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Biology and ecology of *Juniperus phoenicea* – *J. turbinata* – *J. canariensis* complex II. Genetics, physiology, ecology

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Abstract: This is a review of the literature on genetics, physiology, and ecology, which concerns *Juniperus phoenicea*, *J. turbinata*, and *J. canariensis*, forming together the complex *J. phoenicea*. Despite the numerous and varied studies, many gaps and deficiencies have been identified in these fields. Further research is particularly needed on the genetic diversity and differentiation of all three species across their entire geographic ranges, with special attention on the easternmost localities of *J. turbinata*. Additional studies on the real photon flux density requirements, transpiration efficiency, water relations, nutrient demands, and mycorrhizal symbiosis for each species and across different locations, depending on the site conditions, would be highly valuable. The phytocoenological characteristics of *J. turbinata* and *J. phoenicea*, and their roles in particular phytocoenoses are fairly well recognized. However, data on *J. canariensis* and *J. turbinata* on the Arabian Peninsula should be expanded.

Keywords: climate limitation, light demands, genetics, mycorrhiza, nutrient demands, plant communities, transpiration efficiency, water demands

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Introduction

This article is the continuation of a review concerning *Juniperus phoenicea* L., *J. turbinata* Guss. and *J. canariensis* Guyot, which form, due to their affinity, the *J. phoenicea* complex. In the previous contribution, taxonomy, distribution, and morphology were mainly examined (Boratyński et al., 2024). This paper deals with the aspects relating to the genetics, physiology, and ecology of the above-mentioned junipers.

Materials and Methods

The present study is based on a broad literature review. The taxa of the *J. phoenicea* complex have separate geographical ranges (e.g. Mazur et al., 2018; Boratyński et al., 2024); this allows us include data presented by authors who do not distinguish *J. phoenicea* s.s., *J. turbinata* and *J. canariensis*. The plant names follow the International Plant Names Index and Plant of the World Online, accessed in October–December 2024. The syntaxa names and positions are after new synthetic publications of possible large areas (e.g. Rivas-Martínez et al., 2002; Asensi et al., 2007; Rivas-Martínez et al., 2011; Konstantinidis et al., 2012; Mucina et al., 2016; Bonari et al., 2021; Foucault, 2021; Cano et al., 2022) and International Code of Phytosociological Nomenclature (Theurillat et al., 2021).

Genetics

The genus *Juniperus* predominantly contains diploid taxa (Farhat et al., 2019, 2023). In the Mediterranean region, the only exceptions are the tetraploid *J. thurifera* L. and *J. sabina* L. var. *balkanensis* R.P. Adams & Tashev, and the hexaploid *J. foetidissima* L. (Farhat et al., 2019). Junipers exhibit large genome sizes, with the mean for diploid taxa being approximately 25 pg/2C, and the broadest genome range size observed in gymnosperms, from 21.81 to 71.32 pg/2C (Farhat et al., 2019, 2023).

Juniperus phoenicea L. and *J. turbinata* Guss. are diploids, with $2n = 2x = 22$ (Romo et al., 2013; Vallès et al., 2015). The genome size of *J. phoenicea* averages between 20.96 and 21.54 pg/2C, and of *J. turbinata* ranges from 21.32 to 23.23 pg/2C, depending on the geographic origin and sex of the specimens (Romo et al., 2013; Vallès et al., 2015). *Juniperus canariensis* Guyot & Mathou in Guyot from Porto Santo has the largest genome size within the *J. phoenicea* complex, reaching 24.71 pg/2C (Loureiro et al., 2007).

To our knowledge, the juniper species within the *J. phoenicea* complex have not been tested in provenance experiments. Molecular, isoenzymatic, and

biochemical characteristics of the species *J. phoenicea* complex have been used in taxonomic comparisons (Mao et al., 2010, 2019; Adams & Schwarzbach, 2013; Adams, 2014 and references cited). The genetic structure of the *J. phoenicea* complex has been studied multiple times using different markers. The first study indicated the high genetic isolation among five populations of *J. phoenicea* from the Mediterranean region (without distinguishing between *J. phoenicea* and *J. turbinata*) using Inter-Simple Sequence Repeat (ISSR) markers (Meloni et al., 2006).

Isozymes revealed significant genetic differences, often at the 0–1 level between *J. phoenicea* s.s. and *J. turbinata* across several enzymatic systems. The most differentiating alleles were the third of Got1, the fourth of 6Pgd3, the sixth of 6Pgi2, the second of Pgm2, and the first of Shdh2 (Boratyński et al., 2009: Figs 2 and 3).

Random Amplified Polymorphic DNA (RAPD) markers have been used to assess taxonomic and geographic differentiation among populations of *J. phoenicea* s.l. in the western Mediterranean region and the High Atlas Mountains. The results indicated differences between populations identified as *J. phoenicea* and *J. turbinata*, as well as geographic differentiation within each species (Dzialuk et al., 2011). Various genetic and biochemical markers have also been employed to distinguish taxa within the *J. phoenicea* complex (Adams et al., 2002, 2010, 2013, 2014). However, these studies were conducted on individual specimens rather than populations.

Amplified Fragment Length Polymorphism (AFLP) markers were used to evaluate genetic differentiation among populations of *J. phoenicea* s.l. from the Canary Islands, the Atlantic coast of the Iberian Peninsula, and the High Atlas in Morocco. The results distinguished between the Canarian and African populations (Jiménez et al., 2017: Fig. 2a), confirming the taxonomic status of *J. canariensis*. The differentiation within *J. canariensis* showed that the populations from El Hierro were genetically distinct from those sampled in Tenerife and La Palma (Jiménez et al., 2017: Fig. 2b). AFLP markers used in the study of genetic differentiation within the *J. phoenicea* complex across its geographic range detected relatively high levels of genetic differentiation between *J. phoenicea*, *J. canariensis* and *J. turbinata* (Sánchez-Gómez et al., 2018: Figs 2 and 3). Further differentiation was observed within *J. turbinata*, revealing distinctions between populations from the western, central, and eastern Mediterranean regions (Sánchez-Gómez et al., 2018: Fig. 3). Single-nucleotide polymorphism (SNP) markers developed for *J. turbinata* provided more reliable demographic inferences than simple sequence repeat (SSR) markers (García et al., 2018).

Before the advent of biochemical and molecular methods, the morphological differences between

populations were treated as indicative of genetic divergence (e.g. Stebbins, 1950). The phenotypic differentiation of populations within the *J. phoenicea* complex mirrors patterns identified by molecular and biochemical markers. Differences between populations of *J. phoenicea* and *J. turbinata* have been detected through morphological characteristics of cones, seeds, and leaves (Mazur et al., 2003, 2010, 2016). These characteristics also revealed the distinct taxonomic position of *J. canariensis* (Mazur et al., 2018; Fig. 2, but see also Elmir et al., 2024). Geographic differentiation of *J. turbinata* populations based on morphological characteristics corresponds to patterns identified using AFLP markers (compare Mazur et al., 2018; Fig. 1 and Sánchez-Gómez et al., 2018; Fig. 2d).

A moderate level of genetic diversity was found in populations of taxa from the *J. phoenicea* complex using AFLP analysis. Differences in genetic diversity among populations were shaped by Pliocene climate fluctuations (Sánchez-Gómez et al., 2018) and were likely further influenced by modern migration patterns and/or population size restrictions. A moderate level of intrapopulation diversity of *J. phoenicea* and *J. turbinata* was also detected using isoenzymes (Boratyński et al., 2009). Expected heterozygosity, as revealed by RAPD markers, was geographically structured, being higher in European populations than in African ones, and lower in high mountain regions compared to maritime or moderately elevated ones (Dzialuk et al., 2011). Small populations of *J. turbinata* (orig. *J. phoenicea*) composed of only a few, distant from each other specimens, are at risk of inbreeding, leading to reduced growth vigor, and are more vulnerable to climate change (Lloret & Granzow-de la Cerda, 2013; Lloret & García, 2016).

Juniperus turbinata (orig. *J. phoenicea*) from western Saudi Arabia has been shown to exhibit significant genetic differences from *J. procera* Hochst. ex Endl., as revealed by RAPD analysis (Al-Yasi, 2019).

Despite several studies, the investigation of genetic diversity and differentiation of *J. phoenicea*, *J. canariensis*, and *J. turbinata* requires further research using genetic markers other than those used to date. It would be especially important to include more populations from the easternmost parts of *J. turbinata*'s geographic range, particularly from the mountains in Saudi Arabia and Jordan. The populations of *J. phoenicea* s.s. from the northern part of the species' geographic range have not been genetically characterized. Relict populations of *J. phoenicea* s.s. from the cliffs of ravines in France would be especially interesting to study (Boratyński et al., 2024).

Physiology

Plant growth is determined by its photochemical efficiency, the appropriate thermal conditions, and the availability of water and nutrients (e.g. Taiz & Zeiger, 2002; Kochhar & Sukhbir Kaur Gujral, 2020). In the Mediterranean region, CO₂ assimilation is strongly affected by temperature and drought (Allen et al., 2010; Camarero et al., 2021). The intensity of physiological processes in Mediterranean junipers fluctuates throughout the year and is influenced by diurnal changes (Camarero et al., 2021). Physiological research is more advanced for agriculturally important trees and shrubs, somewhat less for significant forest trees, and remains poorly understood for species with local importance, such as junipers (e.g. Kozłowsky & Pallardy, 1997; Pallardy, 2008). This includes the species within the *J. phoenicea* complex. Below we present several findings on some physiological processes analyzed for *J. phoenicea* s.l.

The species in the *J. phoenicea* complex exhibit relatively high structural adaptations to drought conditions and have a relatively high water-use efficiency (Paula & Pausas, 2006). Specific leaf characteristics adapted to drought conditions may reflect a physiological trade-off at the leaf level between drought resistance and carbon gain (Paula & Pausas, 2006). The photochemical efficiency of *J. turbinata* in the Punta Umbria Nature Reserve (Spain) reached its lowest levels in August, with additional midday depression (Castillo et al., 2002). During periods of low water availability and peak temperatures in July and August, stem water potential dropped below -7 MPa. *Juniperus macrocarpa* Sm. and *Pinus pinea* L., co-occurring *J. turbinata*, showed only slight drops in stem water potential during the same period. This suggests that summer drought is a significant cause of photoinhibition, which is severe in southern Spain (Castillo et al., 2002), but less pronounced in southern France (Berger & Heurteaux, 1985). *Juniperus turbinata* showed an increase in stem water potential 10–11 days after rainfall (Castillo et al., 2002). In the western Mediterranean maritime dunes, the highest monthly precipitation occurs from October to January, with almost no rain in July and August. Average annual precipitation is about 250–300 mm, while evapotranspiration reaches approximately 850–860 mm (Álvarez-Rogel et al., 2007).

Water availability is likely a limiting factor for *J. turbinata* on maritime dunes. Its root system is concentrated in the upper soil layers (Castillo et al., 2002), relying mainly on rainfall and avoiding saline groundwater from deeper layers (Armas et al., 2010). In the dune system of the Punta Entinas-Sabinar Nature Reserve (Spain), *J. turbinata* experiences water deficits and reduces gas exchange during summer. The low water content and physiological activity of *J.*

turbinata during this season have been attributed to the depletion of freshwater in the dune system. The species' sensitivity to the saline groundwater means it can absorb water from up to 1 m above the water table (Armas et al., 2010). A year after a fire in the Doñana (SW Spain), *J. turbinata* trees on dunes exhibited high water-use efficiency, even higher than *P. pinea* (Camarero et al., 2022).

Juniperus phoenicea s.s. is a drought-tolerant species. In the region of Teruel (Spain), it exhibited the lowest stem water potential in summer, reaching -3.5 MPa (Martínez-Ferri et al., 2000, 2004; Baquedano & Castillo, 2007). The species increased its stem water potential after rainfall (Baquedano & Castillo, 2007). Gas exchange was highest during spring and summer, peaking in the morning, and was significantly lower at midday (Martínez-Ferri et al., 2004; Baquedano & Castillo, 2007). Similarly, the highest net photosynthetic rate in *J. phoenicea* s.s. was observed during spring mornings (Martínez-Ferri et al., 2004), with a significant midday depression due to decreased gas exchange (Baquedano & Castillo, 2007). Low winter precipitation led to reduced stem water potential in *J. phoenicea*, and similarly, the excessively high summer temperatures (over 35°C) led also to a reduction of water potential, and these environmental limitations are the key factors contributing to photoinhibition (Baquedano & Castillo, 2007).

The concentration of nutrients (NPK) and calcium in the leaves of *J. turbinata* (orig. *J. phoenicea*) in western Anatolia (Turkey) varies seasonally. Nitrogen and phosphorus concentrations peak in autumn, potassium in spring and summer, and calcium in winter. Nutrient levels in older and senescent leaves (over three years old) were significantly lower for N, P, and K, while calcium was highest in these leaves, suggesting the remobilization of N, P, and K (Kutbay et al., 2005).

Seeds of *J. turbinata* (orig. *J. phoenicea*) contain growth inhibitors, which are reduced by stratification (Al-Ramamneh et al., 2012).

In summary, the main physiological processes of species within the *J. phoenicea* complex remain poorly understood and require further basic research.

Outline of ecology

Topography, substrates, and pedology

The species of *J. phoenicea* complex occur on nutrient-poor soils developed from substrates of various origins, from calcareous to siliceous (Quézel & Médail, 2003; Caudullo & de Rigo, 2016). They are well-adapted to well-drained, nutrient-deficient soils, sometimes also to steep slopes covered with

rocky gravel and even to rock fissures. According to range-wide modelling of *J. phoenicea* s.l., clay content in the substrate significantly enhances their occurrence (Dakhil et al., 2022), however, this study bases on localities of *J. phoenicea* s.s., with the erroneously included to this species localities of *J. canariensis* from the Canary Islands and *J. turbinata* from northern Africa and western Asia. High clay content in the soil retains water for a longer period, supporting plant growth in the arid regions of North Africa (Kabieli et al., 2016). However, these results should be verified using data specific for each species in the *J. phoenicea* complex.

Juniperus phoenicea s.s. is a West Mediterranean species. On the Iberian Peninsula, it colonizes slopes of hills, small shelves, cracks, and crevices of limestone, as well as cliffs, dolomite ridges, and limestone walls. It grows on rendzinas or calcareous lithosols, often in small amounts of substrate found in the rock fissures (e.g. Pavón García et al., 2006; Loidi, 2017; Peinado et al., 2017; Camarero & Ortega-Martínez, 2019). In similar orographic and pedological conditions, this species occurs in France and Italy, where it can even grow on the vertical limestone walls in river gorges (e.g. Larson et al., 1999; Garraud, 2003; Mandin, 2005; Tison et al., 2014; Mathaux, 2017). In the Maritime and Apuan Alps of Italy, the species is found on the steep south-facing slopes on the calcareous substrates (authors' personal observations). However, the available data are fragmentary, and specific pedological studies on *J. phoenicea* are lacking.

Juniperus turbinata occurs around the Mediterranean Sea and along the Atlantic coasts, typically in stabilized dune ecosystems and on the slopes close to or not far from the shores (e.g. Browicz & Zieliński, 1982; Paradis, 1991; Géhu et al., 1992; Asensi et al., 2007; Costa et al., 2012; Díez-Garretas & Asensi, 2013; Pavon et al., 2020). Soil profiles at maritime dune summit sites are classified as arenosols, halomorphic arenosols or torripsamments (Berger & Horteaux, 1985; Álvarez-Rogel et al., 2007). The species occurs also on the arenosols of palaeo-psammophytic origin in the mountains of the southern Iberian Peninsula (Hidalgo et al., 2014). In southern Spain, it extends inland and has been observed on gypsum substrates (Pavon et al., 2020). Overall, *J. turbinata* is highly adaptable to various substrates and can be found on a wide range of rock types, from siliceous (e.g. Rubio-Casal et al., 2010; Idbela et al., 2022) to basific (Al-Ramamneh et al., 2012; Abu-Darwish & Ofir, 2014; Alananbeh et al., 2023) or even alkaline with a pH of more than 9.0 (Álvarez-Rogel et al., 2007). In Corsica, it can be found on poorly developed soils or in the fissures of granite, diorite, rhyolite, and limestone (Paradis, 1991).

In Mediterranean Europe, *J. turbinata* frequently colonizes small islets regardless of the substrate type,

aspect, or site exposure (e.g. Christensen, 1997; Gianguzzi et al., 2012; Jeanmonod & Gamisans, 2013; Hidalgo et al., 2014; Tsiourlis et al., 2016; Jasprica et al., 2018). On larger Mediterranean islands, it grows on slopes distant from the seashore, as seen in Corsica (Paradis, 1991; Jeanmonod & Gamisans, 2013), Sicily (Minissale & Sciandrello, 2013), Evvoia (Boratyński et al., 1988), Chios (Boratyński et al., 1987), Crete (Delipetrou et al., 2015), and Cyprus (Meikle, 1977; Anonym, 2009). In continental Greece, *J. turbinata* can be found on metamorphic limestone, often on eroded southern slopes, with altitudinal distribution rarely exceeding 400–500 m a.s.l. In Cyprus, it occurs both at or near the coast and on lower hill slopes, growing on sandstone and limestone (authors' personal observations).

In the Arabian Peninsula, *J. turbinata* occurs predominantly in the mountains influenced by maritime conditions. It grows mainly on the north- and north-west-facing slopes, and in gorges, on sandstone and limestone, also on rocky precipices, and in the rock fissures, typically in poorly developed, clay and/or rocky soils (Kerfoot & Lavranos, 1984; Al-Ramamneh et al., 2012; Danin & Fragman-Sapir, 2016; Alananbeh et al., 2023: Table 7). In North Sinai, *J. turbinata* occurs in the mountains, in desert conditions, primarily in wadis and beneath rocks (Danin, 1983; El-Bana et al., 2010; Magdy et al., 2010; Moustafa et al., 2016). In Cyrenaica, the species occurs on sandy sits under Mediterranean influence (Ali & El Shatshat, 2015; Elmahdy & Mohamed, 2016; Kabieli et al., 2016).

In northwestern Africa, *J. turbinata* occupies a range of habitats, from relatively wet Mediterranean and Atlantic coasts to the subarid and even arid sub-Saharan regions. Along the maritime coasts, it grows on the dunes and the inland hill slopes, regardless of substrate type or site exposure (e.g. Charco, 1999; Benabid, 2000; Pavon et al., 2020; Ayache et al., 2020). In the high mountains, *J. turbinata* occurs regardless of substrate pH or the type of basic rock, typically on slopes, rocky ridges, and steep terrain. In its southernmost localities in the Anti-Atlas, it more frequently grows on the north-facing slopes, and in the western High Atlas, it is also found on west-facing slopes (e.g., Quézel & Barbero, 1981; Quézel et al., 1994; Taleb & Fennane, 2019). In the Saharan Atlas, it has been reported from rendzinas and brown calcareous soils at elevations of 1300–1500 m (Benabderrahmane et al., 2022).

Juniperus canariensis occurs on the westernmost islands, in thermo-sclerophyllous woodlands that develop up to 350 m on the northern slopes and between 500 and 900 m on the southern slopes (Del Arco et al., 2002, 2006, 2010; Del Arco Aguilar & Rodríguez Delgado, 2018). On the north-facing slopes, it grows below the fog and below the evergreen laurel forest

zone, while on the south-facing ones below the *Pinus canariensis* forest. It can thrive in both flat areas and steep slopes, but the flatter areas have been transformed into agricultural and urban areas.

The soils in the localities of *Juniperus canariensis* on El Hierro belong to entisols and andisols (Padrón Padrón, 1993). Entisols lack diagnostic horizons and form on volcanic lava flows from the island's ridges, specifically basaltic "aa" flows, which cover much of the island's surface and have a scoriaceous texture. On tephra cones of the same age, Vitritorrands are found, characterized by an aridic moisture regime. Their profile consists of A, Bw, and C horizons, with the A horizon being less than 10 cm thick, featuring a sandy or sandy-loam texture, a very high percentage of coarse fragments, over 90% glass content, less than 2% organic matter, and a water retention capacity at 1500 kPa below 20%. At higher altitudes and on gentler slopes, Vitrandes have developed. These differ from Vitritorrands by having a thicker A horizon, a silty or silty-sandy texture, slightly higher organic matter content, and more developed andic properties (greater phosphorus retention, higher Fe and Al content, and lower bulk density).

Climate limitations

Light

The species of the *Juniperus phoenicea* complex are heliophilous, preferring full sunlight, and only rarely tolerating partially shaded sites (Martinis et al., 2018). However, this conclusion is based on field observations, and lacks specific measurement data. All three taxa forming the complex are typical components of the maquis vegetation and open woodland. Within forests, *J. phoenicea* s.s. and *J. turbinata* grow beneath the loose, open forest canopies, mainly of *Pinus halepensis* Mill., and/or *P. pinaster* Aiton (e.g. Konstantinidis et al., 2012; Cano et al., 2022), as well as oak species (e.g. Trinajstić, 1987; Tsiourlis et al., 2009). Nonetheless, high light exposure combined with elevated temperatures can cause significant photoinhibition of the photosynthetic capacity of *J. turbinata* (orig. *J. phoenicea*) (Castillo et al., 2002; Rubio-Casal et al., 2010).

In areas where *J. canariensis* coexists with *Pinus canariensis*, they form open forests, but the two species do not share the canopy. The seedlings of *J. canariensis* grow beneath their parent trees rather than under the pines (authors' personal observations).

Despite the data mentioned above, light requirements for *J. phoenicea*, *J. turbinata*, and *J. canariensis* still require further studies.

Temperature

The annual mean temperatures across the potential geographic range of *J. phoenicea* s.l. oscillate between 7.6 °C and 24.6 °C, with a minimum of the coldest month –7.6 °C and maximum of the warmest month 42.8 °C (Salvà-Catarineu et al., 2021: Table S3). According to El-Barougy et al. (2023), temperature-related variables are the key factors influencing *J. phoenicea* s.l. current geographic range, while Salvà-Catarineu et al. (2021: Table 1) found that these variables accounts for about 33% of its current potential geographic range.

Juniperus phoenicea s.s. is associated with a Mediterranean type of bioclimate, occurring mainly in meso- and supra-Mediterranean thermotypes, and its most frequent occurrence is linked to semicontinental bioclimates (Rivas-Martínez et al., 2017). The mean annual temperatures within *J. phoenicea* potential geographic range vary between 3.6 °C and 19.2 °C, with a minimum temperature of –7.4 °C and a maximum of 40.3 °C (Salvà-Catarineu et al., 2021: Table S3).

The potential geographic range of *J. turbinata* covers the Mediterranean zone, including thermo-Mediterranean climates in coastal areas, and meso- and supra-Mediterranean climates in mountainous regions. Winter temperatures typically range between 5 °C and 15 °C, while summer temperatures fluctuate between 25 °C and 30 °C (Ünal et al., 2003; Cámara et al., 2014; Ayache et al., 2020; Sánchez-Salguero & Camarero, 2020). Minimum winter temperatures rarely fall below 0 °C, while maximum summer temperatures frequently reach 32–33 °C, and can even exceed 38–40 °C in desert regions (Arar et al., 2020; Salvà-Catarineu et al., 2021: Table S3). In the Atlas Mountains and southwestern Asia, *J. turbinata* experiences oro-Mediterranean climate conditions, with winter temperatures near 0 °C (Zohary, 1973; Danin & Fragman-Sapir, 2016). Although *J. turbinata* has a wide range in North Africa, from thermophilous coastal areas to colder, continental mountain environments, it does not extend into the Saharan region (Pavon et al., 2020). However, it does grow in desert conditions in the mountains of northern Sinai (El-Bana et al., 2010; Magdy et al., 2010; Farahat, 2020).

Juniperus canariensis is associated with a thermo-Mediterranean climate (Rivas-Martínez et al., 2004; Fernández-Palacios et al., 2008). The Canary Islands have an oceanic climate with low temperature amplitudes (Fernández-Palacios et al., 2008, 2011; Otto et al., 2010, 2012; Romo & Salvà-Catarineu, 2013; Romo et al., 2014; Luis González et al., 2017; Romo, 2018). The annual mean temperatures oscillate between 15.1 °C and 19.5 °C, with an absolute minimum of 7.6 °C and a maximum of 28.4 °C (Salvà-Catarineu et al., 2021: Table S3). In

the juniper woodland of El Julan (El Hierro), temperatures recorded in the years 2012–2023, showed an absolute maximum of 42.7 °C on July 8, 2013, and an absolute minimum of 5.4 °C on February 15, 2014 (Salvà-Catarineu et al., 2016, and unpublished data).

Water relations

Juniperus phoenicea s.s. is considered well-adapted to semi-arid and arid conditions (Quézel & Médail, 2003). It thrives in Mediterranean climates and a variety of bioclimates, ranging from subarid to subhumid and even humid, within the meso-Mediterranean, supra-sub-Mediterranean, and oro-sub-Mediterranean zones (Rivas Martínez et al., 2004; Mazur et al., 2016). However, *J. phoenicea* s.s. experiences greater water stress during summer droughts compared to *Quercus coccifera* L., *Q. ilex* L., and *Pinus halepensis* (Baquedano & Castillo, 2007). Annual precipitation within its distribution area ranges from 350 to 500 mm at lower altitudes, increasing to 800–1000 mm in the mountainous regions (Lionello et al., 2012). The realized niche has an average rainfall of 490 mm, with values ranging between 300 and 1,100 mm (Salvà-Catarineu et al., 2021: Table S3). The current distribution of *J. phoenicea* is heavily influenced by winter precipitation (December to February), which explains over 75% of its geographic range (Salvà-Catarineu et al., 2021). Precipitation during this period ranges from 50 to 150 mm in the Ebro Basin and La Mancha on the Iberian Peninsula, and from 100 to 250 mm in southern France (Lionello et al., 2012).

The geographic range of *J. turbinata* encompasses areas with average precipitation levels between 400 and 800 mm (Türkeş, 2003; Lionello et al., 2012; Elmahdy & Mohamed, 2016; Ayache et al., 2020). These higher values are found in Mediterranean and Atlantic coastal regions exposed to humid winds from the West or North. In the High and Middle Atlas in Morocco, there is significant winter precipitation followed by prolonged drought in late spring and summer (Emberger, 1955; Born et al., 2008). Relict populations of *J. turbinata* on the Sinai Peninsula survive in arid climates with annual rainfall of 80–100 mm, growing in wetter locations such as wadis or gorges (Danin, 1983; El-Bana et al., 2010; Moustafa et al., 2016). Extremely low precipitation leads to very low midday stem water potential values in *J. turbinata* (orig. *J. phoenicea*) in the Dana Nature Reserve in Jordan, reaching as low as –5.3 MPa (Alanbeh et al., 2023).

Juniperus canariensis does not grow on the driest Canary Islands, Lanzarote, and Fuerteventura, which are exposed to dry, warm winds (Cropper, 2013; Bechtel, 2016). However, *J. canariensis* forms homogeneous patches and integrates into shrub communities

on the other islands, even in areas with relatively low rainfall (Fernández-Palacios et al., 2008, 2011; Otto et al., 2010, 2012; Romo & Salvà-Catarineu, 2013; Luis González et al., 2017; Romo, 2018). The climate within its potential geographic range is characterized by low annual precipitation, averaging around 340 mm and not exceeding 420 mm (Salvà-Catarineu et al., 2021). Despite low rainfall, high air humidity helps offset the lack of precipitation (Fernández-Palacios et al., 2008; Otto et al., 2010, 2012). *Juniperus canariensis* has survived years of extreme drought by utilizing water from horizontal precipitation. In El Hierro, there was very little rain in 1946, and none in 1947 and 1948 (Martín Fernández, 2009). Although there are no relative humidity measurements from 1946–1948 in the juniper woodland of El Hierro, between 2012 and 2023, the average relative humidity (RH) was 66.2% in El Julan and 76.6% in Sabinosa (Salvà-Catarineu et al., 2016, and unpublished data).

Fire relations

Junipers in general, including species from the *J. phoenicea* complex, are prone to fires due to their high content of volatile substances, which makes them highly flammable (e.g., Pausas et al., 2004; Pausas & Verdú, 2005). These species are often eliminated by fires, as they do not resprout from the roots.

Phenology

The species in the *J. phoenicea* complex are evergreen, with leaves that live for 3–4 years. The development of apical buds begins in spring, though this is hard to observe. The growing parts of the shoots are light green, lighter than those from the previous year (based on herbarium specimens and field observations). The lateral branchlets stop growing earlier than the main apical shoot, which halts growth when temperatures become excessively high and water deficits occur. In lowland and moderately elevated populations, growth stops at the end of May or the beginning of June. In high-elevation localities and shaded areas in gorges, growth ceases later, sometimes even a month later (authors' personal observations).

Microstrobili start developing in the late summer and autumn, ahead of macrostrobili. The pollen shed in *J. phoenicea* s.s. take place following spring, typically in February–March, while in *J. turbinata* it happens in autumn, in October–November of the same year (Arista et al., 1997). The pollen shed in *J. canariensis* also occurs in autumn (Romo et al., 2019).

The male cones (microstrobili) of *J. phoenicea* s.s. are initiated at the end of summer and develop during autumn, but do not shed pollen grains until the end of winter. The meiosis of the mother cells of

pollen grains is rapid, and take place during late October and November, with simultaneous male cones development (Arista et al., 1997).

The female cones of *J. phoenicea* s.s. are receptive from late February. The meiosis of the megaspore mother cell takes place no earlier than late March or early April, depending on tree location. Interestingly, the gametophyte becomes mature and further stages of female cone development happen during the same period as in *J. turbinata*, in June of the following year (Arista et al., 1997).

Male buds in *Juniperus turbinata* are initiated at the end of August and are visible during autumn as small, light brown cones at the tips of branchlets. The macrostrobili (female cones) of *J. turbinata* consist of 3–4 whorls of opposite or ternate scales at the terminal part of short shoots. They begin developing at the end of summer and are fully developed by the end of October and into November when they start producing droplets to catch pollen grains. The megaspore mother cell undergoes meiosis at the end of the pollination year, followed by a prolonged gametophyte phase with free nuclei, which concludes at the turn of May/June (Arista et al., 1997). The embryo completes its development with fully developed cotyledons, by June of the following year. Macrostrobili develop over two growing seasons after pollination, changing colour from purple, through green, yellowish-green, or purple-green to yellow-brown, red-brown, or purple-black, sometimes pruinose when ripe. The cones reach maturity by the end of the second year of development (Arista et al., 1997). Ripe cones can persist on the trees for one or two years in a dry state (authors' personal observations).

The microstrobili of *J. canariensis* are similar to those of *J. turbinata*, developing during late summer and autumn, and shedding pollen in October and November. The macrostrobili of *J. canariensis* develop and mature in similar periods as those of *J. turbinata* (Romo et al., 2019), though this requires verification through detailed studies. The mature cones with seeds remain on the mother trees at least until the next growing season (authors' personal observations).

Sex ratio

The species of the *J. phoenicea* complex show varying sex expression and sex ratios, year by year (Jordano, 1991). It was previously believed to be the only monoecious species among conifers (Roques et al., 1984), but subsequent studies revealed more species with unstable sex expression (Jordano, 1991 and references cited). A large number of studied individuals of *J. phoenicea* from the Iberian Peninsula and *J. turbinata* (orig. *J. phoenicea*) from the Iberian Peninsula and the High Atlas Mountains revealed

different proportions of unstable individuals between geographic regions, with the majority changing sex from year to year (Jordano, 1991). Populations of *J. phoenicea* s.s. and *J. turbinata* on the Iberian Peninsula showed, on average, 32% unisexual female individuals between 1996 and 1999 (Pavón García et al., 2006).

In the Ardeche region (France), the trees of *J. phoenicea* s.s. were either female or bisexual but none expressed solely male sex traits over the long term. Despite this, the cliff populations exhibited sexual instability, but with a dominance of male individuals. The age did not influence to sex-ratio of *J. phoenicea* (Mandin, 2013). Male dominance was observed in populations of *J. turbinata* growing in North Sinai, Egypt (El-Bana et al., 2010).

Nutrition

To date, specific studies on the nutrition of the species within the *J. phoenicea* complex are lacking. Similarly, the response of these species to an overabundance or deficit of soil micro- and macro-elements, as well as their tolerance to soil and air pollution, has not yet been experimentally verified.

Mycorrhiza

The mycorrhizal symbiosis of the juniper species is generally poorly understood (Thomas et al., 2007; Boratyński et al., 2023). For the species within the *J. phoenicea* complex, mycorrhiza has been documented only for *J. phoenicea* s.s. (Sanguin et al., 2016) and *J. turbinata* (Jadallah et al., 2017; Fakhech et al., 2020; Alananbeh et al., 2023). In *J. phoenicea* s.s., 454-sequencing revealed a complex community of arbuscular mycorrhizal fungi, primarily composed of *Rhizophagus* and Glomeraceae, which are characteristic of arid and semi-arid habitats (Sanguin et al., 2016).

In *J. turbinata* (orig. *J. phoenicea*), the micorrhization of the rhizosphere in Al Jabal Alakhdar in Cyrenaica was found to be high due to the presence of arbuscular symbionts. Fungi isolated from the roots of *J. turbinata* represented taxa of Glomeromycota, mainly *Claroideoglomus eutunicatum* (W.N. Becker & Gerd.) C. Walker & A. Schüssler, *Archaeospora trappei* (R.N. Ames & Linderman) J.B. Morton & D. Redecker, *Glomus eutunicatum* W.N. Becker & Gerd., *Entrophospora infrequens* (I.R. Hall) R.N. Ames & R.W. Schneid., *Gigaspora calospora* (Nicol. and Gerd.) Gerdemann & Trappe, *G. nigra* J.F. Redhead, and *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüssler (Jadallah et al., 2017).

High levels of mycorrhization with arbuscular fungi were also observed in *J. turbinata* roots on the arenosols of the Atlantic shore in Morocco, although fungal species were not identified (Fakhech et al.,

2020). A study conducted in the nature reserves established to conserve *J. turbinata* forests in Jordania, found a high number of fungal spores in the rhizosphere, primarily from the genera *Diplodia* Fr., *Phomopsis* (Sacc.) Bubák, *Mycosphaerella* Johanson, *Cercospora* Fresen., *Kabatina* R. Schneid. & Arx (Alananbeh et al., 2023). The spectrum of fungal taxa and level of mycorrhization were different in each of the four reserves analysed (Alananbeh et al., 2023).

According to Brundrett (2021), earlier reports confirmed ectomycorrhizal associations in *Juniperus* have been mistaken for short roots which often co-occur with ectomycorrhizal (EcM) in conifers, and could be intermingled with studied root samples. The reason for errors in the mycorrhizal assessment of the juniper roots is the possibility of confusing certain cell wall structures in the cortex with the Hartig net. These structures, now known as Phi-thickenings, are characteristic of arbuscular mycorrhizal conifers from the families Ginkgoaceae, Araucariaceae, Taxaceae, and Cupressaceae growing in harsh environmental conditions (Brundrett & Tedersoo, 2020).

Plant communities

Juniperus phoenicea

Juniperus phoenicea s.s. is an important component of associations within the alliance *Pino pinastri-Juniperion phoeniceae* Pérez Latorre et Cabezudo in Pérez Latorre et al. 1998, the thermo- to supra-Mediterranean forest and woodlands in the Luso-Extremaduran Province of the Central Iberian Peninsula (Pérez Latorre et al., 1998; 2014; Mucina et al., 2016) or, in East Spain and South France, as a component of woodlands of meso-supramediterranean belt, belonging to of the alliance *Rhamno lycioidis-Quercion cocciferae* Rivas Goday ex Rivas-Mart. 1975, both included in the order of *Pistacio lentisci-Rhamnetalia alaterni* Rivas-Martínez 1975.

In the Iberian Peninsula, *J. phoenicea* frequently forms shrublands on limestone and dolomites, the associations *Rhamno lycioidis-Juniperetum phoeniceae* Rivas-Martínez & G. López in G. López 1976, and *Buxo sempervirentis-Juniperetum phoeniceae* Rivas-Martínez 1969 (Villar et al., 1997; Peinado et al., 2017). The *Rhamno lycioidis-Juniperetum phoeniceae* occurs in the eastern parts of the central and southern Iberic mountain systems, as well as in the highlands of the Coastal Levantine and La Mancha areas, on the calcareous lithosols, as a relict of xerothermic vegetation of glacial periods (Peinado et al., 2017; Soriano & Costa, 2017; Fernández-González et al., 2017; Molero & Marfil, 2017). The dispersed individuals of *J. phoenicea* grow alongside *Rhamnus lycioides* L. subsp. *lycioides*, *R. alaternus* L., *Jasminum fruticans* L. [= *Chrysojasminum fruticans* (L.) Banfi], *Pistacia terebinthus* L., *Amelanchier rotundifolia* M. Roem., with

clumps of *Erinacea anthyllis* Link, *Genista rigidissima* Vierh. [= *Genista mugronensis* Vierh. subsp. *rigidissima* (Vierh.) Fern.Casas], *Sideritis incana* L. and others. It is replaced by forests composed of *Quercus rotundifolia* Lam., *Q. pyrenaica* Willd., pines, or *Juniperus thurifera* in areas with deeper and better-developed soils (Peinado et al., 2017: 486–487).

The association *Buxo sempervirentis-Juniperetum phoeniceae* occurs in the highlands bordering the Ebro Basin and in the Pre-Pyrenean Mountain Ranges, on calcareous or shale rocks, on calcium-rich soils. Co-dominant or even dominant species is *Buxus sempervirens* L. (Loidi, 2017; Peinado et al., 2017).

In some regions *J. phoenicea* enters the light-full *Pinus halepensis* forest, the associations *Ephedro nebrodensis-Pinetum halepensis* (Braun-Blanquet & Bolòs 1957) Cano et al. 2022 (Cano et al., 2022), and *Pino halepensis-Juniperetum phoeniceae* Pérez Latorre & Cabezudo in Pérez Latorre et al. 1998. These associations are developed locally in the Ebro Basin, bordering in some places specific woodlands, where sparse stands are formed by *Juniperus thurifera* and *J. phoenicea*, with single trees of *Pinus halepensis*, and shrubby components such as *Quercus coccifera*, *Ephedra nebrodensis* Tinio, *Rhamnus alaternus*, *R. lycioides* and others (Loidi, 2017). Additionally, *J. phoenicea* is a component of the evergreen and marcescent oak forests from association *Cephalanthero rubrae-Quercetum fagineae* Rivas-Martínez in Rivas Goday & al. 1960 corr. Rivas-Martínez 1972 (Peinado et al., 2017).

In the hilly areas of southern France, Barbero & Quézel described a pre-forest association, the *Pino salzmannii-Juniperetum phoeniceae*, included in the order *Pistacio-Rhamnetalia alaterni* (Quézel & Barbero, 1988). Overall, in both France and Italy, where populations of *J. phoenicea* s.s. are small, there are limited data on participation of *J. phoenicea* s.s. in natural vegetation. In France, according to Lafon et al. (2024), within the alliance *Rhamno lycioidis-Quercion cocciferae* Rivas Goday ex Rivas Martínez 1975 three plant associations have been identified: *Buxo sempervirentis-Juniperetum phoeniceae* Rivas Martínez 1969; *Junipero phoeniceae-Ficetum caricae* B. Foucault et Julve 1994, and *Pino salzmannii-Juniperetum phoeniceae* Quézel et Barbero 1988.

Juniperus turbinata

According to Mucina et al. (2016), *Juniperus turbinata* is a key woody component of the associations from the alliance *Juniperion turbinatae* Rivas-Mart. 1975 corr. 1987 and *Rhamno graecae-Juniperion lyciae* M. Costa et al. 1984. The first alliance groups dense juniper forests, composed of *J. macrocarpa* Sm. and *J. turbinata*, which develop on coastal dunes in the western and central Mediterranean basin. The second alliance is a type of sclerophyllous woodland of the eastern Aegean region and Cyprus (Mucina et al.,

2016). However, these descriptions do not capture the full complexity and hierarchical arrangement of plant communities formed or co-formed by *J. turbinata*. A comprehensive analysis of plant communities where *J. turbinata* plays a dominant or co-dominant role across its geographic range was done by Asensi et al. (2007). Using statistical and ordination analyses of phytosociological data, they showed the alliances on the scatterplot form one group with outstanding the High Atlas *Ephedro nebrodensis-Juniperion turbinatae* Quézel & Barbero 2007, *Junipero africanae-Quercion rotundifoliae* Quézel & Barbero ex Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988 corr. Barbero, Lebreton & Quézel 1994 and *Tetraclinido-Juniperion turbinatae* Rivas-Martínez, Costa & Izco 1986, the East-Mediterranean *Rhamno graecae-Ceratonion siliquae* Barbero & Quézel in Asensi et al. 2007, and Cyrenian *Aro-Rhamnion lybici* Brullo & Funari 1994 (Asensi et al., 2007: Fig. 1). The syntaxonomic scheme proposed by Asensi et al. (2007: 617–619), places all associations within the class *Quercetea ilicis* Br.-Bl. 1947, and two orders *Ephedro-Juniperetalia* Quézel & Barbero ex Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988, and *Pistacio lentisci-Rhamnetalia alaterni* Rivas-Martínez 1975.

Order *Ephedro-Juniperetalia* includes juniper-dominated woodlands, developed in the pre-steppe, arid, dry regions of the thermo- to oro-Mediterranean climates in the Atlas Mountains of northwestern Africa (see also Benabid, 2000; Taleb & Fennane, 2019). Depending on the geography, geology, and site conditions, this order includes alliances *Ephedro nebrodensis-Juniperion turbinatae* Quézel & Barbero 1981 and *Junipero africanae-Quercion rotundifoliae* Quézel & Barbero ex Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988 corr. Barbero, Lebreton & Quézel 1994 (Asensi et al., 2007; Taleb & Fennane, 2019).

Woodland associations of thermo- and meso-Mediterranean character that cover extended areas in the internal valleys of the High Atlas, are included in the alliance *Ephedro nebrodensis-Juniperion turbinatae*. The main woody taxa, besides *J. turbinata* are *Cupressus atlantica* Gaussen, *Rhus tripartita* DC., and *Warionia saharae* Benth. & Coss. The three associations representing this alliance develop in different regions of the High Atlas. The thermo-Mediterranean association *Coronillo ramosissimae-Juniperetum turbinatae* Quézel & Barbero 1981 (= *Coronillo ramosissimae-Juniperetum phoeniceae* Quézel & Barbero 1981) develops on shallow, rocky soils and covers the northern slopes of the High Atlas at elevations between 1000 and 1900 m (Quézel & Barbero, 1981; Asensi et al., 2007; Taleb & Fennane, 2019).

The association *Warionio saharae-Anthirrhinetum ramosissimi* Quézel & Barbero 1981 has been described from the N'Fiss Valley in the High Atlas,

from poorly developed soils on the volcanic rocks, at elevations 1000 – 1300 m, in arid climate (Quézel & Barbero, 1981; Asensi et al., 2007). Association *Junipero turbinatae-Cupressetum atlanticae* Quézel & Barbero 1981, also known from the N’Fiss Valley, is found within the geographic range of *Cupressus atlantica*. It is formed on shallow, rocky soils derived from shales or calcareous rocks, in arid or semi-arid, thermo- and meso-Mediterranean climate conditions, at elevations of 1000–1700 m (Sękiewicz et al., 2014). The forest is composed of *Cupressus atlantica* and *J. turbinata*, along with species like *Ephedra nebrodensis* Tineo, *Polygala balansae* Coss., *Lavandula dentata* L. (Quézel & Barbero, 1981; Asensi et al., 2007; Taleb & Fennane, 2019). A related association *Micromerio hochreuteneri-Cupressetum atlanticae* Romo ex Sękiewicz et al. 2014, represents forests of *Cupressus atlantica* and *J. turbinata* in the N’Fiss Valley and close parallel valleys of the High Atlas, occurring at elevations between 1100 and 1800 m (Sękiewicz et al., 2014).

The alliance *Junipero africanae-Quercion rotundifoliae* includes associations *Retamo dasycarpae-Juniperetum turbinatae* Quézel & Barbero ex Asensi et al. 2007, and *Bupleuro spinosi-Juniperetum turbinatae* Quézel & Barbero ex Asensi et al. 2007. The first association, consisting of sparse woodlands of *J. turbinata* with *Retama dasycarpa* Coss., develops mainly in the western High Atlas on loamy substrates derived from volcanic rocks, at superior meso- and supra-Mediterranean, cold and relatively humid climates, at elevations between 1300 and 2200 m (Quézel & Barbero, 1981; Asensi et al., 2007; Taleb & Fennane, 2019). Association *Bupleuro spinosi-Juniperetum turbinatae* consists of sparse woodlands dominated by *J. turbinata*. It develops on the volcanic rocks, the limestone, shales, and quartzites of High Atlas and locally in Anti Atlas, at elevations between 1900 and 2100 (2800) m, in the semiarid climate with cold winters (Quézel et al., 1994; Asensi et al., 2007; Taleb & Fennane, 2019).

Order *Pistacio lentisci-Rhamnetalia alaterni* includes woodlands that occur in dry to relatively humid ombroclimates around the Mediterranean basin. Several geographic variants of this vegetation have been distinguished at the alliance level: *Tetraclinido articulatae-Pistacion atlanticae* Rivas-Martínez, Costa & Izco 1986, *Tetraclinido articulatae-Juniperion turbinatae* Barbero, Quézel & Rivas-Martínez 1981 corr. Quézel et al. 1992., *Asparago albi-Rhamnion oleoidis* Rivas Goday ex Rivas-Martínez 1975, *Oleo-Ceratonion* Br.-Bl. Ex Guinochet & Drouineau 1944, *Juniperion turbinatae* Rivas-Martínez 1975 corr. 1987, *Periplocion angustifoliae* Rivas-Martínez 1975, *Rhamno graecae-Ceratonion siliquae* Barbero & Quézel ex Asensi et al. 2007 and *Aro cyrenaici-Rhamnion libyci* Brullo & Funari 1994.

The alliance *Tetraclinido articulatae-Pistacion atlanticae* includes high shrubby or forest associations in semi-arid to dry, thermo- to meso-Mediterranean

regions of northwestern Africa, with occurrence of *J. turbinata* (Asensi et al., 2007). This alliance represents association *Junipero phoeniceae-Tetraclinietum articulatae* Fennane 1982 em. 1988, (= *Tetraclinido articulatae-Juniperetum turbinatae* in remarks, Asensi et al., 2007: 610) developed on the Atlantic coast and in the mountainous regions of the vicinities of Essaouira (Taleb & Fennane, 2019).

The alliance *Tetraclinido articulatae-Juniperion turbinatae* includes several forest or bushy plant communities. The association *Tetraclinido articulatae-Juniperetum turbinatae* Quézel, Barbero, Benabid & Rivas-Martínez 1992 is common in the mountains of northwestern Africa and, depending on plant composition, it can present several variants recognized at the level of subassociations (e.g. Asensi et al., 2007) or independent associations (Meddour et al., 2017; Taleb & Fennane, 2019 and references cited).

The alliance *Asparago albi-Rhamnion oleoidis* includes shrubby plant communities in dry, semi-arid to sub-humid areas along the shores of the Iberian Peninsula and coast of northwestern Africa (Asensi et al., 2007). It comprises several associations that form different aspects of “maquis”. One notable association *Quercu cocciferae-Juniperetum turbinatae* (Rivas-Martínez 1975) Rivas-Martínez, Lousa, T.E. Díaz, Fernández Gonzalez & J.C. Costa 1987 is formed along the Atlantic coast of the Iberian Peninsula. These are small, dense “microforests” that develop primarily on the calcareous hills near the shore (Asensi et al., 2007; Costa et al., 2012; Asensi & Díez-Garretas, 2017). Other associations from this alliance were reported from the southern regions of the Iberian Peninsula and northwestern Africa (Cape-lo et al., 1994; Díez-Garretas et al., 1995; Galán de Mera et al., 1997; Asensi et al., 2007; Hidalgo et al., 2014; Molero & Marfil, 2017; Meddour et al., 2017).

The alliance *Oleo-Ceratonion siliquae* includes the thermo-Mediterranean plant communities, that are widespread along the European coasts of the Mediterranean Sea, from the eastern Iberian to the western Balkan Peninsula shores (Asensi et al., 2007). Several associations within this alliance develop in dry to sub-humid conditions in different geographic regions: *Cneoro tricocci-Pistacietum lentisci* O. Bolòs & Molinier 1958, *Cneoro tricocci-Ceratonietum siliquae* O. Bolòs in O. Bolòs & Molinier 1958, and *Rhamno ludovici-salvatoris-Juniperetum turbinatae* (Camarasa, Cardona, Masalles, Terradas, E. Velasco & Vigo 1976) Gil, Llorens, Tébar & Costa 1995 are developed on calcareous, semi-arid to arid sites of the Balearic Island (Rivas Martínez et al., 1992; Gil et al., 1995; Rivas-Martínez et al., 2002; Stanisci et al., 2004; Asensi et al., 2007; Llorens & Gil, 2017). To *Oleo-Ceratonion siliquae* alliance, Asensi et al. (2007) included association *Oleo sylvestris-Juniperetum turbinatae* Arrigoni, Bruno, De Marco & Veri in De Marco, Dinelli &

Caneva 1985 corr. Biondi & Mossa 1992, the thermo- and meso-Mediterranean, dry woodlands growing on calcium-rich soils, or soils developed from granites or shales along the coast of Corsica and Sardinia. The *Oleo sylvestris-Juniperetum turbinatae* was earlier included in the alliance *Juniperion turbinatae* Rivas-Martínez et al. 1975 corr. 1987 (Paradis, 1991; Biondi et al., 2001; Biondi & Bagella, 2005). Other associations developed mainly on Sardinia are *Euphorbio characiae-Juniperetum turbinatae* Biondi, Filigheddu & Farris 2001, and *Chamaeropo humilis-Juniperetum turbinatae* De Marco, Dinelli & Caneva 1985 corr. Biondi et al. 2001 (Biondi et al., 2001; Asensi et al., 2007).

Other associations included in the *Oleo-Ceratonion* alliance are *Teucrio fruticantis-Juniperetum turbinatae* Arrigoni, Nardi & Raffaelli 1985 corr. Asensi et al. 2007 known from Tuscany, and *Pistacio lentisci-Juniperetum turbinatae* Trinajstić 1987, corr. Asensi et al. 2007 known from the islands along the Adriatic Sea shore (e.g. Trinajstić, 1987; Kovačić et al., 2001; Pandža, 2004; Pandža et al., 2011; Tsiourlis et al., 2016; Jasprica et al., 2018). The latter association was also reported from the Aegean Island of Naxos (Sarika et al., 2015), and could be expected in the southern Peloponnese, where *J. macrocarpa* is frequently found (see Boratyński et al., 1992).

The alliance *Periplocion angustifoliae* includes thermo-xerophilous shrublands distributed throughout the Mediterranean region, within the dry infra- and thermo-Mediterranean regions. To this alliance belongs *Periploco angustifoliae-Juniperetum turbinatae* Bartolo, Brullo, Minissale & Spampinato 1988 described from Lampedusa (Bartolo et al., 1988), reported from Pantelleria (Gianguzzi, 1999), and Chrysi and Gavdos islands in Greece (Brullo & Guarino, 2000; Delipetrou et al., 2015).

The permanent juniper-dominated shrubby communities that grow mainly on coastal sand dunes in the western and central Mediterranean basin, are grouped in the alliance *Juniperion turbinatae*. The associations *Osyrio quadripartitae-Juniperetum turbinatae* Rivas-Martínez ex Rivas-Martínez, Lousa, T. E. Díaz, Fernández González & J. C. Costa 1990, *Rhamno angustifoliae-Juniperetum turbinatae* Rivas-Martínez ex Freitag 1971 corr. Alcaraz, T. E. Díaz, Rivas-Martínez & P. Sánchez 1989, and *Juniperetum turbinatae* Molinier ex O. Bolòs 1967 develop along the coasts of Lusitania, Andalusia, Murcia, Almería, and Valencia to Provença regions, respectively (Asensi et al., 2007; Costa et al., 2012; Alcaraz, 2017; Molero & Marfil, 2017; Asensi & Díez Garretas, 2017). From dunes of the Balearic Islands, the association *Clematido balearicae-Juniperetum turbinatae* (O. Bolòs, Molinier & P. Montserrat 1970) Rivas-Martínez 1975 was reported, and from the Tyrrhenian region of Italy, the association *Phillyreo angustifoliae-Juniperetum turbinatae* Arrigoni, Nardi & Raffaelli 1985 corr. Bartolo et al. 1992

has been described (Bartolo et al., 1992; Asensi et al., 2007; Gianguzzi et al., 2012; Biondi et al., 2014; Lafon et al., 2024). Along the Italian Adriatic coast, the association *Juniperetum macrocarpae-turbinatae* Pedrotti & Cortini-Pedrotti ex Pedrotti et al. 1982, of coastal cliffs has been reported (Pirone, 2014; Veronico et al., 2017).

The local association *Junipero turbinatae-Quercetum calliprini* Bartolo, Brullo & Marcenò 1982 was described from Sicily. This association could correspond with *Junipero turbinatae-Quercetum cocciferae* Hadjadj-Aoul and Loisel 1999, reported from northern Algeria (Meddour et al., 2017), but it differs in that the dominant species is *Quercus coccifera* which several authors (e.g. Paffetti et al., 2001; Brullo & Spampinato, 2004) consider to be quite distinct both in characteristics and distribution from *Quercus calliprinos*, the latter having primarily eastern Mediterranean geographic range. In inland sandy hilly areas of Sicily, another association, *Piptathero caerulescentis-Juniperetum turbinatae* was described by Minissale and Sciandrello (2013).

The association *Clematido cirrhosae-Juniperetum turbinatae* Quézel, Barbero, Benabid Loisel & Rivas-Martínez 1988 was reported from dunes of the Atlantic coast in north-western Africa and *Pino pinastri-Juniperetum turbinatae* Barbero, Banabid, Quézel & Rivas-Martínez 1981 corr. Asensi et al. 2007 from the Tingitanian Peninsula in north-western Africa (Benabid, 2000; Asensi et al., 2007). In the Mediterranean coast dunes in Morocco are developed *Calendulo marginatae-Juniperetum turbinatae* Tregubov 1963 corr. Asensi et al. 2007 and in Algeria *Ephedro fragilis-Juniperetum turbinatae* (Zaffran 1960) Géhu & Sadki 1995 (Benabid, 2000; Asensi et al., 2007).

To the alliance *Rhamno graecae-Ceratonion silique*, the eastern vicariant of the western Mediterranean alliance *Oleo-Ceratonion*, are included thermo-Mediterranean woodland communities of semiarid to sub-humid coastal and subcoastal regions, developed on both calcareous and siliceous substrates. The association *Ephedro campylopodae-Juniperetum turbinatae* Barbero & Quézel in Asensi et al. 2007, was described from Cyprus and reported from Karpathos (Géhu, 1992; Asensi et al., 2007). The association *Ceratonion siliquae-Quercetum calliprini* Knapp 1965 em. Bolòs, Masalles Ninot & Vigo 1996 developed on the calcium-containing substrates in Peloponnese and Aegean Islands (Asensi et al., 2007; Sarika et al., 2015; Tsiourlis et al., 2016). In alliance *Rhamno-Ceratonion* are included also *Junipero turbinatae-Pinetum brutiae* Barbero & Quézel 1980 corr. Asensi et al. 2007, the light-full forests of *Pinus brutia* Ten., growing on calcium-containing substrates on the east Crete (Asensi et al., 2007), and the association *Cyclamino trochop-teranthi-Pinetum brutiae* (Akman, Kurt L., Demiyüre, Quézel, Kurt F., Evren & Küçüködük 1998) Asensi

et al., 2007 developed on calcareous substrates of south-western Anatolia (Akman et al., 1998; Asensi et al., 2007). The last two associations are sometimes included into the alliance *Pinion brutiae* (Bonari et al., 2020). Probably that alliance could include also association *Cupressus sempervirens-Juniperus turbinata* (orig. *J. phoenicea*) reported from Jordan (Zohary, 1973), but it shall be verified. In Mediterranean Syria, alliance *Junipero-Quercion* Barbero & Quezel 1979 was reported as a plant community with *J. turbinata* (orig. *J. phoenicea*) (Ghazal, 2008), but the species occurrence in this region shall be verified.

The additional alliance *Asparago orientalis-Juniperion macrocarpae* (Díez-Garretas & Asensi, 2013) Mucina in Mucina et al. 2016 was recently proposed for the coastal vegetation with *J. turbinata* in the Peloponnese and Aegean Islands (Díez-Garretas & Asensi, 2013; Sarika et al., 2023).

The alliance *Aro cyrenaici-Rhamnion libyci* Brullo & Furnari 1994, which includes only one association *Junipero turbinatae-Arbutetum pavarii* Brullo & Furnari 1994, is found in Cyrenaica (Brullo & Furnari, 1994; Asensi et al., 2007).

In the European Mediterranean region, *Juniperus turbinata* also enters plant communities of *Pinus pinaster*, *P. pinea*, and *P. halepensis*. On the Iberian Peninsula it has been reported from the alliance *Junipero turbinatae-Pinion halepensis*, from associations *Ephedro fragilis-Pinetum halepensis* and *Rhamno lycioidis-Pinetum halepensis*, and from the evergreen oak forests association *Brachypodio boissieri-Quercetum rotundifoliae* (Molero & Marfil, 2017; Asensi & Díez-Garretas, 2017; Espírito Santo et al., 2017; Llorens & Gil, 2017; Peinado et al., 2017; Bonari et al., 2020; Cano et al., 2022). In Sardinia, *J. turbinata* has been reported from the associations *Erico arboreae-Pinetum halepensis* De Marco et Caneva 1984; *Smilaco asperae-Pinetum halepensis* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2022, and *Quercus calliprini-Pinetum pineae* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2022 (Calvia, 2021; Calvia et al., 2022). In the eastern Mediterranean region, *J. turbinata* occurs in the associations formed by *Pinus brutia* (Konstantinidis et al., 2012) and/or *Quercus coccifera* (including *Q. calliprinos* Webb), which are developed in Crete, the Aegean Islands and the Peloponnese (Tsiourlis et al., 2009; Konstantinidis et al., 2012). *Juniperus turbinata* can also enter different stadia of regeneration and/or degeneration of woody vegetation and phryganic communities (e.g. Tsiourlis et al., 2007; Tomaselli et al., 2024), and even cliff vegetation (Terzi et al., 2018).

Juniperus canariensis

Juniperus canariensis is a major component of thermo-sclerophyllous woodland, included in the alliance *Mayteno canariensis-Juniperion canariensis* A. Santos & M. Fernández ex A. Santos 1983 corr. Rivas-Martínez

et al. 1993, endemic to the Canary Islands (Santos, 1983; Del Arco et al., 2006; González Artilles, 2006; Fernández-Palacios et al., 2008; Otto et al., 2012; Romo & Salvà-Catarineu, 2013; Mucina et al., 2016; Del Arco Aguilar & Rodríguez Delgado, 2018). This alliance, endemic to Canary Islands, unlike the continental juniper woodlands, belongs to a special class endemic of the Macaronesian Region *Oleo cerasiformis-Rhamnetea crenulatae* Santos ex Rivas-Mart. 1987, grouping infra-thermomediterranean semiarid and arid matorral on volcanic substrates. The open woodland with *Juniperus canariensis*, locally known as sabinar, is usually found between the cactiform plant community belt at lower elevations and the Canary pine forest or evergreen laurel forest belts at higher altitudes (Romo, 2018). A circuminsular distribution of these juniper woodlands is recognized on the islands of La Gomera, Tenerife, and El Hierro.

On La Gomera, the association *Brachypodio arbusculae-Juniperetum canariensis* M. Fernández 1983 corr. Rivas-Martínez et al. 1993 has been described. This open xeric juniper woodland is endemic to La Gomera. *Juniperus canariensis* forms an open subassociation, *typicum* (Fernández Galván, 1983). In higher areas, it is replaced by the humid subassociation *ericetosum arboreae* Del Arco and O. Rodríguez in Del Arco et al. 2006, which constitutes the transition to the evergreen laurel forest, known as Monteverde.

On Tenerife, the association *Junipero canariensis-Oleatum cerasiformes* O. Rodríguez, Wildpret, Del Arco & Pérez de Paz 1990 corr. Rivas-Martínez et al. 1993 has been reported, with subassociations *typicum* and *ericetosum arboreae* O. Rodríguez, Wildpret, Del Arco & Pérez de Paz, 1990. The *ericetosum arboreae* subassociation corresponds to humid thermo-sclerophyllous woodland. However, juniper plant communities on Tenerife are highly fragmented and degraded (Montesinos et al., 2009).

On La Palma, the association *Rhamno crenulatae-Juniperetum canariensis* A. Santos 1983 corr. O. Rodríguez, Del Arco, García Gallo, Acebes, Pérez de Paz & Wildpret 1998 [nom. inv. propos.] has been described. On La Palma, juniper communities are very small and fragmented (Montesinos et al., 2009).

On El Hierro, the association *Rubio fruticosae-Juniperetum canariensis* A. Santos in Rivas-Martínez et al. 1993 was described, with subassociations *typicum*, *ericetosum arboreae* Del Arco, Acebes & Pérez de Paz 1996, and *pinetosum canariensis* (Del Arco, Pérez de Paz, Wildpret, Lucía & Salas, 1990) Del Arco, Acebes & Pérez, 1996. The *ericetosum arboreae* subassociation represents humid thermo-sclerophyllous woodlands, while *pinetosum canariensis*, located in the southwest of the island below the Canary pine belt, represents more xeric woodland (Salas et al., 1998; Del Arco & Rodríguez Delgado, 2018).

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Supplementary Material

Appendix 1. Syntaxonomic scheme of phytocoenoses with *Juniperus phoenicea*, *Juniperus turbinata* and *J. canariensis* (data compiled from Rivas-Martínez et al., 2001; Asensi et al., 2007; Rivas-Martínez, 2011; Konstantinidis et al., 2012; Díez-Garretas & Asensi, 2013; Mucina et al., 2016; Bonari et al., 2021; Foucault, 2021; Cano et al., 2022)

Class QUERCETEA ILICIS Br.-Bl. 1947

Order *Ephedro-Juniperetalia* Quézel & Barbero ex Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988

Alliance *Ephedro nebrodensis-Juniperion turbinatae* Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007

Associations:

Coronillo ramosissimae-Juniperetum turbinatae Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007
Warionio saharae-Antirrhinetum ramosissimi Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007,
Junipero turbinatae-Cupressetum atlanticae Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007,

Alliance *Junipero africanae-Quercion rotundifoliae* Quézel & Barbero ex Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988 corr. Barbero, Lebreton & Quézel 1991

Associations:

Retamo dasycarpae-Juniperetum turbinatae Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007,
Bupleuro spinose-Juniperetum turbinatae Quézel & Barbero in Asensi, Díez-Garretas & Quézel 2007

Order *Pistacio lentisci-Rhamnetalia alaterni* Rivas-Martínez 1975

Alliance *Pino pinastri-Juniperion phoeniceae* Pérez Latorre et Cabezudo in Pérez Latorre et al. 1998

Associations:

Rhamno lycioidis-Juniperetum phoeniceae Rivas-Martínez & G. López in G. López 1976
Pino halepensis-Juniperetum phoeniceae Pérez Latorre & Cabezudo in Pérez Latorre et al. 1998
Rhamno myrtifolii-Juniperetum phoeniceae Molero Mesa & Pérez Raya 1987
Buxo sempervirentis-Juniperetum phoeniceae Rivas-Martínez 1969

Alliance *Rhamno lycioidis-Quercion cocciferae* Rivas Goday ex Rivas- Martínez 1975

Associations:

Pino salzmannii-Juniperetum phoeniceae Quézel et Barbero 1988

Junipero phoeniceae-Ficetum caricae de Foucault et Julve 1991

Rhamno saxatilis - Juniperetum phoeniceae Roselló 1994

Alliance *Tetraclinido articulatae-Juniperion turbinatae* Barbero, Quézel et Rivas-Martínez 1981 corr. Quézel et al. 1992 (Syn.: *Tetraclinido articulatae-Juniperion phoeniceae* Barbero, Quézel et Rivas-Martínez 1981)

Association:

Tetraclinido articulatae-Juniperetum turbinatae Quézel, Barbero, Benabid & Rivas-Martínez 1992 (syn.: *Junipero phoeniceae-Tetraclinidetum articulatae* Fenane 1988)

Alliance *Asparago albi-Rhamnion oleoidis* Rivas Goday ex Rivas-Martínez 1975

Associations:

Quercu cocciferae-Juniperetum turbinatae (Rivas-Martínez 1975) Rivas-Martínez, Lousa, T.E Díaz, Fernández Gonzalez & J.C. Costa 1987
Phlomido purpureae-Juniperetum turbinatae Capelo, Louisa & J.C. Costa 1994,
Asparago horridi-Juniperetum turbinatae Díez-Garretas, Asensi & Martín 1996
Asparago aphylli-Calicotometum villosae Rivas-Martínez 1975

Alliance *Oleo-Ceratonion siliquae* Br.-Bl. ex Guinochet & Drouineau 1944 em. Rivas-Martínez 1975

Associations:

Cneoro tricocci-Pistacietum lentisci O. Bolòs & Molinier (1969) 1984
Rhamno ludovici-salvatoris-Juniperetum turbinatae (Camarasa, Cardona, Masalles, E. Velasco & Vigo 1976) Gil, Llorens, Tébar & Costa 1996
Cneoro tricocci-Ceratonietum siliquae O. Bolòs in O. Bolòs & Molinier 1958
Oleo sylvestris-Juniperetum turbinatae Arrigoni, Bruno, Di Marco & Veri in De Marco, Dinelli & Caneva 1985 corr. Biondi & Mossa 1992
Erico arboreae-Juniperetum turbinatae De Marco, Dinelli & Caneva 1985 corr. Biondi & Bagella 2005
Euphorbio characiae-Juniperetum turbinatae Biondi, Filigheddu & Farris 2001
Chamaeropo humilis-Juniperetum turbinatae De Marco, Dinelli & Caneva 1985 corr. Biondi et al. 2001

- Teucrio fruticantis-Juniperetum turbinatae* Arrigoni, Nardi & Raffaelli 1985 corr. Asensi et al. 2007 syn.: *Teucrio fruticantis-Juniperetum phoeniceae* Arrigoni, Nardi & Raffaelli 1985
- Pistacio lentisci-Juniperetum turbinatae* (Trinajstić 1987) Asensi et al. 2007, Syn.; *Pistacio lentisci-Juniperetum phoeniceae* Trinajstić 1987
- Alliance *Juniperion turbinatae* Rivas-Martínez 1975 corr. 1987**
- Associations:
- Osyrio quadripatritae-Juniperetum turbinatae* Rivas-Martínez ex Rivas-Martínez, Lousa, T.E. Díaz, Fernández González & J.C. Costa 1990
- Rhamno angustifoliae-Juniperetum turbinatae* Rivas-Martínez ex Freitag 1971 corr. Alcazar, T.E. Díaz, Rivas-Martínez & P. Sánchez 1989
- Juniperetum turbinatae* Molinier ex O. Bolòs 1967 Syn.: *Juniperetum lyciae* Molinier ex O. Bolòs 1967
- Clematido balearicae-Juniperetum turbinatae* (O. Bolòs, Molinier & P. Montserrat 1970) Rivas-Martínez 1975 Syn.: *Clematido balearicae-Juniperetum lyciae* (O. Bolòs, Molinier & P. Montserrat 1970) Rivas-Martínez 1975
- Phillyreo angustifoliae-Juniperetum turbinatae* Arrigoni, Nardi & Raffaelli 1985 corr. Bartolo et al. 1992
- Junipero turbinatae-Quercetum calliprini* Bartolo, Brullo & Marcenò 1982
- Piptathero coerulescentis-Juniperetum turbinatae* Minissale & Sciandrello 2012
- Juniperetum macrocarpae-turbinatae* Pedrotti & Cortini-Pedrotti ex Pedrotti et al. 1976 corr. 1982, syn.: *Asparago acutifolii-Juniperetum macrocarpae* R. & R. Molinier ex O. Bolòs 1962; *Pistacio lentisci-Juniperetum macrocarpae* Caneva et al. 1981
- Clematido corrhosae-Juniperetum turbinatae* Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988
- Pino pinastri-Juniperetum turbinatae* Barbero, Benabid, Quézel & Rivas-Martínez in Barbero, Quézel & Rivas-Martínez 1981 Syn.: *Pino pinastri-Juniperetum lyciae* Barbero, Benabid, Quézel & Rivas-Martínez in Barbero, Quézel & Rivas-Martínez 1981
- Calendulo marginatae-Juniperetum turbinatae* Tregubov 1963 corr. Asensi et al. 2007 Syn.: *Calendulo marginatae-Juniperetum turbinatae* Tregubov 1963; *Rhamno rotundifoliae-Juniperetum turbinatae* Quézel, Barbero, Benabid, Loisel & Rivas-Martínez 1988
- Ephedro fragilis-Juniperetum turbinatae* (Zaffran 1960) Géhu & Sadki 1995
- Rhamno oleoidis-Juniperetum macrocarpae* Rivas-Martínez 1965
- Rubio tenuifoliae-Juniperetum macrocarpae* Géhu et al. 1992
- Prasio majoris-Juniperetum macrocarpae* Brullo et al. 2004
- Alliance *Periplocion angustifoliae* Rivas-Martínez 1975**
- Association:
- Periploco angustifoliae-Juniperetum turbinatae* Bartolo, Brullo, Minissale & Spampinato 1988
- Alliance *Rhamno graecae-Ceratonion siliquae* Barbero & Quézel in Asensi, Díez-Garretas & Quézel 2007, Syn.: *Ceratonio-Pistacion creticum* Zohary & Orshan 1965; *Ceratonio-Rhamnion oleoidis* Barbero & Quézel 1983; *Rhamno graeciae-Juniperion lyciae* Costa, Géhu, Peris & Biondi 1984**
- Associations:
- Ephedro campylopodae-Juniperetum turbinatae* Barbero & Quézel 2007 ex Asensi et al. 2007 Syn.: *Ephedro campylopodae-Juniperetum lyciae* Barbero & Quézel 1979
- Ceratonio siliquae-Quercetum calliprini* Knapp 1965 em. Bolòs, Masalles, Ninot & Vigo 1996 Syn.: *Oleo-Lentiscetum aegeicum* Ludvig, Krause & Seidl 1963; *Prasio majoris-Ceratonietum siliquae* Barbero & Quézel 1980
- Junipero turbinatae-Pinetum brutiae* Barbero & Quézel 1980 Syn.: *Junipero lyciae-Pinetum brutiae* Barbero & Quézel 1980
- Cyclamino trochopteranthi-Pinetum brutiae* Akman, Kurt L., Demiyürek, Quézel, Kurt F., Evren & Küçüköyük 1998 Syn.: *Junipero phoeniceae-Pinetum brutiae* Akman et al. 1998
- Cupressus sempervirens-Juniperus phoenicea* Zohary 1973 (provisional)
- Alliance *Aro cyrenaici-Rhamnion libyci* Brullo & Furnari 1994**
- Association:
- Junipero turbinatae-Arbutetum pavarii* Brullo & Furnari 1994
- Class PINETEA HALEPENSIS Bonari & M. Chytrý 2022**
- Order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi & Vagge in Biondi et al. 2014**
- Alliance *Thymo vulgaris-Pinion halepensis* Biondi & Pesaresi in Pesaresi et al. 2017**
- Associations:
- Ephedro fragilis-Pinetum halepensis* J. Torres, A. García, Salazar, Cano, F. Valle & Rivas-Martínez 2011
- Rhamno lycioidis-Pinetum halepensis* (J. Torres, García-Fuentes, Salazar, Cano & F. Valle 1999) Rivas Mart. 2002

Alliance *Pistacio lentisci-Pinion halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014

Associations:

Erico arboreae-Pinetum halepensis De Marco & Caneva 1984;

Smilaco asperae-Pinetum halepensis Calvia, Bonari, Angiolini, Farris, Fenu & Bacch. 2022,

Quercus calliprini-Pinetum pineae Calvia, Bonari, Angiolini, Farris, Fenu & Bacch. 2022.

Class JUNIPERO-PINETEA SYLVESTRIS Rivas-Mart. 1965

Order *Junipero-Pinetalia sylvestris* Rivas-Mart. 1965

Alliance: *Juniperion thuriferae* Rivas-Martínez 1969

Association:

Juniperetum phoeniceo-thuriferae (Br.-Bl. & O. Bolòs 1958) Rivas-Martínez 1987

Class QUERCO-FAGETEA Br.-Bl. & Vlieger in Vlieger 1937

**Order *Quercetalia roboris* Tüxen 1931, Syn.:
Quercetalia robori-sessiliflorae Tüxen 1937**

Alliance: *Quercion pyrenaicae* Rivas Goday ex Rivas-Martínez 1965

Association:

Cephalanthero rubrae-Quercetum fagineae Rivas-Martínez in Rivas Goday & al. 1960 corr. Rivas-Martínez 1972

Class OLEO CERASIFORMIS- RHAMNETEA CRENULATAE Santos ex Rivas-Mart. 1987

Order *Oleo cerasiformis-Rhamnetalia crenulatae* Santos 1983

Alliance *Mayteno canariensis-Juniperion canariensis* Santos & Galván ex Santos 1983 corr. Rivas-Mart. et al. 1993.

Associations:

Junipero-Rhamnetum crenulatae Santos 1983

Rubio fruticosae-Juniperetum canariensis Santos in Rivas-Martínez & al. 1993;

Brachypodio arbusculae-Juniperetum canariensis F. Galván 1983 corr. Rivas-Mart. et al. 1993

Junipero canariensis-Oleetum cerasiformis Rodríguez, Wildpret, Arco & Pérez 1990 corr. Rivas-Mart. et al. 1993.