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Biology and ecology of *Juniperus phoenicea* – *J. turbinata* – *J. canariensis* complex. III. Reproduction, herbivory, utilization, conservation

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Abstract: This review examines the literature on the reproduction, herbivory, parasitism, utilization, and conservation of *Juniperus phoenicea*, *J. turbinata*, and *J. canariensis*, which constitute the *J. phoenicea* complex. The review of taxonomy, structure, geography, and of genetics, physiology and ecology was presented in two earlier publications. Compared to taxonomy and genetics, as well as phytosociology, we find a relatively high number of studies concerning seed dispersal, but mainly for *J. turbinata*, and the utilization of biochemical components of leaves. The leaves and cones of *J. turbinata* and *J. phoenicea* serve as sources of volatile essential oils (EOS) with numerous chemical compounds traditionally used in local medicine, veterinary applications, and cosmetics. The wood is primarily utilized as fuel, particularly in regions where other tree resources are scarce. Studies in reproduction, herbivory, and conservation are limited in number and predominantly local in character. Thus, further research is particularly needed on seed pretreatment and preparation for germination, seed conservation and storage, vegetative propagation, and micropropagation, which could significantly aid in the restoration of ecosystems for all species of junipers here examined. Data on herbivory and parasitism affecting all three species are incidental, incomplete, and scarce. The conservation needs are determined only locally, and focus primarily on *J. canariensis* and maritime populations of *J. turbinata*. Conservation actions are rare, with efforts mainly directed at *J. canariensis*, while *J. turbinata* and *J. phoenicea* are passively protected in nature reserves, often covering restricted areas. European Union directives on coastal dune vegetation and Macaronesian juniper forest are the only broad international conservation measures for the remnants of *J. turbinata* in maritime dunes, and remnants of *J. canariensis*. However, a comprehensive international program for the conservation of the *J. phoenicea* complex outside Europe and the Canary Islands is lacking.

Keywords: seed germination, damage caused by animals, damage caused by fungi, uses, conservation

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This contribution completes the previously outlined understanding of the *Juniperus phoenicea* complex. Earlier studies have extensively examined its systematics, geographical distribution, genetics, and role in plant communities (Boratyński et al., 2024, 2025) based on a wealth of available literature and personal observations.

Reproduction

Generative reproduction

Seed dispersal

The cones of the species in the *Juniperus phoenicea* L. complex ripen at the end of summer and in the autumn of the second year after pollination. The ripened cones vary in size and weight, depending on the species, specimen, the predominant sex of the specimen (Jordano, 1991; García et al., 2000), and to some extent on geographic location, stand elevation, and climatic conditions (Arista et al., 1997; García et al., 2000; Pavón García et al., 2006; Mazur et al., 2010; Mandin, 2013; Mazur et al., 2016, 2018; Mazur, 2021). In *J. phoenicea* s.l., one kilogram of cones contains between 1,300 and 2,300 pieces, and one kilogram of seeds contains between 32,000 and 50,000 pieces (Piotto et al., 2003).

Juniperus phoenicea L., *J. turbinata* Guss., and *J. canariensis* Guyot & Mathou are predominantly endozoochorous, similar to other juniper species (Bartkowiak, 1970; Jordano, 1993; Thomas et al., 2007 and references cited). Ripened cones often remain on the trees to the autumn of the following year, while some drop to the ground beneath the crown of the mother tree (authors' personal observations). The cones are consumed mainly by birds of the family Turdidae, omnivorous and carnivorous mammals, and locally by lizards (Herrera, 1989; Jordano, 1993; Muñoz-Reinoso, 1993; Rumeu et al., 2009b, 2011; García et al., 2014; Benabderrahmane et al., 2022; González-Varo et al., 2022 and references cited). The seeds are subsequently excreted with feces, sometimes far from the mother tree (Table S1).

In the Saharan Atlas of Algeria, the seeds of *J. turbinata* (orig. *J. phoenicea*) are consumed by *Turdus torquatus* (Linnaeus, 1758), *Sus scrofa* (Linnaeus,

1758), *Genetta genetta* (Linnaeus, 1758), *Canis anthus* (F. Cuvier, 1820), *Vulpes vulpes* (Linnaeus, 1758), and *Meriones shawi* (Duvernoy, 1842). Mammalian ingestion of *J. turbinata* seeds does not significantly enhance their germination rates compared to ingestion by *Turdus torquatus* or seeds collected from the field during winter (Benabderrahmane et al., 2022). This may be due to shorter intestinal passage times in birds compared to mammals. Seeds that pass through mammalian digestive tracts germinate later than those collected directly from trees in winter (Benabderrahmane et al., 2022). However, carnivorous mammals, which occasionally consume juniper cones, have extensive ranges and, due to prolonged passage times in their digestive tracts, may transport seeds over kilometers from the mother trees, facilitating seedling establishment outside forests (Farris et al., 2017; Walton et al., 2018; Benabderrahmane et al., 2022). In the Saharan Atlas, important dispersers of *J. turbinata* seeds also include granivorous birds such as *Emberiza cia* (Linnaeus, 1766), *Fringilla coelebs* (Linnaeus, 1758), *Linaria cannabina* (Linnaeus, 1758), and *Chloris chloris* (Linnaeus, 1758). These birds extract seeds from cones, often losing some during the process (Benabderrahmane et al., 2022). *Chloris chloris* has also been identified as the frequent vector of *J. turbinata* (orig. *J. phoenicea*) seed dispersal in areas recovering from fire, for example in the Doñana National Park in Spain (Isla et al., 2022).

In Parque Nacional de Doñana (Spain), the cones of *J. turbinata* are consumed by *Oryctolagus cuniculus* (Linnaeus, 1758) which also contributes to seed dispersal (Muñoz-Reinoso, 1993). In Sardinia, the cones of *J. turbinata* are frequently eaten by foxes (*Vulpes vulpes* (Linnaeus, 1758) subsp. *ichnusae* (Miller, 1907), which are significant seed dispersers. On average, 84.9 to 116.5 juniper seeds were found in a single fox dung, and from approximately 3,000 to

over 10,000 seeds were found within a 1-hectare area. However, seeds digested by foxes exhibit very low germination rates, roughly half of those collected directly from mother trees (Farris et al., 2017).

The seeds of *J. canariensis* found in the excrement of *Turdus merula* (Linnaeus, 1758) weighed 16.7% less compared to seeds manually removed from cones, though the impact of ingestion on seed germination remains unknown (Rodríguez-Pérez et al., 2005). The cones of *J. canariensis* are eaten by lizards, rabbits, ravens, and blackbirds, among other animals, which contribute to seed dispersal (Nogales et al., 1999; Rumeu et al., 2009a, b, 2011; Valido & Olesen, 2019; Guerrero-Campos et al., 2023). However, dispersal mainly occurs within individual islands (Jiménez et al., 2017). Among these animals, only Corvidae are capable of dispersing seeds between the islands of the Canary archipelago (Nogales et al., 1999, 2012). Long-distance dispersal between islands may also occur as a secondary mechanism, where primary dispersers are hunted by predators and transported from one island to another (Nogales et al., 2002, 2007, 2012; Padilla et al., 2012). While this mechanism has not been confirmed for *J. canariensis*, it is considered plausible and could explain the moderate genetic (Jiménez et al., 2017) and morphological (Mazur et al., 2018) differentiation among *J. canariensis* populations across islands.

Another potential dispersal mechanism for *J. phoenicea* s.l. cones is hydrochory. Dry cones containing viable seeds may float and be transported by rivers or marine currents, though this requires further study. The cones of *J. turbinata* from Sardinia have a significant buoyancy capacity, lasting up to nine weeks (Cuenca-Lombráña et al., 2024). These findings suggest that thalassochory could be a more common dispersal mechanism than previously thought. Nevertheless, the high effectiveness of ornithochory in dispersing seeds of *J. phoenicea* s.s. and *J. turbinata* is indicated by the expansion of these species into abandoned fields and pastures (e.g., Cano-Ortiz et al., 2015; García-Cervigon et al., 2017).

Natural regeneration

The natural regeneration of junipers is generally low (e.g., Piotto et al., 2003; Thomas et al., 2007; Tyłkowski, 2009; Yücedağ et al., 2021), despite relatively abundant cone production, which occurs at least once every two to three years (authors' personal observations). While junipers are pioneer species that colonize open areas (e.g., Cano-Ortiz et al., 2015; García-Cervigon et al., 2017; Camarero et al., 2022), they rarely regenerate in woodlands. This limitation in natural regeneration also affects woodlands dominated by species of the *J. phoenicea* complex across most regions where they occur.

In plant communities featuring *J. phoenicea* s.s. in Spain, seedlings are very rarely found (e.g., Loidi, 2017 and references cited). Regeneration is especially limited at the southern borders of *J. turbinata*'s geographic range in Africa and the Arabian Peninsula. In Cyrenaica, seedlings and saplings of *J. turbinata* (orig. *J. phoenicea*) are exceedingly rare (Kabel et al., 2016), as they are in the mountains of Sinai (e.g., El-Bana et al., 2010; Farahat, 2020). In regions such as Algeria (Benabderrahmane et al., 2022), Sicily (Minissale & Sciandrello, 2013), Morocco (Sahib et al., 2022), Portugal (Capelo et al., 1994), and Greece (authors' personal observations), seedlings and saplings of *J. turbinata* are scarce and rarely observed. This scarcity likely explains the lack of data on seedling density in phytosociological publications. However, on the small Strofades Islands in Greece, regeneration has been reported, with young specimens constituting up to 5% of individuals in some areas (Martinis et al., 2018).

Juniperus canariensis is a monoecious species, but some individuals exhibit a dominance of female, others of male, and some have both types of cones in equal proportions. This could make regeneration more challenging, but further studies are needed (Montesinos et al., 2009). The number of seedlings of *J. canariensis* in Tenerife is generally very low but higher in proximity to mother trees: 76% of the seedlings are found beneath the canopy, 14% at the canopy edge, and 10% outside the canopy. The average distance from the stem of the mother tree is 1.4 m. Adult trees provide abundant seeds and create favorable micro-environmental conditions that support seedling establishment. Deep soils and spiny shrubs also positively influence seedling and sapling recruitment (Fernández-Palacios et al., 2008; Otto et al., 2010).

In the Canary Islands, some juniper forests on less degraded soils with sufficient water resources exhibit significant regeneration (Otto et al., 2006a). However, juniper regeneration is generally very slow due to difficulties with seed germination and seedling establishment. These challenges are exacerbated by water stress, which is often intensified by the absence of shade conditions necessary for seedling development (Rota et al., 2021), as well as the species' inherently slow growth rate. The growth rate of *J. canariensis* under natural conditions ranges from 2 to 4 cm per year, being slightly faster during its juvenile phase (Otto et al., 2006b). The processes of regeneration and colonization in Canary juniper forests, including germination rates, seedling mortality, and the role of nurse plants, particularly concerning the colonization of abandoned agricultural fields, remain largely unstudied (Montesinos et al., 2009).

Viability of seeds and germination

A large number of cones from taxa within the *J. phoenicea* complex only contain empty seeds (Piotto et al., 2003; Hazubska-Przybył, 2019; Tylkowski, personal communication). This is likely due to a lack of pollination or fertilization, cross-pollination with other species, or even interference from dust particles (Gruwez et al., 2013, 2014, 2017). In nursery practices, empty seeds can be identified and eliminated through floating techniques (e.g. Tylkowski, 2016). This method is also effective for seeds of *J. turbinata* (Piotto et al., 2003; Bacchetta, 2015).

The seeds of junipers have predominantly low germination rate and deep physiological dormancy (Piotto et al., 2003; Thomas et al., 2007 and references cited; Tylkowski, 2009, 2010). Seeds of the *J. phoenicea* complex, need a period of cold stratification to germinate (Piotto et al., 2003; Hazubska-Przybył, 2019). *Juniperus phoenicea* s.s., *J. turbinata* and *J. canariensis* grow in diverse site conditions (Mazur et al., 2016; Romo, 2018; Pavon et al., 2020; Salvà-Catari-neu et al., 2021; Boratyński et al., 2024, 2025), and consequently could be adapted to slightly different environmental conditions, and thus demands concerning the stratification conditions of their seeds could also be different, however, this has been only fragmentarily examined.

The seeds of the *J. phoenicea* complex are classified as orthodox (Piotto et al., 2003; Bacchetta, 2015). To germinate in the spring, the seeds need to be stratified at temperatures close to 0°C for 30–90 days (Piotto et al., 2003). Before stratification, seeds should be extracted from cones through maceration, rinsed with water to remove inhibitors present in the cone structure, and dried in the shade. Once their moisture content drops to 10–12%, they can be stored in airtight containers at approximately 3°C (Piotto et al., 2003). Sowing seeds from unripe (green) cones or seeds extracted from ripe cones in autumn can yield good results. Mechanical or chemical scarification methods have also been reported to improve germination rates (Piotto et al., 2003).

The seeds of *J. turbinata* from Sardinia also have an orthodox character. The average weight of 100 seeds is 2.192 g, and approximately 4,500 seeds are found in 100 g of them (Bacchetta, 2015). These seeds require three months of cold stratification at 5°C, after which the best germination occurs at 20°C under alternating light and darkness every 12 hours. Germination efficiency is considered moderate, ranging between 30% and 60% (Bacchetta, 2015).

The seeds of *J. turbinata* (orig. *J. phoenicea*) from the mountains of Jordan germinated at the highest percentages after three months of cold stratification (Al-Ramamneh et al., 2012). Seeds extracted from mature cones and stratified at 5°C for one or three months germinated at rates of 3.2% and 9.3%,

respectively, while unstratified seeds entirely failed to germinate. The lack of germination in unstratified seeds is likely due to inhibitors present in the seed coat, which are inactivated during stratification (Al-Ramamneh et al., 2012).

In Anatolia (Turkey), approximately 30–50 grams of stratified seeds are required to produce 200–300 seedlings of *J. turbinata* (orig. *J. phoenicea*) (Gültekin, 2007). Germination in the first year after sowing ranges from 15% to 60%, while the remaining seeds germinate during the second or even third year after sowing (Yücedağ et al., 2021). To establish a forest of *J. turbinata* in the Mediterranean region of Anatolia, around 5 kg of viable seeds should be sown during autumn and winter directly in the field. Natural seed sources of *J. turbinata* in Turkey are provided by a single stand of 358.5 hectares within the Milas Forest Directorate (Yücedağ et al., 2021).

The seeds of *J. turbinata* from Morocco also require cold pretreatment for germination. Seeds collected from different regions showed germination rates ranging from 60% to 66% after cold stratification (Boumediene et al., 2024).

The seedling production of *J. phoenicea* s.s. and *J. canariensis* remains insufficiently studied and requires further research.

Perennation and vegetative propagation

Branches of junipers lying on the ground sometimes have the ability to root. Within the *J. phoenicea* complex, this phenomenon is observed in *J. turbinata* growing in maritime sandy habitats, where wind-blown sand may bury branches (Debraczy & Rącz, 1999; authors' personal observations). Adventitious roots support the plant and may prolong its lifespan. However, unlike *J. macrocarpa* Sm., sprouting and regeneration from roots or uncovered roots in *J. turbinata* have not been observed. Rooting of branches lying on the ground in *J. phoenicea* and *J. canariensis* has also not been documented. Propagation through cuttings has been successful for *J. turbinata*. The methods employed involve standard horticultural techniques, procedures, and chemicals (Romano et al., 2022).

In recent decades, efforts have been made to develop micropropagation procedures for various juniper species, as reviewed by Hazubska-Przybył (2019). The callus induction depends of media used (Saleh et al., 2022). Micro-cuttings from seedlings of *J. turbinata* (orig. *J. phoenicea*) have been relatively effective in Jordan (Al-Ramamneh et al., 2012, 2017) and Greece (Bertsouklis et al., 2020). Micropropagation was also successful for *J. canariensis* from Porto Santo, with no differences in ploidy among morphotypes or between these and the mother plant, as confirmed by flow cytometry (Brito, 2000; Loureiro

et al., 2007). However, micropropagation using seedlings of *J. phoenicea* s.s. collected in the Alps resulted in a low level of bud-producing callus (Pace & Chiazazza, 2022).

Herbivory and disease

Animal feeders and/or parasites

Reptiles

The cones of *J. turbinata* and *J. canariensis* are consumed by lizards (Lacertidae). Seeds that are not digested and are either regurgitated or defecated retain their ability to germinate (Traveset & Sans, 1994; Fernández-Palacios et al., 2008; Otto et al., 2010; Valido & Olesen, 2019).

Mammals

The high concentration of secondary metabolites, essential oils (EOS), and terpenes in *J. phoenicea* species (Boratyński et al., 2024: Table S1 and S2) likely protects them from extensive grazing by sheep, goats, and other herbivorous mammals by affecting the animals' stomach microflora (Rogosic et al., 2015 and references cited). On Stamphi Island (Strofades Islands, Greece), goats graze on younger parts of *J. turbinata* and can effectively control its growth through decades of grazing (Martinis et al., 2018). On the Adriatic islands of Croatia, sheep and goats consume *J. turbinata* when other forage plants are scarce, although *J. turbinata* may be preferred by goats due to its high terpene content (Rogosic et al., 2009, 2015). In Algeria, moderate browsing by sheep and goats enhances populations of *J. turbinata* (orig. *J. phoenicea*) (Ayache et al., 2020). Branches of *J. turbinata* are also used as forage in arid regions during prolonged droughts, as observed in North Africa (Kabel et al., 2016; authors' personal observations).

Cones from species in the *J. phoenicea* complex are consumed by herbivorous, omnivorous, and carnivorous mammals, which typically do not digest the seeds. These animals act as seed dispersers rather than predators.

In northern Africa, seeds of *J. turbinata* are sometimes gnawed by rodents (Table S1), causing localized damage (Benabderrahmane et al., 2022; Isla et al., 2022). Cone damage by *Oryctolagus cuniculus* has been observed in Parque Nacional de Doñana (*J. turbinata*) (Muñoz-Reinoso, 1993) and the Canary Islands (*J. canariensis*) (Fernández-Palacios et al., 2008). In Anatolia, germinating seeds and young seedlings of *J. turbinata* are affected by rabbits, sheep, and goats (Yücedağ et al., 2021).

Cones of *J. phoenicea* and *J. turbinata* are also consumed by foxes, martens, badgers, and wild boars (Table S1). Although these animals cause minor

damage to the cones, their role as seed dispersers is significant, as undigested seeds are dispersed over long distances.

Birds

Birds frequently consume juniper cones but generally do not digest the seeds. Defecated seeds, often deposited hundreds of meters from mother trees, germinate and colonize new areas. The primary consumers and dispersers of cones from the *J. phoenicea* complex are thrush (Turdidae) species (Jordano, 1993; Rodríguez-Pérez et al., 2005; Fernández-Palacios et al., 2008; Benabderrahmane et al., 2022; Isla et al., 2023), which are considered the main seed dispersers across all juniper species (Table S1). For *J. canariensis*, ravens (*Corvus corax* Linnaeus, 1758) are notable cone consumers and key vectors for seed dispersal between islands in the Canary archipelago (Fernández-Palacios et al., 2008; Jiménez et al., 2017).

In northern Africa, bird species from the families Sylviidae, Emberizidae, Fringillidae, and Muscicapidae consume and occasionally digest seeds. These Passeriformes extract seeds from cones and sometimes remove the seed coat to eat the seeds directly (Table S1).

Insects and Acari

Research on insects associated with species in the *J. phoenicea* complex is limited, as these plants have low economic significance. The list of insects interacting with the Phoenician juniper complex is relatively short, with much of the data coming from isolated reports (Table S2). Most studies describe insect interactions with *J. phoenicea* s.l. without distinguishing among *J. phoenicea* s.s., *J. turbinata*, and *J. canariensis*. In this review, occurrences of insect interactions are attributed to specific species within the *J. phoenicea* complex, based on their geographic range.

Different taxonomic groups of insects feed on and damage various parts of junipers. Moths (Lepidoptera) are primarily folivorous species belonging to the families Argyresthiidae, Gelechiidae, Geometridae, Lasiocampidae, Noctuidae, and Tortricidae.

Leaf-eating species whose larvae move freely on the shoots include the oligophagous *Eupithecia phoeniceata* (Rambur, 1834) (Geometridae) and *Lithophane leautieri* (Boisduval, 1829) (Noctuidae). Leaf-mining *Gelechia senticetella* (Staudinger, 1859) of the Gelechiidae family can also damage cone bases (Cleu, 1957; Bland et al., 2002). On the other hand, larvae of *Mesophleps oxycedrella* (Millière, 1871) (Gelechiidae) and two species of tortricid moths (Tortricidae) develop inside female, mature cones (Guido & Roques, 1996; Ruseva et al., 2020).

The development of conospermatophagous *Pamene oxycedrana* (Millière, 1876) on *J. phoenicea* has

been described (Roques, 1983). In contrast, the biology of *P. blockiana* (Herrich-Schäffer, 1851) is less understood but is likely analogous to that of *P. oxycedrana*, as is typical for members of the genus *Pammene* Hübner, 1825 (Guido & Roques, 1996; Brown, 2022).

Insects damaging the cones of *J. phoenicea* s.l. include the parasitic wasp *Megastigmus amicornum* Bouček, 1969, the beetle *Nanodiscus transversus* (Aubé, 1850), and *Ernobius juniperi* Chobaut, 1899 (Cleu, 1957; Guido & Roques, 1996; Roques & Skrzypczyńska, 2003; Ribes Escolà & Askew, 2009). Certain Hemipterans, such as *Cyphostethus tristriatus* (Fabricius, 1787) (Acanthosomatidae), *Gonocerus juniperi* Herrich-Schäffer, 1839 (Pentatomidae), *Orsillus depressus* (Mulsant & Rey, 1852), and *O. maculatus* (Fieber, 1861) (Lygaeidae), are also responsible for seed and cone damage.

True bugs (Hemiptera), including aphids, capsid bugs, and scales, feed on plant sap from various parts of *J. phoenicea* s.l. Among these, the conifer aphid genus *Cinara* Curtis, 1835 is represented by four oligophagous species that feed on Cupressaceae, notably *C. cupressi* (Buckton, 1881), a serious pest of these plants (Kairo & Murphy, 1999; Watson et al., 1999; Durak, 2012; Rosagro et al., 2020). Regularly observed phytophagous Hemipterans on *J. phoenicea* s.l. include *Holcogaster fibulata* (Germar, 1831), *Piezodorus lituratus* (Fabricius, 1794), and *Gonocerus juniperi* Herrich-Schäffer, 1839 (Cleu, 1957).

Thysanoptera (thrips) species such as *Frankliniella intonsa* (Trybom, 1895), *Tenothrips discolor* (Karny, 1907), and *Tenothrips frici* (Uzel, 1895) are highly polyphagous, feeding on plants from multiple families. Additionally, *Ankothrips niezabitoskii* (Schille, 1910) and *Scirtothrips dignus* zur Strassen, 1986 are associated with *Juniperus* spp. While these species are considered palynivores (Table SA), they may occasionally feed on young cone and leaf tissues (Marullo, 2004).

Under the bark of *J. phoenicea* s.l., three bark beetle species (Curculionidae: Scolytinae) develop (Balachowsky, 1949; Cleu, 1957; Pfeffer, 1994; Bright & Skidmore, 1997; Lieutier et al., 2016), along with four longhorn beetle species (Cerambycidae) and three jewel beetle species (Buprestidae) (Cleu, 1957; Mikšić & Georgijević, 1973; Sama, 2002). While some species, such as *Phloeosinus aubei* (Perris, 1855), have been reported to kill Cupressaceae plants (Fiala & Holuša, 2019), no widespread tree mortality has been attributed to these beetles in *J. phoenicea* s.l. However, *Delagrangeus schurmanni* Sama, 1985, a monophagous longhorn beetle endemic to the Canary Islands, develops exclusively on *J. canariensis* branches (Sama, 1985).

The only mite (Acari) species known to develop on the *J. phoenicea* complex is *Trisetacus quadrisetus* (Thomas, 1889), the juniper berry mite, which

induces galls on female cones (Ribes Escolà & Askew, 2009). However, knowledge regarding its development on the *J. phoenicea* complex remains limited.

Despite the various taxa mentioned above (Table S2), the data on insects feeding on and damaging species within the *J. phoenicea* complex remain scarce and fragmentary. Further studies, particularly in the context of climate change and its impact on host plant and invertebrate ranges, would be highly valuable.

Fungi

Phytopathological studies on species within the *J. phoenicea* complex are limited, random, and scattered. The list of fungal species associated with the Phoenician juniper complex is relatively short (Table S3) and surely incomplete.

The branch and shoot dieback of *J. turbinata* (orig. *J. phoenicea*) on Island Caprera (Maddalena Archipelago, Italy) was caused by *Diplodia africana* Damm & Crous (Linaldeddu et al., 2011). This fungus can kill entire trees over several years by producing afritoxins and other metabolites (Evidente et al., 2012). Similarly, branch dieback in *J. turbinata* from Cyrenaica, characterized by necrosis progressing from the tips of branches to the trunk, was caused by *Sordaria fimiicola* (Roberge ex Desm.) Griffiths & Seaver (Zaetout et al., 2023).

The wood of the *J. phoenicea* complex is generally considered resistant to fungal infections (Anonym, 2009). However, the sapwood of dead *J. turbinata* (originally *J. phoenicea*) is highly susceptible to decay by *Coniophora puteana* (Schum.: Fr.) P. Karst. and *Rhodonia placenta* (Fr.) Niemelä, K.H. Larss. & Schigel, while its heartwood remains durable and resistant to fungal decomposition (Lykidis et al., 2023).

The wood of *J. turbinata* (originally *J. phoenicea*) is a substrate for 38 wood-decay fungal species (Saitta et al., 2011). These include rare and endangered species such as *Echinodontium rywardenii* Bernicchia & Piga, *Hyphoderma etruriae* Bernicchia, *Lenzitopsis oxycedri* Malençon & Bertault, *Neolentiporus squamosellus* (Bernicchia & Rywarden) Bernicchia & Rywarden, *Piloporia sajanensis* (Parmasto) Niemelä, and *Trametes junipericola* Manjón, G. Moreno & Rywarden. These aphylloroid wood-decay fungi are closely associated with Mediterranean juniper wood, including *J. turbinata* (Saitta et al., 2011).

Unidentified fungal species pose a significant challenge to the *in vitro* propagation of *J. phoenicea* from the Rocca San Giovanni-Saben Nature Reserve (Maritime Alps, Italy) (Pace & Chiavazza, 2022).

Plant parasites

The only known plant parasite associated with the *J. phoenicea* complex is *Arceuthobium oxycedri* (DC.) M.Bieb. (Viscaceae). This hemiparasitic plant targets

several species of the genus *Juniperus*. It has been reported on *J. phoenicea* s.s. in Spain (Bolòs & Vigo, 1990; Villar et al., 1997; Catalán, 1997) and in France (Mandin, 2003; Ciesla et al., 2004). Interestingly, *A. oxycedri* has not been documented parasitizing *J. turbinata* in Europe, though it has been observed on this species (orig. *J. phoenicea*) in Morocco and Algeria (Ciesla et al., 2004).

Utilization

Different parts of junipers or their extracts have been used by local populations in regions where the species occur, and in some cases, transported to distant countries. The relatively high content of EOS and other secondary metabolites in the leaves, cones, seeds, and wood of the *J. phoenicea* complex contributes to their diverse uses, primarily pharmacological but also veterinary and cosmetic. The species within the *J. phoenicea* complex are among the most frequently exploited medicinal agents, used also for insect crop protection, and as repellents against nuisance insects for humans and animals.

The biomass of *J. turbinata* (originally *J. phoenicea*) on the Adriatic islands of Croatia serves as an important fuel source for local populations. The average calorific value of 1 kg of biomass and biochar was 20.45 MJ and 29.01 MJ, respectively (Peter et al., 2022).

Wood

Historically, juniper wood was highly valued, especially in southern regions where species of the genus *Juniperus* were often the only trees. The wood of *J. phoenicea* species is known for its hardness, reddish color, fragrance, and high resistance to destruction by insects and fungi (Danin, 1983; Lykidis et al., 2023), making it a valuable material for tools, weapons, and construction (Anonym, 2009). The earliest record of Phoenician juniper wood usage is a ritual harpoon from the time of King Djoser (ca. 2667–2648 BC) discovered in Saqqara, Egypt (<http://saqqara.uw.edu.pl/pl/obiekty/cor1/>). Due to its durability, the wood was used in antiquity for constructing coffins and its resin for producing incense (Anonym, 2009). It was also utilized in roofing, fencing (Teofrast, 1961), and other outdoor structures, including treadmill propellers (Anonym, 2009). These records primarily pertain to the eastern part of the geographic range of the *J. phoenicea* complex, specifically *J. turbinata*. During the Bronze and Iron Ages in antiquity, *J. turbinata* wood served as fuel for copper and iron smelting in regions such as modern-day Jordan, Saudi Arabia, and the Negev Desert (Collenette, 1985; Engel & Frey, 1996). In these regions, the species became

extinct due to overexploitation (Vardi et al., 2023). In the Edom Highlands (Jordan), an estimated 86 tons of dry *J. turbinata* wood per hectare were available, making it the second richest fuel resource and a frequently used material during the Bronze Age (ca. 3,000 to 1,000 BC) (Engel & Frey, 1996).

In North Africa, *J. turbinata* wood is utilized in carpentry, as fuel, and for charcoal production. In the Atlas and Anti-Atlas Mountains, *J. thurifera* is a primary fuel source (Romo & Boratyński, 2005; Sękiewicz et al., 2014). However, in regions of the High Atlas, Anti-Atlas, and Saharan Atlas without *J. thurifera*, *J. turbinata* wood remains a crucial fuel resource for local populations. Similarly, the wood of *J. canariensis* was an essential fuel source in the past (Tomé et al., 2022).

The wood of *J. turbinata* and other parts of the plant are believed to repel insects. In rural Cyprus, pieces of the wood were placed in wardrobes to protect clothes from moths (Anonym, 2009).

On the Canary Islands, Guanches used *J. canariensis* wood for tools, weapons, body ornaments, coffered ceilings in caves, and funerary boards as biers (Del Arco & Rodríguez Delgado, 2018). After colonization of the Canary Islands by Castilians, the wood of this species, and *Juniperus cedrus* L. F., *Visnea mocanera* (Cav.) A.Braun, *Apollonias barbujana* (Cav.) A.Braun, *Pistacia atlantica* Desf., and *Olea cerasiformis* Rivas Mart. & del Arco were widely used in furniture making and folk handicrafts, particularly during the 16th and 17th centuries (Del Arco & Rodríguez Delgado, 2018). The wood of *J. canariensis* was highly valued for its quality in traditional artisanal uses, including carpentry (Fernández-Palacios, 2008).

Tar extracted from *J. turbinata* (orig. *J. phoenicea*) wood demonstrates significant antifungal activity, particularly against six strains of *Fusarium oxysporum* von Schlechtendal f. sp. *albedinis* W.L. Gordon, effectively inhibiting their growth. This tar also exhibits broad-spectrum antifungal potential against various filamentous fungi (Terfaya et al., 2021).

Leaves

The leaves of species in the *J. phoenicea* complex contain EOS with many components (for a review, see Boratyński et al., 2024 and references cited). These oils have applications in medicine, cosmetics, veterinary science, agriculture, food conservation, and protection against insect predation and fungal destruction.

The biological activity and cytotoxicity of various leaf extracts have been extensively studied in Africa and the Arabian Peninsula, where traditional uses remain prevalent (e.g. El-Sawi et al., 2007; Abu-Darwish et al., 2013, 2014; Ghouti et al., 2018; Miara et al., 2018, 2019; Belhouala & Benarba, 2021; Er

Kemal et al., 2023). EOS extracted from *J. turbinata* leaves or leaves with branchlets show specific antifungal activity against *Fusarium oxysporum*, *Candida albicans* (C.P. Robin) Berkhout, *C. tropicalis* (Castellani) Berkhout, and *C. glabrata* (Anderson) Meyer et Yarrow (Chelouati et al., 2024). However, studies on the EOS and bioactive compounds of *J. phoenicea* s.s. and *J. canariensis* remain scarce and require further research.

In Algeria, decoctions made from the leaves of *J. turbinata* (orig. *J. phoenicea*) are commonly used by nomads to treat illnesses in goats, sheep, and cattle, as well as in human medicine (Miara et al., 2019). In veterinary medicine, they are used for digestive disorders, scabies, pulmonary tuberculosis, and kidney problems. In traditional human medicine in Algeria, Morocco, and other regions, decoctions of *J. turbinata* leaves are used to treat ulcers, diarrhea, stomach ailments, nausea, inflammation (Ghouti et al., 2018), lung diseases, poisoning, and kidney problems (Miara et al., 2018, 2019 and references cited).

Extracts of *J. turbinata* containing EOS have demonstrated insecticidal properties. They cause high larval mortality and moderate adult mortality in *Tribolium castaneum* J.F.W.Herbst, 1897 but have an inverse effect on *Trogoderma granarium* Everts, 1898, with high adult mortality and lower larval impact (Papanikolaou et al., 2022). A combination of *J. turbinata* (orig. *J. phoenicea*) EOS with *Artemisia herba-alba* Asso and *Rosmarinus officinalis* L. has proven effective in killing *T. castaneum* and serves as a good insect repellent (Boukraa et al., 2022). The effectiveness of extracts depends on the solvent used, with the highest impact observed when water with acetone is used, achieving over 50% adult mortality in *T. castaneum* (Saada et al., 2022).

In Jordan, infusions and aqueous extracts of *J. turbinata* leaves (and cones) have been used for centuries as steam inhalants to treat bronchitis and arthritis, improve digestion, and alleviate gas and stomach cramps (El-Sawi et al., 2007). Decoctions are also used in baths to alleviate rheumatism (Abu-Darwish et al., 2014; Keskes et al., 2017). In southern Jordan, decoctions of *J. turbinata* leaves are recommended for treating rheumatism (Al-Qura'n, 2009) and aqueous extracts for diarrhea and gout (Qnais et al., 2005). In Morocco, powdered leaves are employed as diuretics and hypoglycemic agents (Bellakhdar, 1997; Maamoun et al., 2016). In Tunisian folk medicine, *J. turbinata* leaves are used to treat diarrhea, rheumatism, gonococcal infections, eczema, dysmenorrhea, and sunstroke. The efficiency of extracts varies depending on the extraction method, solvent, plant material origin, season of gathering, and pretreatment (Hayouni et al., 2007).

EOS extracted from *J. turbinata* leaves also show cytotoxic effects against human cancer cell lines,

including A549 lung cancer cells and prostate cancer cells (PC3), with high cytotoxic selectivity (Al Groshi et al., 2019; Venditti et al., 2018). These oils also possess significant antioxidant potential (Elmhawi et al., 2015; Venditti et al., 2018).

EOS from the leaves and branches of *J. turbinata*, sourced from various countries, inhibit the growth of bacteria, yeasts, molds, and wood-rot fungi. Targeted organisms include *Escherichia coli*, *Micrococcus luteus*, *Klebsiella pneumoniae*, *Bacillus subtilis*, *Staphylococcus aureus*, *Streptococcus mutans*, *Pseudomonas aeruginosa*, *Candida albicans*, *Fusarium oxysporum*, *Aspergillus niger*, *Penicillium digitatum*, *Penicillium expansum*, *Saccharomyces cerevisiae*, *Macrophomina phaseolina*, *Rhizopus stolonifer*, *Gloeophyllum trabeum*, *Poria placenta*, *Coniophora puteana*, *Coriolus versicolor*, and *Geotrichum candidum* (Stassi et al., 1996; Angioni et al., 2003; El-Sawi et al., 2007; Bouzouita et al., 2008; Ennajar et al., 2009; Derwich et al., 2010; Mazari et al., 2010; Mansouri et al., 2011; Papanikolaou et al., 2022). The antibacterial activity of *J. turbinata* (orig. *J. phoenicea*) leaf extracts has been reported in several studies from Africa, Asia, and Europe (e.g., Cosentino et al., 2003; Cavaleiro et al., 2006; Fouad et al., 2011). Phenolic-enriched fractions from juniper species in Portugal, including *J. phoenicea* and *J. turbinata*, show neuroprotective potential (Tavares et al., 2012). Additionally, EOS from *J. turbinata* leaves and cones exhibit moderate antihypertensive activity (Yvon et al., 2012).

EOS from the leaves of *J. turbinata* (orig. *J. phoenicea*) demonstrate acaricidal activity, achieving 100% mortality of *Ixodes ricinus* (Linnaeus 1758) nymphs within two hours at appropriate concentrations (Elmhawi et al., 2021). EOS from the aerial parts of *J. turbinata* exhibit moderate larvicidal and adult-repellent effects against *Aedes albopictus* (Skuse, 1894) (Giatropoulos et al., 2013).

EOS extracted from the aerial parts of *J. turbinata* suppress the seedling growth of several common weeds in Algeria, including *Daucus carota* L., *Ampeodesmos mauritanicus* (Poir.) T.Durand & Schinz, *Cynodon dactylon* (L.) Pers., *Poa annua* L., and *Avena fatua* L. This indicates the potential for high concentrations of EOS to act as an effective herbicide through allelopathy (Sabrine & Tarek, 2023).

Additionally, the leaves of *J. turbinata* possess the ability to synthesize titanium dioxide nanoparticles (TiO₂ NPs), which exhibit antibacterial, antifungal, and cytotoxic activities. These nanoparticles have potential applications in medicine and *in vitro* technologies (Al Masoudi et al., 2023).

Leaves of *J. canariensis* were used as infusions for medicinal purposes and as an abortifacient (Fernández-Palacios et al., 2008).

Cones

The cones of *J. turbinata* were historically utilized in medicine, cosmetics, and as a kitchen spice. In the mountains of Morocco, cones served as famine food when families faced food shortages. Even today, shepherds consume ripe cones as a snack (Bellakhdar, 2023). Juniper cones contain EOS that had long been used for their antibacterial and antifungal properties, particularly in pharmacy and cosmetics (e.g. Filipowicz et al., 2003; Er Kemal et al., 2023). The cones of *J. communis* L. and other juniper species are widely known for flavoring gin, a key ingredient in dry martinis (Abu-Darwish et al., 2014; Borkowski, 2024). In ancient Greece, juniper cones were used to scent wine (Dioscorides, as cited in Anonym, 2009). They were also employed to anoint the bodies of deceased kings and have been found in Pharaohs' tombs (Manniche, 1999, as cited in Al Masoudi et al., 2023).

In Jordan, cones of *J. turbinata* are traditionally used to treat diabetes mellitus (Hamdan & Afifi, 2004), edema, and urinary tract diseases (Shkukani et al., 2008). Similarly, in Morocco, a decoction made from a mixture of leaves and ripened cones is used for diabetes treatment (Bellakhdar, 2023).

While some studies reviewed by Afifi and Kasabri (2013) suggest that *J. phoenicea* s.l. (mostly *J. turbinata*) cone extracts lack significant antidiabetic efficacy, they highlight the presence of components beneficial for treating various human diseases. Cone extracts contain anticancer compounds, exhibit cytotoxicity against five cell lines, and possess antioxidant properties (Öztürk et al., 2011; Maamoun et al., 2016; Laouar et al., 2017; Ghouti et al., 2018). They may also have hepatoprotective properties (Maamoun et al., 2016), therapeutic potential against hepatotoxicity and nephrotoxicity, wound-healing effects (Aboul-Ela et al., 2005; Tumen et al., 2012), and anticholinesterase activity. Additionally, they show antifungal activity against *Candida albicans* and have antiparasitic and nematocidal applications in traditional medicine across North Africa and the Arabian Peninsula (Afifi & Kasabri, 2013 and references cited; Laouar et al., 2017). Cone extracts are also valuable in food conservation, preventing aflatoxin contamination during storage, and displaying antimicrobial and antifungal properties (Cosentino et al., 2003; Abu-Darwish et al., 2013; Afifi & Kasabri, 2013 and references cited). EOS extracted from *J. turbinata* cones in Italy have been shown to reduce the proteolytic activity of *Pseudomonas fluorescens* KM24 on refrigerated salmon stored at 4°C (Myszka et al., 2021).

In Jordan, the cone EOS of *J. turbinata* (orig. *J. phoenicea*) demonstrated significant antifungal effects against dermatophytes (*Epidermophyton floccosum*, *Microsporum canis*, *M. gypseum*, *Trichophyton*

mentagrophytes, *T. rubrum*, *T. verrucosum*), yeasts (*Candida albicans*, *C. guilliermondii*, *C. krusei*, *C. parapsilosis*, *C. tropicalis*, *Cryptococcus neoformans*), and *Aspergillus* species (*A. flavus*, *A. fumigatus*, *A. niger*). Although the effects varied among pathogens, they were generally high (Abu-Darwish et al., 2013, 2014).

Ornamental purposes

Species within the *J. phoenicea* complex are valued for their decorative qualities, including evergreen foliage and the conical crown shape, particularly in young specimens. These species, especially *J. turbinata*, have low water requirements, making them suitable for urban greenery. However, they are rarely used in landscaping (Farjon, 2005, 2010). The lack of widespread plantations has resulted in an absence of decorative varieties and forms, despite their ability to thrive under harsh conditions (Auders & Spicer, 2012). Known forms have been described from wild populations (Debreczy & Rácz, 1999) and are not cultivated.

Other uses

The potential of *J. turbinata* for coastal area restoration and conservation has been studied in Apulia and Sicily, Italy (La Mantia et al., 2012; Romano et al., 2022). In Apulia, seedlings of *J. turbinata* were planted in highly eroded areas near the seashore. While the species exhibited an adaptive period to the dune's edaphic conditions, the stabilization results were less effective compared to *Pistacia lentiscus* L. (Romano et al., 2022). However, on steep, eroded slopes of Lampedusa Island (Sicily), *J. turbinata* achieved a very high establishment rate (97%), outperforming other shrubs (La Mantia et al., 2012).

Threats and protection need

Species threat

Species within the *J. phoenicea* complex have been exploited for millennia (Le Houérou, 1980) and face various environmental challenges and anthropogenic pressures in the Mediterranean region. According to the IUCN, *J. phoenicea* s.s. is categorized as "Least Concern" (LC) with a stable global population trend (Allen, 2017). However, climate change can pose a significant threat. High levels of warming (8.5 W/m² scenario) could reduce the current distribution area of *J. phoenicea* by over 90% by 2070 (Salvà-Catarineu et al., 2021). Drought-related mortality in many individuals of this species has been observed around the Sierra de Guara hills in Spain, particularly on rocky ridges (Camarero et al., 2020). Conversely, the

decline of intensive agriculture in dry, infertile areas and reduced grazing pressure due to declining flocks of sheep may facilitate the expansion of *J. phoenicea* into abandoned fields and pastures (Farris et al., 2009; García et al., 2014; Cano-Ortiz et al., 2015; García-Cervigon et al., 2017). However, reduced grazing can increase the risk of wildfires by allowing the accumulation of highly flammable dry organic matter. Consequently, the fires could potentially further reduce juniper populations. Post-fire regeneration in juniper species relies solely on seed germination (JM Montserrat personal communication; Camarero et al., 2022).

Juniperus phoenicea s.s. is conserved in areas across Spain, France, and Italy, established to protect terrestrial ecosystems (Picchi, 2008; Montesinos et al., 2009). The species has low economic value in forestry and, currently, no gene conservation programs are known to exist.

Juniperus turbinata is recognized as Near Threatened (NT) by the IUCN due to threats from expansion of tourism, and recreation (Farjon, 2020). These pressures are most significant on Mediterranean maritime sandy dunes (e.g., Mota et al., 1996; Kutbay et al., 2005; Anonym, 2009; Minissale & Sciandrello, 2013; Mazur et al., 2016, 2018), where intensive development of holiday resorts has extensively displaced natural habitats. Conversely, the Atlantic shores of Morocco and Portugal have experienced less invasive recreation pressure. During last decades, the intensive development of agriculture in the maritime regions around the Mediterranean Sea also substantially restricted occurrence of *J. turbinata* (Mota et al., 1996; authors' personal observations).

In semi-arid and arid regions of northern Africa and the Arabian Peninsula, *J. turbinata* remains an important source of wood for rural communities. Young twigs are also used as forage for goats and sheep during extremely dry periods. While grazing pressure may hinder regeneration (Martinis et al., 2018), *J. turbinata* is generally unpalatable to livestock (Rogosic et al., 2009, 2015). Overgrazing, dieback, and insufficient regeneration have been documented in Saudi Arabia near the species' southernmost range (El-Juhany, 2009, 2015). Similarly, grazing and tourism threaten *J. turbinata* in the forest reserves in Jordan (Alananbeh et al., 2023).

The dieback of *J. turbinata* due to drought and high temperatures is most severe in African and Arabian regions, including Cyrenaica (Libya), where abundant *J. turbinata* communities experience cyclical drought effects and high mortality during extremely dry periods (El-Barasi & Saaed, 2013; Moustafa et al., 2016; Al-Shaikhly et al., 2023). Similar patterns of drought-induced dieback have been observed in Sinai (Danin, 1983; El-Bana et al., 2010; Farahat et al., 2020) and Jordan (Alananbeh et al., 2023).

Climate models indicate that under high warming scenarios (8.5 W/m²), *J. turbinata*'s occurrence area may shrink by over 53% by 2070 (Salvà-Catarineu et al., 2021: Table 2; see also Arar et al., 2020; Dakhil et al., 2022; El-Barougy et al., 2023). The species' moderate longevity may allow persistence in some areas for a limited time, but trunk rot (Martinis et al., 2018) and winter or early spring droughts exacerbate dieback (Sánchez-Salguero & Camarero, 2020). Long-term reductions are also likely due to summer droughts and water deficits, which cause tree mortality across the species' range (Körner et al., 2005; Armas et al., 2010; Lloret & Granzow-de la Cerda, 2013; Díaz-Delgado et al., 2014; Lloret & García, 2016; Arar et al., 2020; Camarero et al., 2020).

Summer droughts increase the flammability of juniper plant communities, making wildfires a significant threat to *J. turbinata* (e.g. Pausas & Verdú, 2005; Pausas et al., 2004; Kutbay et al., 2005; Paula & Pausas, 2006; Papagiannaki et al., 2020). Frequent Mediterranean fires often kill *J. turbinata*, as the species does not regenerate from roots after fire events (Quevedo et al., 2007; Camarero et al., 2020). Although fires can restrict the occurrence of *J. turbinata* for extended periods, they may also promote expansion in some cases by eliminating competing tree species.

Juniperus turbinata currently occupies a relatively extensive geographic range (Boratyński et al., 2024), but its distribution is fragmented, with some populations consisting of a small number of individuals. These small populations are vulnerable to inbreeding and other threats (Lloret & García, 2016). In addition to the African populations mentioned earlier, small populations of *J. turbinata* are scattered along the Mediterranean coast in Spain and Italy. In Italy, efforts are underway to support the species through *ex situ* breeding and reintroduction programs (La Mantia et al., 2012; Minissale & Sciandrello, 2013; Romano et al., 2022).

The conservation status of *Juniperus canariensis* has not yet been formally evaluated using IUCN criteria. Historically, this species formed extensive forest communities in the Canary Islands and on the Madeira archipelago, but it has been significantly reduced. In Tenerife, the Guanches used juniper wood extensively for fuel (Tomé et al., 2022), and areas originally covered by juniper plant communities have been transformed into agricultural land (De Nascimento et al., 2016). Today, *J. canariensis* forms only scattered populations in the Canary Islands. Its historical exploitation, current fragmented distribution, and vulnerability to fires suggest that it may warrant a classification of Vulnerable or Endangered, though this should be verified.

Climate change poses an additional threat to *J. canariensis*, with models predicting a reduction in

its potential occurrence area by nearly 60% by 2070 (Salvà-Catarineu et al., 2021, 2023). On the Madeira archipelago, only a few isolated individuals remain, making the species nearly extinct locally, despite isolated specimens being planted in botanical gardens in Funchal and along roadsides. Efforts to reintroduce *J. canariensis* in the Canary Islands are ongoing (Boratyński et al., 2025) but need to be intensified.

Threats to Plant Communities

The juniper communities in southern Europe are primarily part of the order *Pistacio lentisci-Rhamneta-lia alaterni* and are protected under the Habitats Directive (92/43/CEE, 2013). These include habitats classified as “Arborescent matorral with *Juniperus* spp” (Annex I, code 5210) and “Coastal dunes with *Juniperus* spp” (Annex I, code 2250), the latter being a priority habitat for conservation. These habitats are often threatened by agricultural transformation, dune flattening, urbanization, and reforestation with alien tree species, which have significantly reduced their extent in regions like Sicily (Minissale & Scian-drello, 2013) and Sardinia (Pinna et al., 2015) and Crete (Delipetrou et al., 2015). On Lampedusa, agricultural activities initiated in the 1800s led to the near-total disappearance of *J. turbinata* scrub, leaving only a few relic individuals (Bartolo et al., 1988; La Mela Veca et al., 2003). Similar actions to conserve the coastal dune vegetation with junipers were conducted in Greece (LIFE+ programme, <http://junicoast.maich.gr/>), and in Cyprus (LIFE10 NAT/CY/000717/, <https://webgate.ec.europa.eu/life/publicWebsite/project/LIFE10-NAT-CY-000717/improving-the-conservation-status-of-the-priority-habitat-type-9560-endemic-forests-with-juniperus-spp-in-cyprus#description>). Restoration efforts on Lampedusa in recent years have shown promising results, with successful regrowth of junipers (La Mantia et al., 2012).

The Habitats Directive also recognizes “Endemic forests of *Juniperus* spp” (Annex I, code 9560), which include *Juniperus canariensis* forests classified as *Mayteno canariensis-Juniperion canariensis*. These mid-altitude forests are found on Tenerife, La Palma, El Hierro, Gran Canaria, and La Gomera and are characterized by a high number of endemic species. In all these islands, the extent of juniper forests has been significantly reduced due to historical exploitation for wood and the conversion of forests into agricultural or urban areas. Inaccessible areas such as ravines or steep slopes in Gran Canaria, Tenerife, and La Palma have allowed some individuals to survive. The best-preserved populations are found in La Gomera and El Hierro. In Tenerife, ecological restoration projects have been implemented in the Teno Massif, supported by the LIFE04/NAT/ES/000064 project (Otto

et al., 2006a; Fernández-Palacios et al., 2008). These projects have highlighted the difficulty of restoring areas where juniper forests have been completely lost, as seedling survival is higher in the presence of adult trees, which provide protection. Additionally, the climatic conditions during the first years after planting are crucial for restoration success.

Conclusions and perspectives

The understanding of the biology and ecology of the species within the *Juniperus phoenicea* complex has expanded significantly in recent decades due to research on their taxonomy, biogeography, morphology, biochemistry, genetics, ecology, and physiology (Boratyński et al., 2024, 2025). These studies have predominantly focused on *J. turbinata*, particularly its biochemistry, essential oil (EOS) composition, and traditional medicinal applications. In contrast, relatively fewer studies have been dedicated to *J. phoenicea* and *J. canariensis*. Nevertheless, the diversity and differentiation within the complex are now better understood, largely due to biochemical, genetic, and morphometric research. However, comprehensive studies across the entire distribution range of these species are still needed, particularly to clarify the unresolved intra-species diversification of *J. turbinata*.

The nutritional and pharmaceutical properties of the cones, as well as the medicinal and veterinary applications of various plant organs, are locally recognized but require further investigation. Similarly, research on overcoming seed dormancy and enhancing seed conservation is incomplete, despite its importance for long-term seed storage, *ex situ* breeding, and reintroduction efforts. Significant gaps remain in our understanding of the environmental requirements of these species, their interactions with other organisms, and their potential applications for ornamental purposes and erosion control. Several studies have highlighted the need for further research, such as those on dispersal, zoochory, germination, and resilience to climate change.

To address these gaps, future research should focus on:

- completing the chorological data and understanding the environmental conditions of species occurrence, particularly in the Arabian Peninsula and North Africa,
- establishing genetic resource banks and protected areas to conserve a sufficiently high number of populations across the geographic ranges of all species,
- experimental investigations of the relationships between these species and environmental factors such as light, temperature, and water availability in different regions of their distribution,

- examining interactions with animals, fungi, and other plant species.

Enhancing knowledge in these areas will enable better utilization of the species' unique properties and provide more effective protection for them.

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