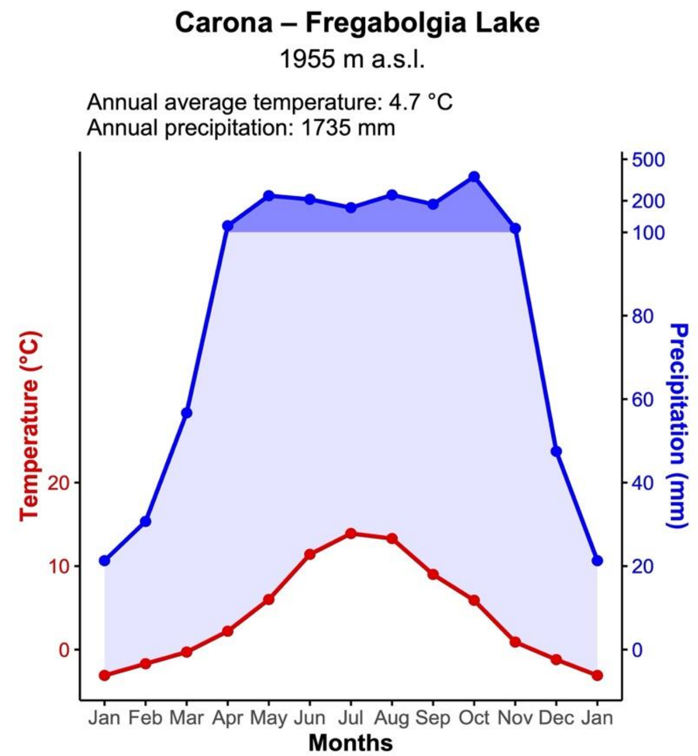

Figure 2. Ombrothermic diagram of the weather station of Fregabolgia Lake (Carona - BG, latitude: 46°01’27’’N, longitude: 9°51’43’’E). Data source: ARPA Lombardia, 2015-2024.

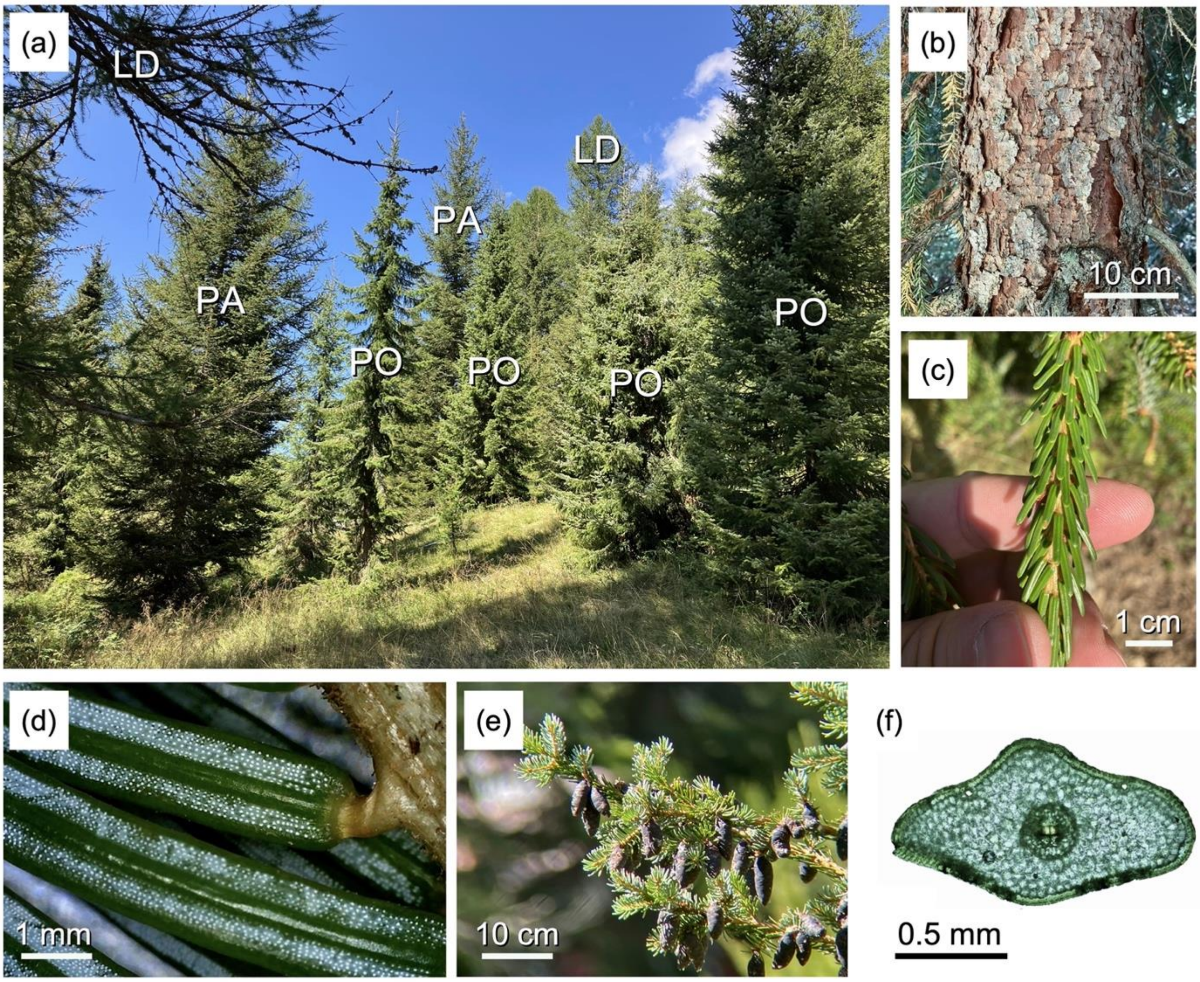

Figure 3. Morphological characteristics of *P. omorika* growing in the study area. (a) General view of the stand showing *P. omorika* (PO) surrounded by *Picea abies* (PA) and *Larix decidua* (LD). (b) Bark of *P. omorika*, showing thin, scaly plates with reddish-brown tones. (c) Shoot with slender, keeled needles, 0.8-1.8 cm long and 1.1-1.8 mm wide. (d) Needle underside with two broad white stomatal bands composed of 4-6 lines each. (e) Female cones at the upper part of the crown; they are pendulous, resinous, dark bluish-violet, ovoid to oblong, and reach up to 6.5 cm in length when mature. (f) Microscopic section of a needle showing its bilaterally flattened shape.

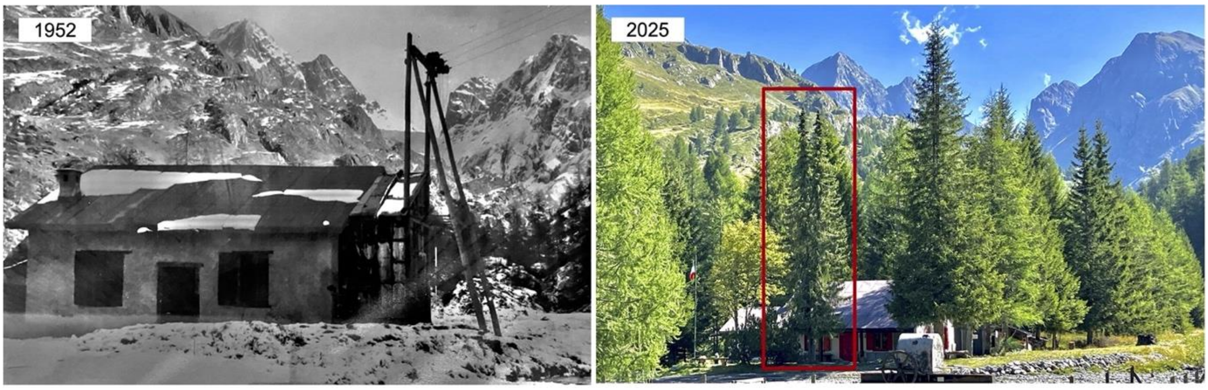

Figure 4. Armentarga hut in 1952 (photo from the archive of the "Penne Nere" Alpine Group) and in 2025 (photo by Giupponi L.). The red box marks the Serbian spruce located near the hut, currently surrounded by Norway spruces and larches that were not present in 1952.

Materials and methods

Dendrochronological analysis

The age and growth dynamics of the *P. omorika* stand were assessed on a sample of 12 trees, selected to include individuals of varying heights and sizes to be as representative as possible of the stand. The sample also included the only Serbian spruce growing near the Armentarga hut.

Wood cores were collected from each tree at breast height (1.3 m above ground level) using a Pressler increment borer, and stem circumference at breast height (CBH) was measured with a tape measure. In the laboratory, the cores were examined under a stereomicroscope, and annual growth rings were counted to determine the age of each tree. Based on these data, the age of the sampled trees was established, and a growth model of stem circumference over time was developed. The model was constructed using linear regression analysis in the R environment (R Core Team 2025).

Vegetation data collection and analysis

In the study area, 3 phytosociological relevés were carried out on 100 m² (10 × 10 m) following the classical Zürich-Montpellier school approach (Braun-Blanquet, 1964). For each relevé, topographic data (elevation, aspect and slope angle) were recorded, and total cover of trees, shrubs, herbaceous vegetation and litter was estimated. The vascular plants were identified using the dichotomous keys of Pignatti (2017-2019) and for each plant species was assigned a cover-abundance index according to the Braun-Blanquet scale: r, rare species in the relevé; +, cover <1%; 1, cover 1-5%; 2, cover 5-25%; 3, cover 25-50%; 4, cover 50-75%; 5, cover 75-100%.

For the phytosociological analysis of the *P. omorika* plant community in the study area, various bibliographic sources were consulted (Aeschimann et al. 2004; Ubaldi 2008a; Ubaldi 2008b; Andreis et al. 2009; Landolt et al. 2010) as well as online portals, including "Prodromo della vegetazione italiana" (Biondi and Blasi 2014) and "FloraVeg.EU" (Chytrý et al. 2024).

The mean Ellenberg Indicator Values (EIVs), weighted by species cover, were calculated for each relevé in order to assess the ecological characteristics of the vegetation in the study area and compare these values with those recently assigned to *P. omorica* (Tichý et al. 2023). This study used the EIVs recently updated and extended for the entire European vascular flora by Tichý et al. (2023): light (L), temperature (T), soil moisture (M), soil reaction (R), nutrients (N), and salinity (S). The mean EIV values were calculated after transforming the Braun-Blanquet cover-abundance indices according to the ordinal scale proposed by van der Maarel (1979): r = 1; + = 2; 1 = 3; 2 = 5; 3 = 7; 4 = 8; 5 = 9.

The scientific names of the species mentioned in this research follow Pignatti (2017-2019), while the names of syntaxa (from class to alliance level) are in accordance with Mucina et al. (2016).

Functional strategy evaluation
CSR functional strategy of *P. omorika* was assessed following the procedure described by Pierce et al. (2017). In particular, 50 healthy leaves were collected from the lower branches (at least 2 years old) of 10 different individuals. All samples were wrapped in moist paper and stored at 4 °C for one night. Fresh weight of saturated leaves was determined using an analytical balance (Precisa XB 220A). Leaf area was obtained by scanning the samples with a digital scanner and processing the images with ImageJ (Schneider et al. 2012). Dry weight was measured after oven-drying the leaves at 105 °C for 24 h. CSR values and the functional strategy were calculated using the "StrateFy" spreadsheet (Pierce et al. 2017). In addition, both weighted (according to species cover values) and unweighted mean CSR strategies of the whole plant community were computed. For this purpose, CSR values of the species within the community were retrieved from the field-portable list of CSR strategies (Pierce et al. 2017). CSR values were then visualised in the ternary CSR graph using the "ggplot2" package of R, highlighting point/species density levels through kernel density analysis.

Results

Stand age and growth
Dendrochronological analysis of Serbian spruces revealed that the wood pasture supports an uneven-aged stand, comprising both young individuals (only a few years old) and mature trees exceeding 30 years (Figure 5). The graph in Figure 5 illustrates a linear increase in CBH with tree age. The Serbian spruce near the Armentarga hut was found to be the oldest (54 years at breast height), despite exhibiting a CBH value comparable to that of 30-35-year-old trees in the wood pasture (Figure 5).

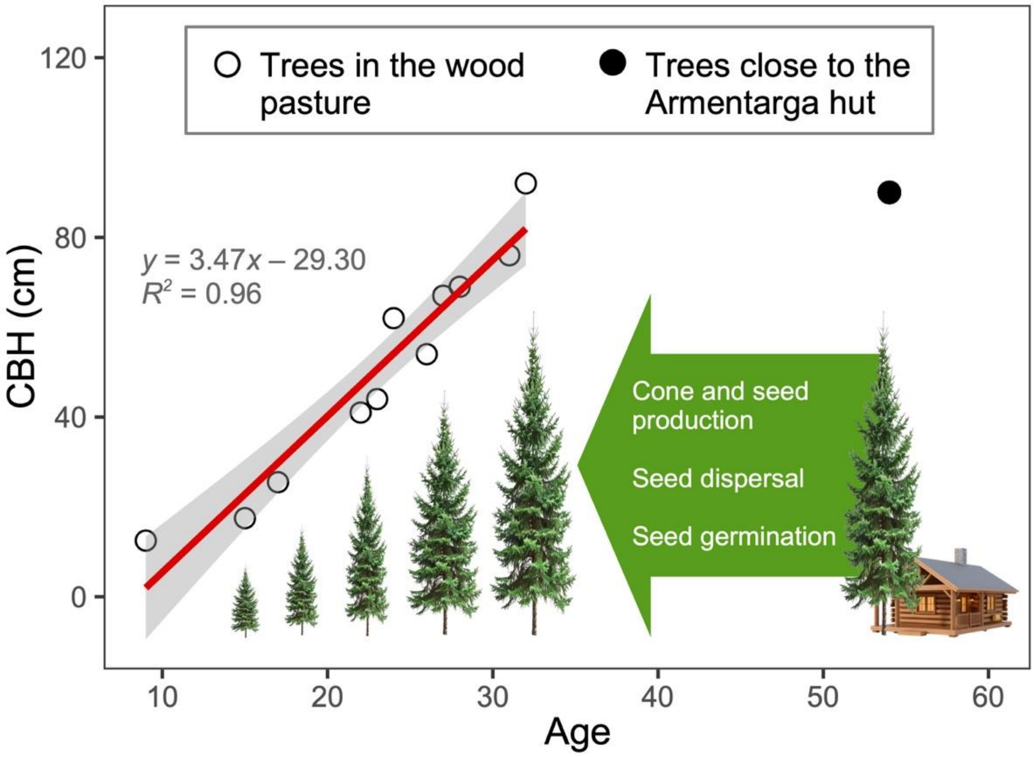

Figure 5. Relationship between tree age (years) and circumference at breast height (CBH). Open circles denote trees located within the wood pasture, whereas the filled circle represents a tree growing in proximity to the Armentaraga hut. The red line indicates the fitted linear regression (based on open circles only), with the shaded area representing the 95% confidence interval. The regression equation and the coefficient of determination value (R^2) are reported in the figure.

Plant community

In the study area, 58 plant species were identified (Table 1), of which 75% are perennial herbs (hemicryptophytes: 66%; geophytes: 10%), and the remaining species are trees (9%) and shrubs (15%). Most of the species are European montane species (orophytes), and some are endemic to the Alps, including *Sanguisorba dodecandra*, which is endemic to the Orobic Alps. *Picea omorika* is the only non-native species recorded.

The data reported in the phytosociological table of the relevés (Table 1) indicate that the *P. omorika* plant community is composed of species from different vegetation types and that secondary succession is occurring in the study area. In fact, alongside species of subalpine acidic pastures (*Nardion strictae*) with plants of nutrient-rich and moist mountain habitats of the classes *Molinio-Arrhenatheretea* and *Mulgedio-Aconitetea* (particularly in relevé 1, carried out on a flat surface), the community also includes shrubs of ecotonal/mantle communities dynamically connected to forests (*Robinietea* and *Crataego-Prunetea*), as well as species of mature oro-boreal coniferous forests (*Piceion excelsae* and *Piceetalia excelsae*) (Tab. 1).

Table 1. Phytosociological table of relevés.

Biological Form	Chorological Type	Relevé code	1	2	3
		Area (m²)	100	100	100
		Slope (°)	0	32	20
		Aspect (°)	-	157	127
		Elevation (m a.s.l.)	1780	1778	1770
		Trees cover (%)	40	70	30
		Shrubs cover (%)	5	50	25
		Grass cover (%)	95	30	75
		Litter cover (%)	0	20	0
		Number of species	24	38	32
		Target species			
P scap	Endem. W-Balkans	*Picea omorika* (Pančić) Purk.	1	2	2
		***Nardion strictae* Br.-Bl. 1926**			
H caesp	Circumbor.	*Agrostis capillaris* L.	1	1	2
H scap	Orof. SE-Europ.	*Centaurea nervosa* Willd.	+	+	1
H scap	Eurasiat.	*Potentilla erecta* (L.) Raeusch.	+	+	+
H caesp	Eurosib.	*Nardus stricta* L.	+	+	2
H scap	Endem. Alp.	*Campanula barbata* L.	.	r	r
H scap	Orof. SE-Europ.	*Campanula scheuchzeri* Vill.	.	+	.
H ros	Centr.-Europ.	*Carlina acaulis* L.	.	+	.
H ros	Europ.-Caucas.	*Pilosella officinarum* Vaill.	.	+	.
H ros	Alp.-Piren.	*Plantago alpina* L.	.	.	+
		***Festucetalia spadiceae* Barbero 1970 and *Juncetea trifidi* Hadac in Klika et Hadac 1944**			
H scap	Alp.-Carpat.	*Carduus defloratus* L.	.	+	+
H caesp	Endem. Alp.	*Festuca scabriculmis* (Hack.) K.Richt.	.	1	+
Ch suffr	Endem. Alp.	*Daphne striata* Tratt.	.	.	+

H scap	Orof. SE-Europ.	*Ranunculus montanus* Willd.	.	.	+
		***Molinio-Arrhenatheretea* Tx. 1937**			
H caesp	Subcosmop.	*Deschampsia cespitosa* (L.) Beauv.	4	+	3
H scap	Eurosiber.	*Achillea millefolium* L.	.	+	1
H rept	Subcosmop.	*Trifolium repens* L.	.	+	+
G rhiz	Eurasiat.	*Bistorta officinalis* Delarbre	+	.	+
H scap	Subcosmop.	*Rumex acetosa* L.	+	.	.
H scap	Subcosmop.	*Silene vulgaris* (Moench) Garcke	.	+	.
H caesp	Circumbor.	*Phleum alpinum* L.	.	.	+
		***Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944**			
H scap	Orof. Europ.	*Chaerophyllum hirsutum* L.	+	1	1
H scap	Endem. Ital.	*Sanguisorba dodecandra* Moretti	.	+	+
H scap	Eurasiat.	*Hypericum maculatum* Crantz	.	.	1
H scap	Alp.-Piren.	*Molopospermum peloponnesiacum* (L.) W.D.J.Koch	.	.	+
G rhiz	S-Europ.	*Veratrum album* L.	+	.	.
H ros	Subcosmop.	*Athyrium distentifolium* Tausch ex Opiz	+	.	.
H scap	Orof. Europ.	*Imperatoria ostruthium* L.	1	.	.
G rhiz	Orof. Centr.-Europ.	*Petasites albus* (L.) Gaertn.	+	.	.
G rhiz	Circumbor.	*Streptopus amplexifolius* (L.) DC.	r	.	.
G bulb	Eurasiat.	*Lilium martagon* L.	r	.	.
H scap	Circumbor.	*Epilobium angustifolium* L.	.	.	+
		***Robinietea* Jurko ex Hadač et Sofron 1980 and *Crataego-Prunetea* Tx. 1962**			
NP	Circumbor.	*Rubus idaeus* L.	1	2	2
P caesp	Orof. S-Europ.	*Laburnum alpinum* (Mill.) Bercht. & J.Presl	.	+	.
		***Vaccinio-Abietenion* Oberd. 1962 and *Piceion excelsae* Pawłowski et al. 1928**			
G rhiz	Circumbor.	*Phegopteris connectilis* (Michx.) Watt	+	.	.
H scap	Orof. SW-Europ.	*Astrantia minor* L.	+	.	.
H ros	Orof. Centr.-Europ.	*Homogyne alpina* (L.) Cass.	+	.	.
		***Piceetalia excelsae* Pawłowski et al. 1928 and *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939**			
P scap	Eurosiber.	*Picea abies* L.	2	3	1
P scap	Orof. Centroeurop.	*Larix decidua* Mill.	2	1	1
Ch frut	Circumbor.	*Vaccinium myrtillus* L.	+	1	1
NP	Circumbor.	*Juniperus nana* Willd.	.	2	1
Ch frut	Circumbor.	*Vaccinium vitis-idaea* L.	.	+	+
Ch rept	Orof. Eurasiat.	*Veronica officinalis* L.	+	+	.
H scap	Circumbor.	*Solidago virgaurea* L.	+	+	.
NP	Orof. S-Europ.	*Rosa pendulina* L.	.	1	.
H caesp	Orof. SW-Europ.	*Luzula nivea* (L.) D.C.	.	+	.
H scap	Europ.	*Laserpitium krapfii* Crantz	.	+	.
		Other species			
H ros	Eurosiber.	*Alchemilla vulgaris* L.	.	+	+
H ros	Orof. SE-Europ.	*Aposeris foetida* (L.) Less.	.	+	+
H scap	Orof. S-Europ.	*Prunella grandiflora* (L.) Scholler	.	+	+
H scap	SE-Europ.	*Knautia drymeia* Heuff.	.	+	+
Ch frut	Orof. S-Europ.	*Erica carnea* L.	.	1	.
Ch suffr	Orof. S-Europ.	*Polygala chamaebuxus* L.	.	+	.
P caesp	Circum-Artic-Alp.	*Alnus viridis* (Chaix) DC.	.	+	.
H rept	Cosmop.	*Fragaria vesca* L.	.	+	.
H scap	-	*Viola* spp.	.	+	.

H scap	Eurasiat.	*Polygala vulgaris* L.	.	.	+
H scap	Eurosiber.	*Hieracium murorum* L.	+	.	.

Figure 6 shows the results of the application of EIVs. The *P. omorika* community is mainly composed of heliophilous species occurring in the high-mountain vegetational belt, on moderately moist, nutrient-poor, slightly acidic, and non-saline soils.
The comparison between the EIVs of the plant community in the study area and those assigned to *P. omorika*, based on the floristic-ecological features of the vegetation where it occurs in Serbia and Bosnia-Herzegovina, indicates that the mean M value of the community is similar to that of *P. omorika*, whereas the community values for the L and T indices are respectively higher and lower than those of *P. omorika*.

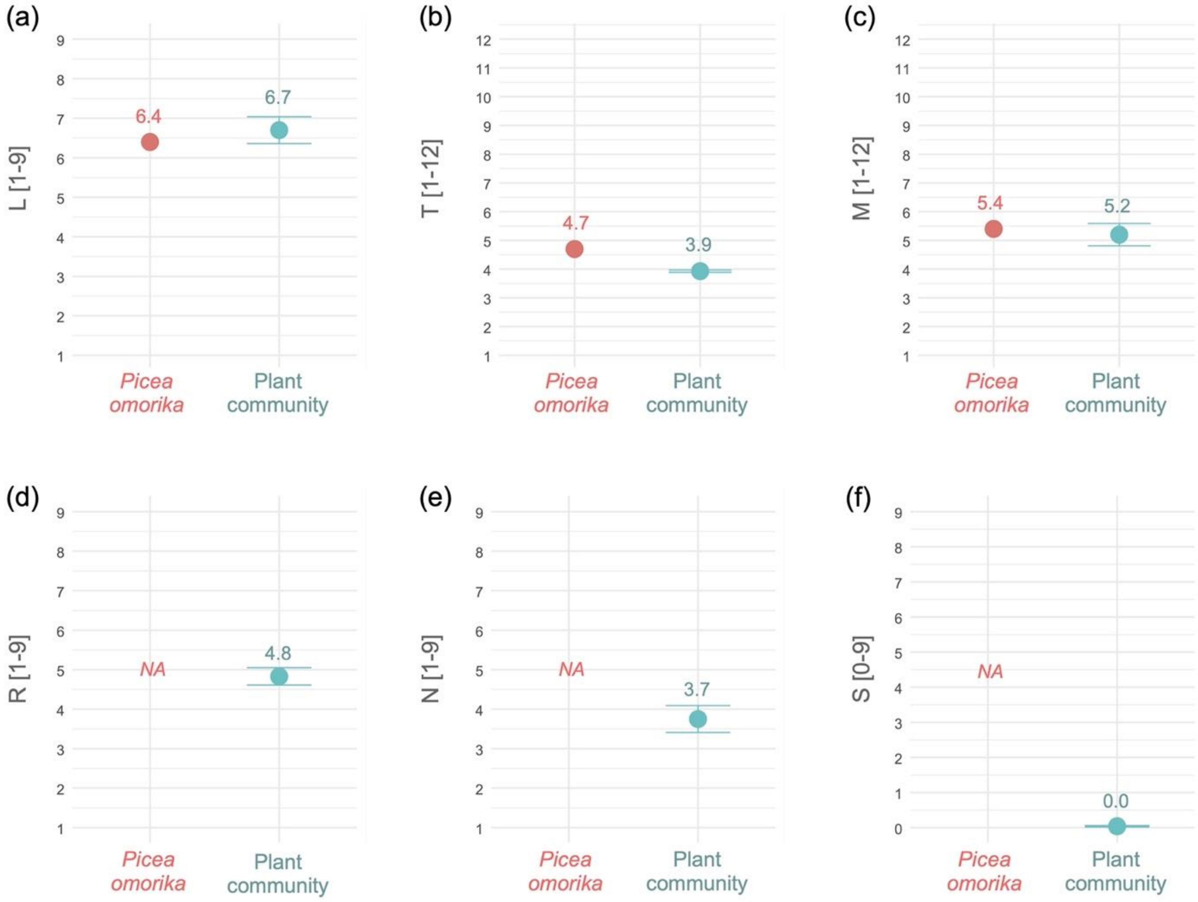

Figure 6. Comparison between the EIVs assigned to *P. omorika* (Tichý et al. 2023) and those of the plant community in the study area. Key: L, light (a); T, temperature (b); M, moisture (c); R, reaction (d); N, nutrients (e); S, salinity (f); NA, not available data.

Functional strategy

All 50 leaves analyzed for Grime's functional strategy showed the same values of C, S, and R (C = 0.0%, S = 100.0%, R = 0.0%), allowing *P. omorika* to be classified as a strictly stress-tolerant species. The triangular diagrams in Figure 7 indicate that the *P. omorika* community is composed of species with different functional strategies, as they are distributed across the entire diagram except near the R vertex. Nevertheless, the community mean values and the kernel density distributions reveal a higher representation of stress-tolerant species, particularly when CSR values are weighted by species cover (Figure 7b).

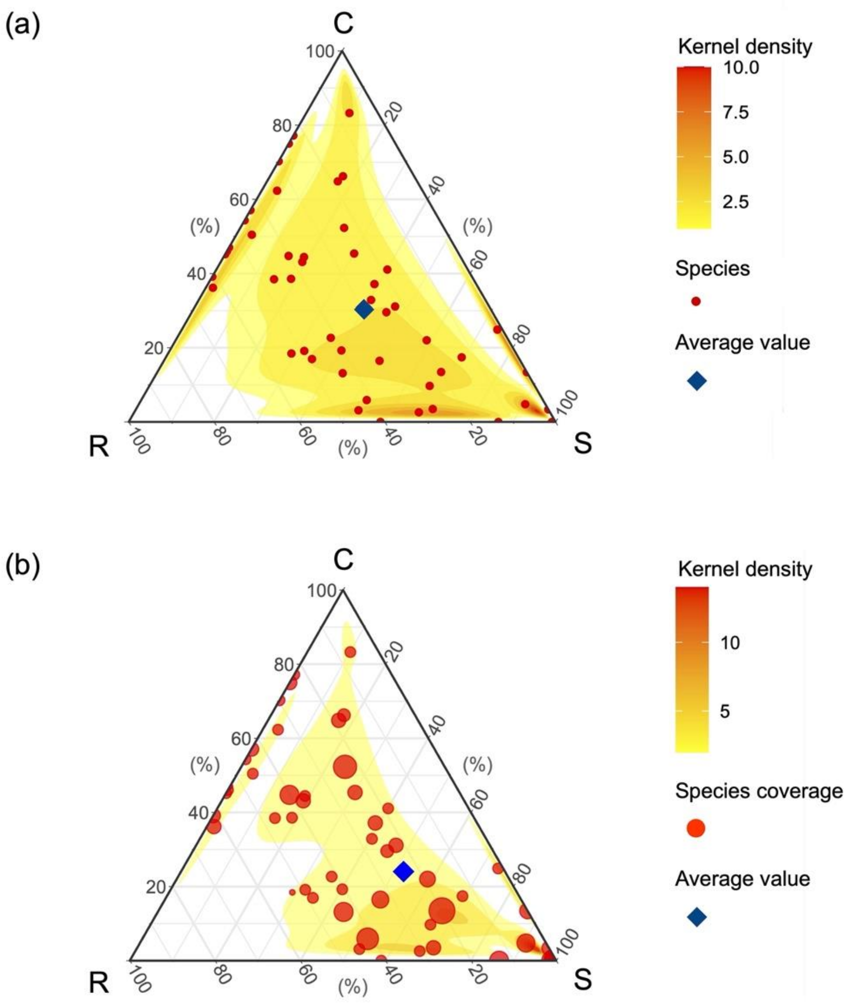

Figure 7. Species distribution within Grime's CSR ternary plot (C = competitor, S = stress-tolerant, R = ruderal): (a) kernel density of species positions (red circles), with the blue diamond indicating the average value; (b) kernel density weighted by species coverage (circle size), with the blue diamond showing the average weighted value.

Discussion

Dendrochronological analysis revealed that the study area hosts *P. omorika* individuals of varying ages, including both young and mature trees (Fig. 5). This finding confirms that the stand is not the result of a forest plantation (which in the past typically consisted of even-aged individuals) but instead demonstrates the naturalisation of *P. omorika* within the area. According to Richardson et al. (2000), naturalised species are alien plants that reproduce consistently and maintain self-sustaining populations over multiple generations without direct human intervention (or even despite it). *P. omorika* therefore represents a newly naturalised species enriching the alien vascular flora of Italy, which currently comprises 1782 taxa (Galasso et al. 2024).

Among the dated trees, that located near the Armentarga hut was found to be considerably older than the others, suggesting that it was the first to produce viable seeds and initiate the species' establishment in the study area. Its presence near the hut for approximately 55-60 years makes it plausible that it was planted for ornamental purposes following the building's restoration, although current members of the "Penne Nere" Alpine Group have no recollection of such an event (personal communication). It is, however, unlikely that *P. omorika* represents a glacial relict in this area, as no particularly old individuals were detected and the site was glaciated during the Würm glacial period (Ivy-Ochs 2015).

The absence of Serbian spruce individuals aged between 32 and 54 years (Fig. 5) may be attributed to a combination of ecological and physiological factors. From the late 1960s, when the first tree was likely planted near the Armentarga hut, until the mid-1990s, when *P. omorika* began reproducing, local climatic conditions may have been unfavourable for seed production or germination. Furthermore, this tree, which would have been approximately 25 years old in 1995, may not have reached reproductive maturity, as the species typically requires 20-30 years to produce fertile cones, according to experiments conducted at the Bedgebury National Pinetum (Kent, UK) (Dallimore 1945).

Figure 5 also shows that the tree near the Armentarga hut has a CBH comparable to those of individuals roughly twenty years younger. The reduced radial growth of this tree may reflect less favourable climatic conditions during its first two decades, compared with those prevailing in subsequent years. Conversely, the group of *P. omorika* trees growing in the wood-pasture exhibits a nearly linear increase in CBH over time, indicative of stable and suitable environmental conditions (West 2024). These conditions correspond to a sub-oceanic climate, with moderately moist, nutrient-poor, and slightly acidic soils under cold, high-light conditions, as a result of the application of the EIVs (Fig. 6).

The synecological analysis also revealed differences between the EIVs assigned to *P. omorika* in Serbia and Bosnia-Herzegovina and the mean EIVs of the vegetation of the study area (Fig. 6). Such discrepancies may help explain the ecological and conservation challenges affecting *P. omorika* in its native range. In Brembana Valley, the species benefits from colder temperatures and open, well-lit habitats - conditions that differ markedly from the shaded forests it occupies in the Balkans, where it competes with several tree species such as beech (*Fagus sylvatica* L.) (Burschel 1965; Savill et al. 2017), a more thermophilous broadleaved species capable of forming dense, low-light stands.

Beech is absent from the study area (Table 1) because, in the upper Brembana Valley, beech forests of *Fagetalia sylvaticae* Pawłowski 1928 occur at lower elevations (800-1500 m a.s.l.), whereas the high mountain and subalpine belts are characterised by open conifer forests dominated by spruce, larch, and Swiss stone pine (*Pinus cembra* L.) (Del Favero 2002; Verde et al. 2010). The latter is a relict species in the South-Orobic District and, although absent from the relevés (Table 1), occurs near the Fregabolgia Lake (Andreis et al. 2005; Martini et al. 2012).

Although the study area provides ecologically suitable conditions for *P. omorika*, the species does not display invasive behaviour, meaning it lacks the capacity for rapid spread or for generating negative impacts on native ecosystems (Richardson et al. 2000). Indeed, over the past three decades, only a few dozen individuals have established within a limited area. While these trees can create shaded microsites unsuitable for *Sanguisorba dodecandra* (similarly to *P. abies*), they do not threaten the persistence of this endemic species of the Orobic Alps, which is widespread and abundant, often dominating pastures, meadows, avalanche tracks, and stream margins (Pirola 1964; Giupponi et al. 2022).

Although Richardson and Pyšek (2012) noted that all naturalised species possess potential invasiveness, *P. omorika* is unlikely to exhibit such behaviour due to its strongly stress-tolerant functional strategy. Dalle Fratte et al. (2019) showed that invasive alien plants in southern Europe typically display a CSR strategy with higher competitive (C) values than native species, suggesting that invasive plants in this biogeographic region are associated with relatively productive habitats. Consequently, native species inhabiting resource-poor environments are less likely to experience competitive pressure from aliens. In the present case, the habitat is characterised by low productivity due to nutrient limitation and low temperatures. Moreover, *P. omorika* competes primarily with *P. abies*, which shares the same CSR strategy (C = 0.0%, S = 100.0%, R = 0.0%), and with *Larix decidua*, which, although slightly less stress-tolerant, remains predominantly S-strategist (C = 0.0%, S = 99.2%, R = 0.8%) (Pierce et al. 2017).

The functional CSR strategy of *P. omorika* also suggests that this species becomes part of the plant communities in mature forests. Indeed, according to Grime (2001), the final stages of plant succession (whether primary or secondary) are characterised by the predominance of stress-tolerant species. In this study, the plant community of *P. omorika* was composed of species with different strategies, although most were stress-tolerant (Fig. 7). This pattern is explained by the ongoing secondary succession in the study area, which involves the gradual replacement of *Nardion strictae* pastures with meadow species (*Molinio-Arrhenatheretea*) and megaphorb species of *Mulgedio-Aconitetea* (initial stage with some competitive species), leading to the high-montane coniferous forest of *P. excelsae* (final stage). Intermediate stages, based on the interpretation of phytosociological data, may include the *Rubetum idaei* association, dominated by *Rubus idaeus*, which in the Alps develops following the abandonment of mountain pastures or in Norway spruce forests affected by disturbance events (Verde et al. 2010; Giupponi et al. 2023, 2025).

Future studies focusing on vegetation dynamics in the area would be valuable to determine whether and how *P. omorika* might influence the floristic and physiognomic features of intermediate and mature successional stages. In particular, it would be useful to define the syntaxonomic framework of the mature forest that *P. omorika* may form in Brembana Valley. Phytosociological analysis (Tab. 1) suggests that *P. omorika* may establish within forest communities of *Piceion excelsae* (*Vaccinio-Piceetea*), which are very different from those of *Erico carneae-Piceion omorikae* (*Erico-Pinetea* Horvat 1959) communities described in Serbia and Bosnia-Herzegovina (Mucina et al. 2016).

Gaining a better understanding of the ecological role and effects of *P. omorika* on the ecosystems of the Brembana Valley, as well as monitoring its spread, would be important, if only because the study area lies within the Orobie Bergamasche Regional Park, a protected area of high natural value and rich in endemic species (Andreis et al. 2017; Giupponi and Giorgi 2017, 2019). Such knowledge would support land managers in making scientifically informed decisions regarding nature conservation actions. In this specific case, given that *P. omorika* is an endangered species with a low invasive potential, its eradication in the Brembana Valley should be avoided; on the contrary, the study area could even be considered for potential translocation efforts aimed at preserving the species.

Conclusion

This study reported the first documented case of *P. omorika* naturalisation in Italy - and, more broadly, in an area outside Serbia and Bosnia-Herzegovina - thereby adding the species to the list of alien vascular flora of Italy.

Stand-age analysis indicated that this population likely originated from the planting of a Serbian spruce near the Armentarga hut in the late 1960s for ornamental purposes. Environmental conditions in the study area over the past decades have proven favourable for *P. omorika*, allowing the development of an uneven-aged population of approximately 50-60 individuals within a pasture of *Nardion strictae*. Here, an active secondary succession is currently underway, which is expected to lead to the formation of a high-montane coniferous forest of *Piceion excelsae*. In addition to the sub-oceanic pre-Alpine climatic context, Serbian spruces in the upper Brembana Valley grow on moderately moist, nutrient-poor, and slightly acidic soils, under cold and high-light conditions, as inferred from the application of the EIVs.

The open woodland structure (wood pasture) and the low temperatures typical of the high-montane vegetation belt are the two ecological factors that most distinguish the *P. omorika* community in Brembana Valley from those in its native range in Serbia and Bosnia-Herzegovina. Moreover, the stress-tolerant strategy of *P. omorika* supports its ability to grow in cold environments with nutrient-poor soils, and also suggests a low invasive potential.

Acknowledgments
We would like to thank the "Penne Nere" Alpine Group for providing valuable information on the Armentarga hut and for granting us access to their photographic archive. We also thank the "Comunità Montana Valle Brembana" and the Municipality of Carona for sharing information regarding the absence of *P. omorika* forest plantations in the upper Brembana Valley. We are grateful to Mr. Pietro Giupponi for his logistical support and for assisting us in collecting *P. omorika* samples.

References

Aeschimann D, Lauber K, Moser DM, Theurillat JP (2004) Flora alpina. Haupt Verlag, Bern, Stuttgart, Wien.

Aleksić JM, Ballian D, Isajev D, Mataruga M, Christian T, Gardner M (2017) *Picea omorika*. The IUCN Red List of Threatened Species 2017: e.T30313A84039544. https://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T30313A84039544.en [accessed 7 September 2025].

Andreis C (2002) I distretti geobotanici. In: Del Favero R (Ed) I tipi forestali della Lombardia. Cierre Edizioni, Verona, pp 36-40.

Andreis C, Armiraglio S, Caccianiga M, Bortolas D, Broglia A (2005) *Pinus cembra* L. nel settore Sud-Alpino lombardo (Italia settentrionale). Annali del Museo Civico di Scienze Naturali di Brescia 34: 19-39.

Andreis C, Armiraglio S, Caccianiga M, Cerabolini B (2009) La vegetazione forestale dell'ordine *Piceetalia excelsae* Pawl. in Pawl. et al. 1928 nelle Alpi Lombarde. Fitosociologia 46: 49-74.

Andreis C, Armiraglio S, Caccianiga M, Cerabolini B (2017) Alpi Orobie e Prealpi Carbonatiche: un hotspot di endemicità. In: Blasi C, Biondi E (Eds) La flora in Italia. Sapienza Università Editrice, Roma, pp 100-103.

Ballian D, Ravazzi C, Caudullo G (2016) *Picea omorika* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds) European Atlas of Forest Tree Species. Publications Office of the European Union, Luxembourg, pp e0157f9+.

Bertolli A (Ed) (2024) Flora endemica nel Nord Italia. Athesia, Bolzano.

Biondi E, Blasi C (2014) Plant communities of Italy: The Vegetation Prodrome. Plant Biosystems 148(4): 728–732. https://doi.org/10.1080/11263504.2014.948527

Braun-Blanquet J (1964) Pflanzensoziologie, 3rd ed. Springer, Wien.

Burschel P (1965) Die Omorikafichte. Forstarchiv 36: 113-131.

Chytrý M, Tichý L, Agrillo E, De Cáceres M, Doležal J, Hájek M, Jansen F, Jiménez-Alfaro B, Landucci F, Lenoir J, Midolo G, Nobis MP, Pignatti A, Rūsiņa S, Šilc U, Škvorc Ž, Van Meerbeek K, Wohlgemuth T, Zelený D (2024) FloraVeg.EU: an online database of European vegetation units. Applied Vegetation Science 27: e12798. https://doi.org/10.1111/avsc.12798

Cislaghi A, Giupponi L, Tamburini A, Giorgi A, Bischetti GB (2019) The effects of mountain grazing abandonment on plant community, forage value and soil properties: observations and field measurements in an Alpine area. Catena 181: 104086. https://doi.org/10.1016/j.catena.2019.104086

Dalle Fratte M, Bolpagni R, Brusa G, Caccianiga M, Pierce S, Zanzottera M, Cerabolini BEL (2019) Alien plant species invade by occupying similar functional spaces to native species. Flora 257: 151419. https://doi.org/10.1016/j.flora.2019.151419

Dallimore W (1945) Two possible forest trees for Britain. Quarterly Journal of Forestry 39: 88-91.

Del Favero R (2002) I tipi forestali della Lombardia. Cierre Edizioni, Verona.

EUFORGEN (2024) *Picea omorika*. European Forest Genetic Resources Programme. https://www.euforgen.org/species/picea-omorika [accessed 7 September 2025].

Galasso G, Conti F, Peruzzi L, Alessandrini A, Ardenghi NMG, Bacchetta G, Banfi E, Barberis G, Bernardo L, Bouvet D, Bovio M, Castello M, Cecchi L, Del Guacchio E, Domina G, Fascetti S, Gallo L, Guarino R, Gubellini L, Guiggi A, Hofmann N, Iberite M, Jiménez-Mejías P, Longo D, Marchetti D, Martini F, Masin RR, Medagli P, Musarella CM, Peccenini S, Podda L, Prosser F, Roma-Marzio F, Rosati L, Santangelo A, Scoppola A, Selvaggi A, Selvi F, Soldano A, Stinca A, Wagensommer RP, Wilhalm T, Bartolucci F (2024) A second update to the checklist of the vascular flora alien to Italy. Plant Biosystems 158(2): 297-340. https://doi.org/10.1080/11263504.2024.2320129

Giupponi L, Giorgi A (2017) Mount Cavallo Botanical Path: a proposal for the valorization of an area of the Orobie Bergamasche Regional Park (Southern Alps). eco.mont 9: 5-15. https://doi.org/10.1553/eco.mont-9-2s5

Giupponi L, Giorgi A (2019) A contribution to the knowledge of *Linaria tonzigii* Lona, a steno-endemic species of the Orobie Bergamasche Regional Park (Italian Alps). eco.mont 11: 16-23. https://doi.org/10.1553/eco.mont-11-1s16

Giupponi L, Leoni V, Gianoncelli C, Tamburini A, Giorgi A (2022) Endemic plants can be resources for mountain agro-ecosystems: the case of *Sanguisorba dodecandra* Moretti. Sustainability 14: 6825. https://doi.org/10.3390/su14116825

Giupponi L, Leoni V, Pedrali D, Giorgi A (2023) Restoration of vegetation greenness and possible changes in mature forest communities in two forests damaged by the Vaia storm in Northern Italy. Plants 12: 1369. https://doi.org/10.3390/plants12091369

Giupponi L, Panza R, Pedrali D, Sala S, Giorgi A (2025) Ecology, floristic-vegetational features, and future perspectives of spruce forests affected by *Ips typographus*: insight from the Southern Alps. Plants 14: 1681. https://doi.org/10.3390/plants14111681

Grime JP (2001) Plant strategies, vegetation processes and ecosystem properties. Wiley, Chichester.

Ilić T, Kuzmanović N, Vukojičić S, Lakušić D (2022) Phytogeographic characteristics of montane coniferous forests of the central Balkan Peninsula (SE Europe). Plants 11: 3194. https://doi.org/10.3390/plants11233194

Ivy-Ochs S (2015) Glacier variations in the European Alps at the end of the last glaciation. Cuadernos de Investigación Geográfica 41(2): 295-315. https://doi.org/10.18172/cig.2750

Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schweingruber FH, Theurillat JP, Urmi E, Vust M, Wohlgemuth T (2010) Flora indicativa. Ecological indicator values and biological attributes of the flora of Switzerland and the Alps. Haupt-Verlag, Bern.

Martini F, Bona E, Federici G, Fenaroli F, Perico G (2012) Flora vascolare della Lombardia centro-orientale. Lint, Trieste.

Mataruga M, Piotti A, Daničić V, Cvjetković B, Fussi B, Konnert M, Vendramin GG, Aleksić JM (2020) Towards the dynamic conservation of Serbian spruce (*Picea omorika*) western populations. Annals of Forest Science 77: 1. https://doi.org/10.1007/s13595-019-0892-1

Mucina L, Bültmann H, Dierssen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, Gavilán RG, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniels FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachović M, Schaminee JHJ, Lysenko T, Didukh YP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19(Suppl. 1): 3-264. https://doi.org/10.1111/avsc.12257

Nikolić BM, Ballian DA, Đorđević IŽ, Rajčević NF, Todosijević MM, Stanković Jeremić JM, Mitić ZS, Bojović SR, Tešević VV (2023) n-Alkanes variability in natural populations of *Picea omorika* (Pančić) Purk. from Bosnia and Herzegovina. Biochemical Systematics and Ecology 106: 104544. https://doi.org/10.1016/j.bse.2022.104544

Nikolić BM, Mitić ZS, Ballian D, Todosijević MM, Nikolić JS, Ivanović S, Tešević VV (2025) Morpho-anatomical properties and terpene composition of *Picea omorika* (Pančić) Purk. needles from Bosnia and Herzegovina. Forests 16: 791. https://doi.org/10.3390/f16050791

Nikolić BM, Rajčević NF, Mitić ZS, Jovanović SS, Čule NM, Mladenović K, Marković MS, Marin PD (2024) Diversity of *Picea omorika* (Pančić) Purk. populations based on morpho-anatomical needle traits and bioclimatic parameters. South-east European Forestry 15(2): 131–139. https://doi.org/10.15177/seefor.24-17

Pierce S, Negreiros D, Cerabolini BEL, Kattge J, Díaz S, Kleyer M, Shipley B, Wright SJ, Soudzilovskaia NA, Onipchenko VG, van Bodegom PM, Frenette-Dussault C, Weiher E, Pinho BX, Cornelissen JHC, Grime JP, Thompson K, Hunt R, Wilson PJ, Buffa G, Nyakunga OC, Reich PB, Caccianiga M, Mangili F, Ceriani RM, Luzzaro A, Brusa G, Siefert A, Barbosa NPU, Chapin III FS, Cornwell WK, Fang J, Fernandes GW, Garnier E, Le Stradic S, Peñuelas J, Melo FPL, Slaviero A, Tabarelli M, Tampucci D (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Functional Ecology 31: 444-457. https://doi.org/10.1111/1365-2435.12722

Pignatti S (2017-2019) Flora d'Italia. Edagricole, Bologna.

Pirola A (1964) Ricerche su *Sanguisorba dodecandra* Moretti. Atti dell'Istituto Botanico e del Laboratorio Crittogamico dell'Università di Pavia 21: 69-104.

Provincia di Bergamo (Ed) (2002) Carta geologica della Provincia di Bergamo 1:50.000. Grafica Monti s.n.c., Bergamo.

R Core Team (2025) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ [accessed 28 September 2025]

Ravazzi C (2002) Late Quaternary history of spruce in southern Europe. Review of Palaeobotany and Palynology 120: 131-177. https://doi.org/10.1016/S0034-6667(01)00149-X

Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383-396. https://doi.org/10.1111/j.1469-8137.2012.04292.x

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity and Distributions 6: 93-107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Savill P, Wilson S, Mason B, Jinks R, Stokes V, Christian T (2017) Alternative spruces to Sitka and Norway. Part 1 - Serbian spruce *Picea omorika*. Quarterly Journal of Forestry 111(1): 32-39.

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671-675. https://doi.org/10.1038/nmeth.2089

Tichý L, Axmanová I, Dengler J, Guarino R, Jansen F, Midolo G, Nobis MP, Van Meerbeek K, Aćić S, Attorre F, Bergmeier E, Biurrun I, Bonari G, Bruelheide H, Campos JA, Čarni A, Chiarucci A, Ćuk M, Ćušterevska R, Didukh Y, Dítě D, Dítě Z, Dziuba T, Fanelli G, Fernández-Pascual E, Garbolino E, Gavilán RG, Gégout JC, Graf U, Güler B, Hájek M, Hennekens SM, Jandt U, Jašková A, Jiménez-Alfaro B, Julve P, Kambach S, Karger DN, Karrer G, Kavgacı A, Knollová I, Kuzemko A, Küzmič F, Landucci F, Lengyel A, Lenoir J, Marcenò C, Moeslund JE, Novák P, Pérez-Haase A, Peterka T, Pielech R, Pignatti A, Rašomavičius V, Rūsiņa S, Saatkamp A, Šilc U, Škvorc Ž, Theurillat JP, Wohlgemuth T, Chytrý M (2023) Ellenberg-type indicator values for European vascular plant species. Journal of Vegetation Science 34(1): e13168. https://doi.org/10.1111/jvs.13168

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1968) Flora Europaea. Cambridge University Press, Cambridge.

Ubaldi D (2008a) Le vegetazioni erbacee e gli arbusteti italiani: tipologie fitosociologiche ed ecologia. Aracne, Roma.

Ubaldi D (2008b) La vegetazione boschiva d'Italia: manuale di fitosociologia forestale. Clueb, Bologna.

Vacek Z, Vacek S (2023) Challenges and risks of Serbian spruce (*Picea omorika* [Pančić] Purk.) in the time of climate change - a literature review. Central European Forestry Journal 69(3): 152-166. https://doi.org/10.2478/forj-2022-0016

van der Maarel E (1979) Transformation of cover-abundance values in phytosociology and its effect on community similarity. Vegetatio 39(2): 97-114. https://doi.org/10.1007/BF00052021

Verde S, Assini S, Andreis C (2010) Le serie di vegetazione della Regione Lombardia. In: Blasi C (Ed) La vegetazione d'Italia. Palombi and Partner S.r.l., Roma, pp 181-203.

West PW (2024) A review of the growth behaviour of stands and trees in even-aged, monospecific forest. Annals of Forest Science 81: 34. https://doi.org/10.1186/s13595-024-01250-x