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Distribution, floristic and ecological characterization of Sardinian Gymnospermae communities

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General introduction

1.1 **General information about Gymnosperms**

Gymnosperms represent an important part of the plant world. Despite being only 0.29% of the entire plant kingdom, compared to a total 89.4% of Angiosperms (Crepet & Niklas 2009), Gymnosperms are widespread in many areas of the world, sometimes dominating in density, cover and biomass over the other taxa (Farjon 2017). They are present in all continents, excepted Antarctica, and their distribution has often been enlarged by human activities (Eckenwlder 2009; Farjon 2017).

Conflicting studies about the origin of Gymnosperms and Angiosperms had been carried out, but it is still not well clear which were the dynamics related to speciation and separation of the various groups (Farjon 2008; Christenhusz *et al.* 2011). The Gymnosperms had been considered for a long time a distinctive group of plants and many unresolved problems and debates get involved the different groups (Earle 2021). Currently, molecular analyses have not removed issues as the origin of a presumed common ancestor within the different Gymnosperms. Besides, it is not resolved the doubt about the existence of a common ancestor shared both by the Gymnosperms and the flowering plants or Angiosperms (Eckenwalder 2009). According to Armstrong & Brasier (2005), Angiosperms would have been evolved from an advanced group of gymnosperms, but still controversial relationships occur between the two groups of seed plants. Palynological data report a first appearance of Angiosperms during the Early Cretaceous (Hughes & McDougall 1987) same era where the first record of the genus *Pinus* is known (Ryberg *et al.* 2012), while the earliest seed plants are known from the early Devonian (Hill 2005).

All the Gymnosperms are woody, mostly trees, shrubs, and vines (Earle 2021). Their name derives from the ancient Greek word *γυμνόσπερμος* (γυμνός, gymnós, "naked" and σπέρμα, spérma, "seed"), meaning "naked seeds". That is due to the condition of their ovules, which are not enclosed in a capsule (ovary) but are often naked (Farjon 2017).

The Gymnosperms are separated in two divisions, Gnetophyta and Pinophyta (Earle 2021): to Gnetophyta Bessey 1907 belong the three sub-classes Cycadidae Persoon ex Bercht. et J. Presl, Ginkgoidae Engl. and Gnetidae Pax ex Pranti.

Cycadidae is a subclass represented by the only order Cycadales Persoon ex Bercht. et J. Presl, in which are included three families: Cycadaceae L., Stangeriaceae L.A.S.Johnson, and Zamiaceae Horianow, for a total extent of about 290 species, mostly resembling palms (Earle 2021). All the species grow at tropical and subtropical latitudes, in all the continents excepted Europe (Jones 1993).

The subclass Ginkgoidae includes the order Ginkgoales Gorozh., with a single family, Ginkgoaceae Engl., consisting of the monotypic *Ginkgo biloba* L., which is considered a living fossil and is today very rare in the wild, being known in some small areas of south-western China, in the provinces of Guizhou and Zhejiang (Gong *et al.* 2008; Earle 2021).

The subclass Gnetidae has three orders: Ephedrales Dumort., Gnetales Blume ex von Martius, and Welwitschiales Skottsburg ex Reveal (Christenhusz *et al.* 2011). In the order Ephedrales is included one single family (Ephedraceae Dumort.) and one genus (*Ephedra* L.) composed by 61 taxa (Earle 2021). Many species grow in the Eurasia, others in Americas and Africa, normally in arid and semiarid environments from the sea level up to 5000 m a.s.l. in the Himalayan and Andean Chains (Price 1996). The order Gnetales is represented by the only family Gnetaceae Blume, with one genus (*Gnetum* L.) and 44 species (Earle 2021). Many of the species belonging to this family are vines and grow in south-eastern Asia (Carlquist 1996), while a smaller number of species is known in South America and in western Africa (Price 1996). Finally, the order Welwitschiales is represented by the monotypic family Wellwitschiaceae Caruel, with *Welwitschia mirabilis* Hooker, one of the strangest plants in the world, having only two leaves that constantly grow during all its life. It is limited to a small area of south-western Africa (Namib desert; Eller *et al.* 1983).

The division Pinophyta Raveal includes the only subclass Pinidae Cronquist, Takhtajan et Zimmermann, which is divided in three orders: Pinales Gorozh., Araucariales Gorozh., and Cupressales Link. To the order Pinales belongs the family Pinaceae Spreng. ex Rudolphi, with 232 species included in 11 genera (Farjon 2017). Almost all the entities of this family grow in the northern hemisphere, both in temperate and sub-arctic environments, as well as in sub-tropical areas (Farjon 2017). On the other hand, the order Araucariales includes two families, Araucariaceae Henkel et W. Hochstetter and Podocarpaceae Endl., that are mostly distributed in the southern hemisphere, while in the northern one they grow only on tropical regions (Farjon 2017): the Araucariaceae are divided in three genera (*Araucaria* Jussieu, *Agathis* Salisb., and *Wollemia* Jones, Hill et Allen) and about 40 species. The family Podocarpaceae is larger, including 18 genera and 174 species (Farjon 2017). The order Cupressales comprises three different families (Sciadopityaceae Luerss., Cupressaceae Rich. ex Bartling and Taxaceae Gray). The family Sciadopityaceae is monotypic, represented only by *Sciadopitys verticillata* (Thunberg) Siebold et Zuccarini, a tree growing in Japan (Tsukada 1963). The Cupressaceae family is the richest within conifers in genera, being 27, which include a total 143 species and subspecies (Eckenwalder 2009). It is also the most widespread conifer family, being known in all the continents excepted Antarctica (Earle 2021). Molecular analyses showed the former family Taxodiaceae C.N.Page was to include within Cupressaceae (Brunsfeld *et al.* 1994). Finally, the family Taxaceae is represented by 6 genera and 28 species, mostly diffused in the boreal hemisphere (Earle 2021).

This PhD research is focused on a specifical group of Gymnosperms, i.e. conifers (Pinophyta). Conifers characterise many natural environments, mostly in the northern hemisphere of the world (Eckenwlder 2009; Debreczy & Racz 2011; Farjon 2017).

Conifers can be distinguished from the other groups because they have some typical peculiarities: they are all shrubs or trees having secondary wood built of tracheids with large-bordered pits and narrow rays into their wall; simple leaves, single or parallel veined; reproductive organs divided in male (pollen cones) and female (seed cones) which can be compound or reduced. Almost all conifers have resin produced in the wood or in the leaves, which is conduced through resin canals. Moreover, they have a single copy of a large-inverted repeat in the chloroplast DNA, while the other plants have two copies (Farjon 2008).

The history of conifers dates to the late Carboniferous and is dotted with divergences and extinctions. Only 8 families out of 20 recorded by fossil records have reached the present time (Farjon 2008). The Mesozoic era, and particularly Cretaceous, can be called the “age of conifers” since they were then dominating among the vegetational stages worldwide. On the contrary, from the late Eocene (Tertiary era) a slow and constant decline of conifer species started, together with the retreat of remnant conifer stands to refugia where they became more adapt than their coexistent angiosperms (Farjon 2008). Another drastic conifer’s extinction phase began with the Pleistocene glaciations, which caused, especially in Europe, a stronger retreat of species previously diffused, so that this continent became poorer than other temperate zones (Farjon 2008). The Mediterranean basin excepted, since climatic conditions were more favourable for species more adapt to more temperate sites such as conifers (Farjon 2008).

In the last millennia, because of the anthropic interest for natural resources, since the Bronze Age (near 5000 years ago in the Near and Middle East), many conifers raised the attention of mankind, being them useful for naval industry, building, carpentry and arts (Atzei 2003; Debreczy & Raczy 2011; Farjon 2017). This interaction between humans and conifers concerned mostly the areas closely related to Mediterranean Basin (Barbéro *et al.* 1998): e.g. the massive cut of the Lebanon cedar forests for the ship industry and carpentry already started during the trade expansion of Phoenicians (Mikesell 1969). In the same way is attested the usage of cutting junipers for buildings in different countries of west-Mediterranean regions (Ruiz-Checa & Cristini 2013). *Pinus pinea* L. was already exported by Etruscan, Greeks and Romans because of its economic importance (Fady *et al.* 2004).

Thus, in addition to the natural woods, during the centuries several conifer species were planted worldwide for their timber, resins, bark, pine nuts, or ornamental purposes (Richardson 1998; Farjon 2008, 2017). In this respect, pines were among the most used trees for commercial, industrial and forestry meanings in the world (FAO 2001). Extended afforestation and reforestations with conifers, mainly pines, are now widespread in all continents inhabited by humans (Richardson 1998).

In Italy, and in other European countries besides, the extensive reforestations with exotic species started during the 19th century, later spreading for most of the 20th (Pavari & De Philippis 1941; D'Autilia *et al.* 1967; Richardson 1998). On the other hand, as reported before (Farjon 2008), the decrease of many taxa from their natural ranges, as well as their drastic reduction until the brink of extinction in the wild is not an exception in several contexts, as in the case of the following examples: - *Abies nebrodensis* (Lojac.) Mattei in the Madonie Mountain, in Sicily (Pasta & Troìa 2017): - *Picea omorika* Purkyne, that is now confined in a restricted area at the borders of Bosnia and Serbia (Aleksić *et al.* 2017): - *Pinus heldreichii* Christ subsp. *leucodermis* (Antoine) E. Murray, localised in a small part of southern Apennines and in the Balkan peninsula (Gargano & Bernardo 2006).

1.2 **Study area: the island of Sardinia**

The study area is the island of Sardinia (Italy). This is the second largest Mediterranean island after Sicily, with a surface area of about 24,090 km^2. Sardinia is located in the central-western part of the Mediterranean Basin and, together with Corsica and the Tuscan Archipelago, it constitutes an independent biogeographical province (Bacchetta *et al.* 2012; Fenu *et al.* 2014). This island has a high variety of geological substrates and of landscapes as well (Carmignani *et al.* 2001; Fois *et al.* 2017b). The climate is influenced by its current position in the centre of the western Mediterranean Sea, between 38° 51′ N and 41° 15′ N latitude and between 8° 8′ E and 9° 50′ E longitude. For this reason, its climate is typically Mediterranean, with dry summers and relatively wet and mild winters (Bacchetta *et al.* 2009; Canu *et al.* 2015).

For the high concentration of endemic plant species, Sardinia has been identified as a biodiversity hotspot of global and regional importance (Medail & Quezel 1997; Bacchetta *et al.* 2012; Cañadas *et al.* 2014). Woodlands and forests of Sardinia are mainly represented by oaks, both evergreen (*Quercus ilex* L. and *Q. suber* L.) and deciduous (*Q.* gr. *pubescens* Willd.). These formations have a wide ecological range and are widespread from coastal areas up to 1550 m a.s.l. (Bacchetta *et al.* 2009). Furthermore, particular soil-climatic conditions support the presence of mesophilic (e.g. *Ilex aquifolium* L., *Ostrya carpinifolia* Scop., *Populus tremula* L., *Taxus baccata* L.) as well as edafoxerophilous woods (*Juniperus* spp., *Olea europaea* L. var. *sylvestris* Brot., *Phillyrea latifolia* L., *Pinus pinaster* Aiton subsp. *pinaster*), often confined in small areas, which make the island very diverse in the vegetational aspect (Bacchetta *et al.* 2009).

In recent decades, Sardinia is experiencing a significant increase in the wooded areas (Puddu *et al.* 2012), a process that is characterizing also other European and Italian regions (Poyatos *et al.* 2003; Falcucci *et al.* 2007; Gehrig-Fasel *et al.* 2007; Barbati *et al.* 2013; Smiraglia *et al.* 2015). Nonetheless, in Sardinia as in other regions, from Punic and Roman ages, human activities often compromised many environments (Barreca 1974; Meloni 1975), through a constant impoverishment of natural resources due to long-term actions such as deforestations, industries, mining, quarries, wildfires, grazing, charcoal burning, agricultural and silvicultural practices (Saur 1929; Pavari 1935). This long process, which involved vast forested areas that were almost totally deprived of the earlier covering, became more evident especially during the 19th century (Beccu 2000; Caterini 2013). Furthermore, these areas were transformed in pastures by the intensive pastoralism and periodical wildfires (Desole 1964; Beccu 2000; Caterini 2013). The descriptions of Sardinia provided by the geographers during the first half of the 20th century (e.g. Le Lanneau 1941), as well as the aerial photographs, reflect this situation, showing it as an arid, poor, dry and woodless island. During this period, many tree species suffered a great decreasing, and between them several conifers such as pines and yews (*Taxus baccata*) (Desole 1948, 1960, 1964, 1966; Arrigoni, 1967). Several species of plants suffered a strong pressure, even finding themselves to the brink of the extinction (Fois *et al.* 2017a). Nonetheless, nowadays the island still retains fragmented old-growth forests. Among them, remarkable remnant stands with old-growth yews persist (Fantini *et al.* 2020). A complete and updated knowledge of the distribution, ecology and floristic aspects of these rare and scattered woods was not available in Sardinia, nor a comprehensive information on their conservation status and threats that might affect them as well.

1.3 **Conifer species in Sardinia**

From a distributional point of view, Europe is poorer in conifers than other regions of the Northern hemisphere, with only 36 native taxa (Tutin *et al.* 1993). The most represented family is Pinaceae, with 26 taxa included in four genera (*Abies* Mill.; *Larix* Mill.; *Picea* A. Dietrich; *Pinus* L.); the richest genus in Europe is *Pinus*, with 17 taxa, followed by the genus *Juniperus* L. with 13 taxa (Tutin *et al.* 1993). Additional 35 conifer species were introduced in Europe from other continents, mainly for timber, reforestations and dune stabilization works (Tutin *et al.* 1993).

In Italy, among a total occurring checklist of 8195 vascular plants taxa, only 24 native conifers (Pinopsida) are present (Conti *et al.* 2005; Bartolucci *et al.* 2018).

In Sardinia, 10 conifers grow, according to Bartolucci *et al.* (2018). Almost all these taxa are trees or tall shrubs (more than 5 m tall), while only one (*Juniperus communis* L. var. *saxatilis* Pallas) is strictly a shrub. In the island there are not endemic conifers, despite the high number of endemics (290 following Bacchetta *et al.* 2012). If compared to the neighbouring island belonging to the same biogeographical province, Sardinia is poorer than Corsica in the extent of conifer's woods. Despite the total extent of conifers occurring in Corsica is similar to Sardinian one, 10 taxa, some of them dominate vast portions of the first island, characterising the plant landscape, especially of the mountain areas (Reymann *et al.* 2015). On the other hand, in Sardinia the natural conifer dominated woods are more scattered and isolated (Bacchetta *et al.* 2009).

Among the Sardinian conifers, the family Cupressaceae, with the genus *Juniperus*, is richer than the others (*J. communis* s.l. - present with the var. *communis* and var. *saxatilis*, *sensu* Adams 2014 - *J. macrocarpa* Sibth. et Sm., *J. oxycedrus* L., *J. phoenicea* L. and *J. turbinata* Guss.). Pinaceae follow, with three species belonging to the genus *Pinus* (*P. halepensis* Mill., *P. pinaster* subsp. *pinaster*, *P. pinea* L.). Finally, the family Taxaceae is represented by only *Taxus baccata*. Among them, in this study we considered the species belonging to two families: Pinaceae and Taxaceae.

Studies on Sardinian conifers were rare during the 20th century and regarded mostly the distribution or the phytosociology of some species such as pines (Desole 1960, 1964; Arrigoni 1967; De Marco *et al.* 1984; Mossa 1990), and the distribution of yew as well (Desole 1948, 1966). On the other hand, during the first two decades of the 21st century several studies involved many different conifer species and habitats. Specifically, *Juniperus communis* var. *saxatilis* scrublands were described by Brullo *et al.* (2001); *J. macrocarpa* and *J. turbinata* coastal habitats were studied by Pinna *et al.* (2014, 2015); *Taxus baccata* phytosociological traits, habitat characterisation and response to browsing were studied by Bacchetta & Farris (2007); Farris & Filigheddu (2008); Farris *et al.* (2012). Nevertheless, many other features remain to be studied about conifers, as their distribution, ecology and floristic composition of their stands.

1.4 **The selected conifers and their features**

The analysed taxa in this study are the native conifers growing in Sardinia. Specifically, this work has been concentrated on four species, three of them belonging to the family *Pinaceae* (i.e. *Pinus halepensis*, *P. pinaster* subsp. *pinaster* and *P. pinea*) and *Taxus baccata*.

Pinus halepensis is considered a circum-Mediterranean species (Mauri *et al.* 2016; Farjon 2017; Pesaresi *et al.* 2017), although it has maximum presence in the western side of the basin (Fady *et al.* 2003; Mauri *et al.* 2016). Its altitudinal range is conditioned by its high distribution along the Mediterranean Basin, where it is normally limited to lowlands, reaching a maximum altimetry of 700-800 m a.s.l. in several countries, but even 2000 m a.s.l. in North Africa. This species is native also in Sardinia (Arrigoni 1967; Tutin *et al.* 1993; Bacchetta 2006; Arrigoni 2006; Farjon 2017, Pignatti 2017).

On the last decades, several studies have been carried out on *P. halepensis* stands, both from a distributional point of view and phytosociological (Arrigoni 1967; De Marco & Mossa 1980; De Marco & Caneva 1984). More recently, another work regarded the phytosociological study of woods growing in central-eastern Mediterranean area (Pesaresi *et al*. 2017).

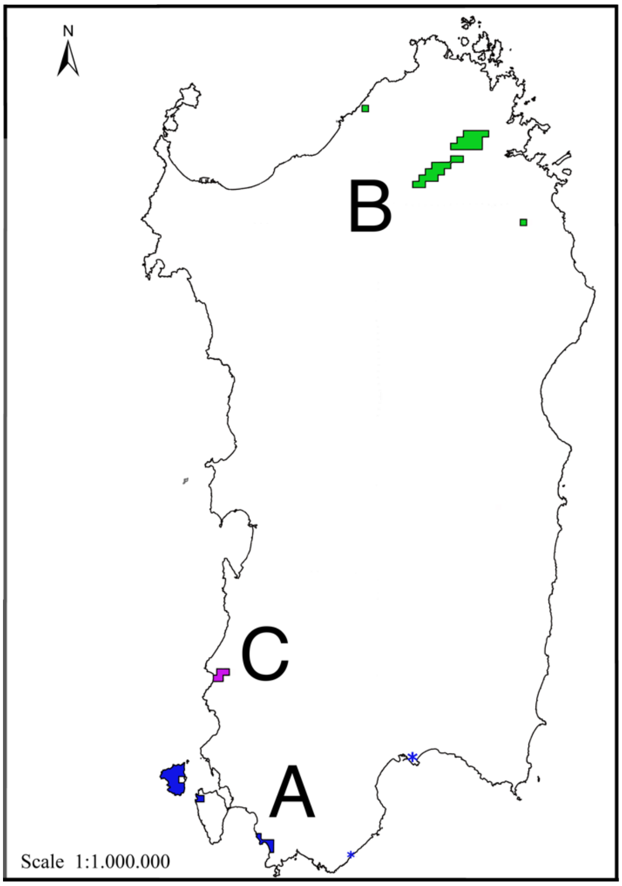

Figure 1 – Map of Sardinia showing the distribution of the three pine species considered native in Sardinia. A (blue) = Pinus halepensis *area; B (green) =* Pinus pinaster *subsp.* pinaster *area; C (purple) =* Pinus pinea *area. Asterisks show the doubtful stands of* P. halepensis *(Figure from chapter 2).*

Nowadays, the natural distribution of *P. halepensis* in Sardinia is restricted to the south-western part of the island, in the Sulcitano-Iglesiente sector: Island of San Pietro and coast between Porto Pino and Capo Teulada. Another small population exists at the extreme north-western border of the Island of Sant'Antioco (Figure 1). In the Island San Pietro, this species is the most typical tree, as well as along the coastal area between Porto Pino and the dune system of Is Arenas Biancas, then becomes scattered towards Capo Teulada in the municipalities of Sant'Anna Arresi and Teulada. On the contrary, it is difficult to establish whether on the Island of Sant'Antioco there would have been similar conditions to those of the neighbouring Island of San Pietro, since the tree cover of that island is, almost everywhere, disappeared after drastic cuts and wildfires. Doubtful stands are known in the hills around the city of Cagliari and along the southern coast (Santa Margherita di Pula).

Pinus pinaster subsp. *pinaster* has a distribution typically west-Mediterranean Atlantic, being naturally spread from the Tyrrhenian coasts of Italy to Portugal and from North-Africa to the Atlantic coasts of Spain and France (Richardson 1998; Farjon 2017). Some different subspecies were described: the subsp. *pinaster*, the typical subspecies, has been located only in the continental Atlantic sector of France, Spain and Portugal. The subsp. *renoui* (Villar) Maire, diffused in the western side of the Mediterranean area, should be located between the Tunisia, Algeria, Morocco and along the Spanish part of the Iberian Peninsula (Debreczy & Racz 2011). A third subspecies [*P. pinaster* subsp. *hamiltonii* (Ten.) Vill.] has been variously considered endemic to Sardinia and Corsica (Barbéro *et al*. 1998; Arrigoni 2006; Camarda & Valsecchi 2008), as well as of Pantelleria Island (Gianguzzi 1999a, 1999b). Otherwise, it is indicated another subspecies, *P. pinaster* subsp. *escarena* (Risso) K. Richt., spread in the Italian regions Latium, Liguria, Tuscany (Conti *et al*. 2005; Debrezcy & Racz 2011) and along the French Mediterranean coastal area. Recent studies tried to clarify the systematic differences among subspecies, showing that *P. pinaster* has a certain variability, but it is considered as a unique entity (Mariette *et al*. 2001, Bucci *et al*. 2007). More recently, *P. pinaster* subsp. *pinaster* has been reported in Latium, Liguria, Sardinia, Sicily, Tuscany (Biondi & Vagge 2015; Bartolucci *et al*. 2018).

The Sardinian distribution of *P. pinaster* subsp. *pinaster* is limited to four areas, all scattered on the Gallurese biogeographic sub-sector: Monti di Lu Pinu (near Costa Paradiso), Monti Ultana, Limbara massif and Monte Nieddu di Padru (Figure 1; Desole 1960, 1964; Veri & Bruno 1974; Brigaglia 1994; Calvia & Ruggero 2020). Historical data reported an older diffusion southward until the Baronico sub-sector (Angius 1851). *P. pinaster* subsp. *pinaster* is the pine species having, in Sardinia, the natural highest variety in elevation and ecological trends, growing from the coast to the tops of the Limbara massif (from 90 to 1250 m a.s.l.). Here too, the species has a current non-natural distribution in Sardinia, due to abundant reforestations throughout the island (Pavari 1935).

Sardinian woods dominated by *P. pinaster* subsp. *pinaster* were not framed into any plant association, unlike other Italian regions (Biondi & Vagge 2015) or Corsica (Reymann *et al*. 2015).

All the natural *P. pinaster* subsp. *pinaster* woods of Sardinia fall within the habitat 9540, while no natural stands are included in the priority habitat 2270* (European Commission 2013).

Pinus pinea is a broadly Mediterranean species diffused in many countries from Portugal and Spain to Turkey (Abad-Viñas *et al*. 2016). *P. pinea* had probably a wide distribution throughout the Mediterranean region, but it was enlarged (also in Sardinia) by abundant introductions in reforestations (Pavari 1935; D'Autilia et al. 1967) and plantations aimed at producing edible seeds (Richardson 1998). For this reason, it is unknown the original distribution area of the species (Abad-Viñas *et al*. 2016). *P. pinea* is typical of coastal areas, although capable of living inland (especially in Spain), and rarely reaches 500-600 m a.s.l. (Farjon 2017). From a geological point of view, it often thrives on sandy soils and siliceous substrates (Abad-Viñas *et al*. 2016).

The distribution of *P. pinea* in Italy is limited to the peninsular administrative regions, as well as in the islands of Sardinia and Sicily, but it is often originated by plantations (Pignatti 2017).

The first mention of this species in Sardinia was due to Moris (1827, *sub P. laricio*) in the area of Fluminimaggiore, Sulcitano-Iglesiente biogeographic sector of the island (Arrigoni 1967). Small, isolated stands still survive in the area between Fluminimaggiore and Buggerru, but they are currently surrounded by extended reforestations that today cover almost completely the vast dune system in where these pines grow naturally (Figure 1; Mossa 1990).

Despite in other regions phytosociological analyses were provided for *P. pinea* (Brullo *et al*. 2000), in Sardinia there were not yet deepened studies on this species (Bacchetta *et al*. 2009).

The priority habitat 2270* "Wooded dunes with *Pinus pinea* and/or *P. pinaster"* (Biondi *et al*. 2010; Bonari *et al*. 2018), mostly includes the reforestations with *P. pinea* sparsely spread on the island's dune systems.

Taxus baccata L. is a paleo-temperate species, which can be shrub or even becomes a large tree, long living and reaching a height of about 28 m (Thomas & Polward 2003). This species is spread in almost all continental areas of Europe and in Iran, appearing also in the Maghreb mountains (Algeria, Morocco) and the Azores Archipelago (Gianguzzi & La Mantia 2004; Schirone *et al*. 2010; Benham *et al*. 2016; Ahmadi *et al*. 2020). It is present also in Sicily, Sardinia and Corsica (Mazzola & Domina 2006; Bacchetta & Farris 2007; Jeanmonod & Gamisans 2013).

This species is currently considered rare and endangered in many countries (Thomas & Polwart 2003). Indeed, it is now locally extinct or progressively decreasing in many parts of Europe (García *et al*. 2000; Thomas & Polwart 2003; Iszkuło *et al*. 2016). The main causes of yew decline are climatic factors, human pressure, grazing, poor competitive ability, changes in rain distribution, droughts, fungal infections, dioecy related problems (Svenning & Magärd 1999; Thomas & Polwart 2003; Devaney *et al*. 2015). In southern Europe, and especially in the Mediterranean area, that represents the southern border of the species range, yew decline was often attributed to climate change (Thomas & García-Martí 2015).

The critical conditions of yew populations across their range have led to many concerns over its long-term future (Dhar *et al*. 2006; Linares 2013). The habitats with *T. baccata* are now protected and have priority status under the EU Habitats Directive (European Commission 2013). Its habitats (9580* - Mediterranean *Taxus baccata* woods and 9210* - Apennine beech forests with *Taxus* and *Ilex*) are listed as priority habitats in the European Habitat Directive 92/43/EEC (European Commission 1992).

In Italy, *T. baccata* is diffuse in all the administrative regions, although often rare (Pignatti 2017). In recent years, some studies have been carried out to explain different features concerning yew ecology and regeneration (e.g., Piovesan *et al*. 2009; Scarnati *et al*. 2009; Salis 2011). Between them, some studies interested specifically Sardinian yew populations (Bacchetta & Farris 2007; Farris & Filigheddu 2008; Farris *et al*. 2012).

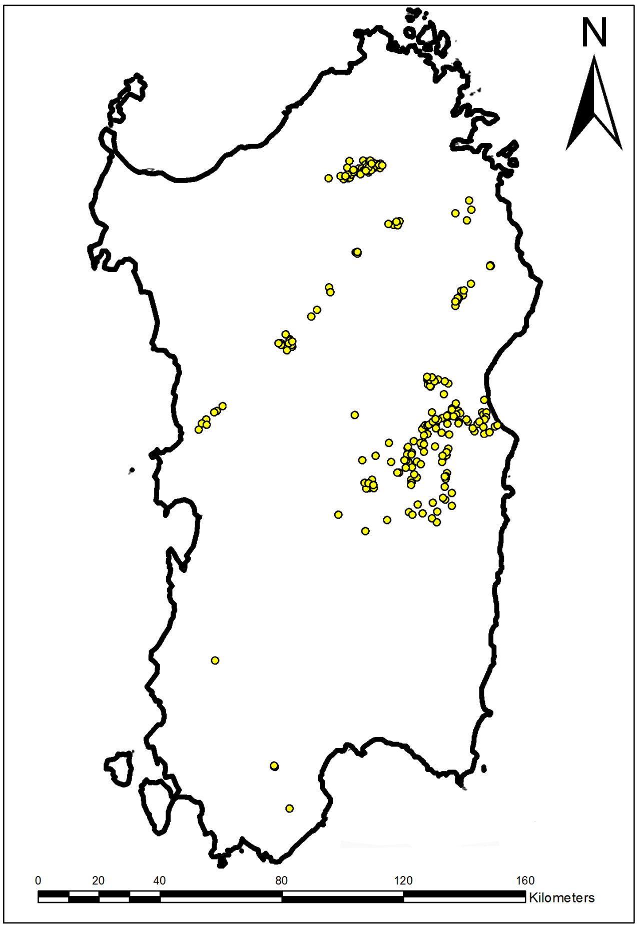

Figure 2 – Distribution of Taxus baccata *in Sardinia (Figure from chapter 3).*

In Sardinia *T. baccata* is scattered in almost all the mountain areas, being mainly diffuse in central and northern sectors, while only a few sites are known in the south-western one (Figure 2; Bacchetta & Farris 2007). In the past, yew has been studied by Desole (1948, 1966) and Chiappini *et al.* (1983). More recently its range was enlarged by Farris *et al.* (2012). In Sardinia, such as other Mediterranean areas (García *et al.* 2000; Thomas & Polwart 2003), yew occurrence is often limited to scattered individuals or small groups of trees within the understorey, located mainly in mountain areas, on shady northern slopes. Its elevation range in the island was reported to be comprised between 800-1200 m, but in particular conditions it grows at lower elevation, until 400-500 m and exceptionally at 45 m a.s.l. (Bacchetta & Farris 2007).

1.5 **Research objectives and structure of this thesis**

By updating the present and past distribution of native *Pinus* spp. and *Taxus baccata* in Sardinia, this thesis aimed at gathering both qualitative and quantitative data on populations and communities' extension, structure, and floristic composition. Diachronic analyses were also applied to better understand *Pinus* spp. expansion or contraction through time, in order to define long-term variation trends, while modelling the ecological niche of Sardinian *T. baccata* allowed us to compare its real vs potential distribution. All this information was

analysed in the framework of the Habitats Directive 43/92/EEC, with the aim to define the conservation status of the community habitats identified by native *Pinus* spp. and *T. baccata* stands.
During the first months of the study, the work was focused both on the literature search and on the analysis of all the information available through maps issued by the Military Geographic Institute (IGM, maps 1:25,000) and Local Ecological Knowledge (LEK). A following survey campaign was carried out from spring-summer 2018 to autumn 2020 in order to verify all the acquired information, provide phytosociological analyses (particularly for pine woods) and collect all the ecological information needed.

Chapter 1 –The knowledge of phytosociological features of the three types of pine woods growing naturally in Sardinia has been improved. *Pinus halepensis* plots (24) are located in south-western Sardinia and in the Island of San Pietro, growing often in coastal areas. Three different associations were found in this study: one typical of rhyolitic substrates on the Island of San Pietro, one new association typical of limestones on coastal areas and one new on sand dunes. *P. pinaster* subsp. *pinaster* plots (32) were analysed in the north-eastern sector of Sardinia, thriving on granitic substrates. They revealed the existence of a new association with two sub-associations, differentiated by climatic diversity. *P. pinea* plots (10) are confined in a dune system of the south-western Sardinia. The analysis showed the existence of a new association. This work produced a first characterization of the residual pine woods of Sardinia.

Chapter 2 – A diachronic analysis of the distribution of the three native or putative pine species of Sardinia was undertaken. We discussed where and how natural pine stands are currently diffused, emphasizing the increasing of two out of three wood types (i.e. *Pinus halepensis* and *P. pinaster* subsp. *pinaster*) in ca. 60 years. On the other hand, through literature, phytotoponyms and Local Ecological Knowledge (LEK) we were able to define a past reduction of the Sardinian areas where the two mentioned species grew. This reduction occurred mainly during the 19th century and the first half of the 20th century. Moreover, we defined the current amount of natural pine woods included in the two EU Habitats, priority habitat 2270* - "Wooded dunes with *Pinus pinea* and/or *P. pinaster"* and habitat 9540 - "Mediterranean pine forests with endemic Mesogean pines", highlighting how their total areas do not correspond to previous knowledges.

Chapter 3 – The distribution and ecology of *Taxus baccata* in Sardinia were studied. This work showed the current potential distribution of the species and its strong correspondence to the real distribution. In the field, we found a recent or current presence of yews in 234 localities, although most of these communities are mainly represented by a few samples per site, old trees and a scarce to absent renewal. Some exceptions were found in restricted areas. The presence of dead yews was also detected, highlighting how, in the absence of an adequate natural regeneration, the conservation value of this species is high and deserves future implementations at a regional level.

Chapter 4 – With the aim of evaluating the differences between *Taxus baccata* old-growth stands and younger ones, we evaluated several old-growth features such as amount of large size and old trees, tree species composition, canopy heterogeneity, amount of deadwood and recruitment, compared with different past and present human impacts. This work highlighted how the current human disturbance often affects residual stands with yews of Sardinia, thus not allowing a clear recognition of old growth stands even in those stands where larger trees are present. Moreover, this study showed that Sardinian woods with yew are suffering a general lack of renewal. Among the most disturbing human activities, livestock grazing has appeared to be the crucial factor that conditioned their conservation. Finally, we proposed conservation measures for the protection and recovery of the priority habitat 9580 in the island.

1.6 **References of introduction**

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Chapter 1

Classification of the Sardinian pine woods

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This manuscript is currently under review

Contribution to the project – I collected the data and organised the dataset. I participated to the analyses and realised the figures. I leaded the preparation of the manuscript, which was implemented and reviewed by the contributions of the co-authors.

Abstract – We described the woods dominated by *Pinus halepensis*, *P. pinaster* subsp. *pinaster*, and *P. pinea* in Sardinia (Italy). We analysed old and new data to test their differences and clarify their syntaxonomic position. We compiled a dataset of 66 original vegetation plots, complemented with the holotypes of similar vegetation types formerly described for Italy and Corsica (France). We classified *P. halepensis* woods, native to the Island of San Pietro (south-western Sardinia), to the association *Erico arboreae-Pinetum halepensis*. Also, we classified *P. halepensis* woods of south-western coast of Sardinia growing on limestones to the new association *Smilaco asperae-Pinetum halepensis* and stands typical of coastal dune to a new association *Asparago horridi-Pinetum halepensis*. We described the north-eastern Sardinia *P. pinaster* subsp. *pinaster* woods as the new association *Arbuto unedonis-Pinetum pinastri*, of which we recognised two new sub-associations, *pinetosum pinastri* and *cephalantheretosum longifoliae*, ecologically distinguished by the xerophilous and mesophilous conditions, respectively. Furthermore, we classified *P. pinea* woods, putatively native only to stabilised sand dunes of south-western Sardinia, in the new association *Querco calliprini-Pinetum pineae.* This study represents the first complete survey and classification of Sardinian pine woods, highlighting the relevance of these communities in the Mediterranean Basin.

Keywords – classification; Mediterranean Basin; phytosociology; *Pinetea halepensis*; *Pinus halepensis*; *Pinus pinaster*; *Pinus pinea*; Sardinia; vegetation.

1. **Introduction**

Mediterranean pine woods are one of the most common wooded types across the Mediterranean Basin (Barbéro *et al.* 1998). Many studies have analysed these communities, with an increasing ecological and phytosociological attention in the last decade (Biondi & Vagge 2015; Pesaresi *et al.* 2017; Bonari *et al.* 2018; Sarmati *et al.* 2019; Bonari *et al.* 2021). Recently, the new class *Pinetea halepensis* Bonari et Chytrý 2021 has been proposed. This class comprehends pine woods, specifically dominated by *Pinus brutia* Ten., *P. halepensis* Mill., *P. pinaster* Ait. subsp. *pinaster* and *P. pinea* L., thus resulting physiognomically different from the Mediterranean oak woods of the class *Quercetea ilicis* Br. Bl. ex A. Bolòs et O. de Bolòs in A. Bolòs y Vayreda 1950 (Bonari *et al.* 2021). Also, a large amount of information that was previously scattered among tens of local studies, was integrated in a specific electronic vegetation database (*CircumMed Pine Forest Database*, Bonari *et al.* 2019) that contributed to facilitate studies on pine woods. Nonetheless, a gap of knowledge remains concerning the phytosociology of these natural formations in some areas of the Mediterranean Basin. In this respect, the island of Sardinia results of crucial importance, being placed at the centre of the Tyrrhenian Sea and hosting three Mediterranean pines (*Pinus halepensis*, *P. pinaster* subsp. *pinaster*, and *P. pinea*) with an indigenous status (Arrigoni 2006; Pignatti 2017-2019).

From the phytosociological point of view, early studies about *P. halepensis* communities in Italy started in the second half of 20th century (Agostini 1964; De Marco & Mossa 1980; De Marco & Caneva 1984; De Marco *et al.* 1984). More recently, the phytosociological aspects of *P. halepensis* woods of the central-eastern Mediterranean area were reviewed (Pesaresi *et al.* 2017). The authors recognised five alliances and 25 associations, 15 of them diffused in Italy, while others present in France, Croatia, Albania and Greece (Pesaresi *et al.* 2017).

A few studies focused on *Pinus pinaster* woods in recent decades in Italy. These works considered the species' woods of the Island Pantelleria (Sicily; Brullo *et al.* 1977; Gianguzzi 1999) and the communities of north-western Italy as well, i.e. Liguria and Tuscany (Biondi & Vagge 2015). Other contributions exist for the nearby island of Corsica (France), where these woods have been classified at the syntaxonomic rank of sub-association (Gamisans 1977; Reymann *et al.* 2016). On the other hand, phytosociological analyses of *P. pinaster* subsp. *pinaster* stands are currently lacking for Sardinia (Bacchetta *et al.* 2009).

Italian studies regarding the phytosociological aspects of *Pinus pinea* woods are generally scarce. This is primarily linked to the fact that many stands have been planted. The natural communities are classified in two associations described for Sicily (Bartolo *et al.* 1994; Brullo *et al.* 2002). In Sardinia, the only putative native *P. pinea* population, firstly reported by Moris (1827), was studied by Mossa (1990), who provided a phytosociological table, without describing any association.

Mediterranean pine woods have a great conservation importance (Bonari *et al.* 2020), because they are included in different habitats of European interest (Habitats Directive 92/43/EEC). In coastal dunes, the habitat with Mediterranean and Atlantic thermophilous pines (*P. pinea*, *P. pinaster* subsp. *pinaster* and *P. halepensis*), including long-established plantations within their natural area of occurrence, is identified with the priority code 2270* (Wooded dunes with *Pinus pinea* and/or *P. pinaster*), while the other habitat with Mediterranean pines is identified with code 9540 (Mediterranean pine forests with endemic Mesogean pines) (European Commission 2013). Mediterranean pine woods are also classified under the code T3A in the EUNIS classification system (Chytrý *et al.* 2021).

In this study, we aim at describing the natural pine woods of Sardinia. Our specific aims were: (i) to test the differences of Sardinian relevés with previously described syntaxa from the Italian Peninsula, Sicily and Corsica, and (ii) to build an updated syntaxonomic scheme of Sardinian native pine woods.

2. **Material and methods**

2.1 Study area

Sardinia is the second largest island of the Mediterranean Basin, with an area of 24090 km², including manifold smaller islands and islets. The Hercynian granitic basement characterises the eastern half of the island, while effusive rocks predominate in the western part. Other important geologic formations are represented by metamorphic rocks, and sedimentary carbonate reliefs, which are present in many parts of the island from north to south, with a patchy distribution (Carmignani *et al.* 2001).

The climate of Sardinia is characterised by a typical Mediterranean seasonality, with mild-wet winters, and dry-hot summers. Mean annual temperature ranges between 11.6 °C and 18 °C, while annual rainfall ranges from 441 mm to 1134 mm (Bacchetta *et al.* 2009). Overall, two macro-bioclimates, seven thermotype belts, and 43 iso-bioclimates have been identified and mapped (Canu *et al.* 2015).

In the framework of the Italo-Tyrrhenian biogeographic super-province (Ladero-Alvarez 1987; Bacchetta *et al.* 2012), Sardinia falls in the context of the Sardinian-Corsican biogeographic province (Bacchetta *et al.* 2012), having a complex biogeography (Fenu *et al.* 2014).

2.2 Pine species of interest

Pinus halepensis (Aleppo pine) is a Circum-Mediterranean species (Fady *et al.* 2003; Mauri *et al.* 2016; Farjon 2017; Pesaresi *et al.* 2017). It is considered native to Spain, Balearic Islands, France, Italy, Sardinia, Sicily, Bosnia Herzegovina, Croatia, Montenegro, Albania, Greece, Turkey, Lebanon, Syria, Jordan, Israel, Morocco, Algeria, Tunisia and Libya, while it is doubtfully native to the Greek islands, Crete and Cyprus (Euro+Med 2006-2020). In Italy, *P. halepensis* is reported as native to many administrative regions, including Sicily and Sardinia, while it is absent in Piedmont and Val d'Aosta, casually introduced in Lombardy, Veneto and Friuli-Venezia Giulia, and naturalised in Trentino-Alto Adige (Bartolucci *et al.* 2018; Bartolucci *et al.* 2020). Its elevation range is normally limited to lowlands but can reach 1600 m a.s.l. in Spain (López González 2004), and 1700 m a.s.l. in Morocco (Farjon 2017). The species occurs on various substrates, but its optimum is on marls and limestones (Mauri *et al.* 2016), is thermophilous and drought-resistant, therefore preferring semi-arid to sub-humid ombrotypes, with an annual average rainfall comprised between 350 and 700 mm (Barbéro *et al.* 1998; Mauri *et al.* 2016). The woods dominated by this species are concentrated mainly in the western half of the Mediterranean Basin, while they are more scattered in the eastern half (Pesaresi *et al.* 2017). These woods have a typical open canopy and are frequently reported as aspects of garrigues or scrubland vegetation with scattered pines (e.g. Mauri *et al.* 2016).

Pinus pinaster s.l. (Maritime pine) is a western Mediterranean species (Abad Viñas *et al*. 2016a). It is native to Portugal, Spain, Balearic Islands, France, Corsica, Italy, Sardinia, Sicily, Morocco, Algeria, and Tunisia (Euro+Med 2006-2020). In Italy, *P. pinaster* subsp. *pinaster* is native only to Liguria, Tuscany, Sicily, and Sardinia (Bartolucci *et al*. 2018). This species grows in a broad elevation range, from the sea level to 1600 m a.s.l., in Spain and Corsica but can reach 2000 m a.s.l. in Morocco (Abad Viñas *et al*. 2016a). It is usually a heliophilous, thermophilous species, which prefers a climate with oceanic influence, and a minimum annual average rainfall of about 600 mm. For what concerns geology, it usually thrives on siliceous substrates, rarely growing on limestones (Abad Viñas *et al*. 2016a). The woods dominated by *P. pinaster* subsp. *pinaster* have an open canopy. They can be either mixed with oaks or monospecific, with a more or less thick understorey of sclerophyllous shrubs (Farjon 2017).

Pinus pinea (Stone pine) is a typical Mediterranean species, although its native distribution remains controversial due to long-established plantations (Bonari *et al*. 2017). This species grows in many Mediterranean countries, such as Portugal, Spain, Balearic Islands, France, Italy, Sardinia, Sicily, Croatia, Montenegro, Albania, Greece, Cyprus, Turkey, Syria and Lebanon (Euro+Med 2006-2020). In Italy, it is present in the peninsular regions, in Sicily and Sardinia, but widely planted (Pignatti 2017-2019). *P. pinea* is primarily a species of coastal areas, while in Spain and Portugal it grows also inland (Abad Viñas *et al*. 2016b) and can reach elevations up to 600 m a.s.l. (Farjon 2017). It has been defined as a heliophilous, xerophilous, and thermophilous plant, having an optimum of 600 mm per year (Abad Viñas *et al*. 2016b). In natural or semi-natural conditions, this species forms woods with an open canopy and a shrub layer that varies in thickness. Normally it is taller than the other co-occurring trees, sometimes forming mixed woods with other pines or oaks, e.g. *Quercus ilex* (Farjon 2017).

2.3 Data collection

To obtain an accurate distributional update of Sardinian natural pine woods, we retrieved references related to the natural distribution of the three pine species in Sardinia (Moris 1827; Desole 1960, 1964; Arrigoni 1967; De Marco & Mossa 1980; Mossa 1990; Bacchetta 2006; Bacchetta *et al*. 2009; Calvia 2016). During the years 2017-2019, we accomplished a vegetation survey of the natural stands growing in Sardinia, mainly based on the available cartography, but also making use of the knowledge of local people. Then, we performed vegetation plots within each of the areas dominated by one pine species. We also collected environmental features at each site, including elevation, slope, and substrate.

All the phytosociological sampling was carried out following the Zürich-Montpellier method (Braun-Blanquet 1965; Rivas-Martínez 2005). The names of vegetation ranks follow Mucina *et al*. (2016). We followed the fourth edition of the Internationale Code of Phytosociological Nomenclature (ICPN; Theurillat *et al*. 2020) for phytosociological nomenclature. We identified all plant species using Arrigoni (2006-2015), Jeanmonod & Gamisans (2013) and Pignatti (2017-2019). The plant names follow Euro+Med PlantBase (Euro+Med 2006-2020) and Bartolucci *et al*. (2018).

2.4 Data preparation and analyses

To investigate the differences in species composition in each of the three pine wood types, meaning that we followed the criterion of the pine species dominance, we prepared likewise comparative datasets comprising all the type relevés published, at the best of our knowledge (see the list of associations in the Appendix 1, Brullo *et al*. 1977; De Marco *et al*. 1984; De Marco & Caneva 1984; Bartolo *et al*. 1994; Brullo *et al*. 2002; Biondi & Vagge 2015; Pesaresi *et al*. 2017), for pine woods of Italy and Corsica, by requesting data to *CircumMed Pine Forest Database* (Bonari *et al*. 2019). Overall, we retrieved 14 relevés for *Pinus halepensis* woods from Italy and one from Corsica, 4 for *P. pinaster* subsp. *pinaster* woods from Italy and 2 for *P. pinea* woods from Sicily. Old data were merged with the new 66 relevés of our survey, overall resulting in 24, 32 and 10 plots for *P. halepensis*, *P. pinaster* subsp. *pinaster*, and *P. pinea* woods, and analysed together, thus obtaining one dataset for *P. halepensis* woods (39 relevés × 171 species; see Table 1 and Appendix 2), one dataset for *P. pinaster* subsp. *pinaster* (36 relevés × 107 species; see Table 2 and Appendix 2) and one dataset for *P. pinea* (12 relevés × 70 species; see Table 3 and Appendix 2). Before the analysis, we combined the cover values of same species present in different layers in a single layer. The cover of aggregation was calculated under the assumption that covers can overlap and that they do so independently of each other (see Tichý & Holt 2006).

We used TWINSPAN (Hill 1979) to classify the phytosociological relevés, setting the parameters of three pseudospecies cut levels (the "pseudospecies cut levels" value is the number of cut levels, while "values of cut levels" are the percentages corresponding to each cut level - Tichý & Holt 2006) of species percentage cover (0, 10, 25%) and minimum group size of two plots. We used different numbers of division for each dataset, resulting in eight, six and two for *P. halepensis*, *P. pinaster* subsp. *pinaster* and *P. pinea* clusters, respectively. We interpreted all the TWINSPAN clusters by comparing species composition, ecological characteristics and literature data, subsequently merging clusters in case of no substantial dissimilarities between them.

We defined diagnostic species for the clusters obtained by TWINSPAN and used the phi coefficient of association as fidelity measure calculated for equalised size of clusters following Tichý & Chytrý (2006). Diagnostic species were determined as species with phi coefficient ≥0.3 and Fisher's exact test value of the probability of the given concentration of species occurrences within the cluster <0.05. We defined constant species as those species with percentage occurrence frequency >20%, and dominant species as those occurring with a cover >20%.

The analyses were performed in JUICE program (Tichý 2002).

To display the accepted syntaxa in comparison with the holotypes of the previously described vegetation types, we plotted three DCA ordinations (Hill & Gauch 1980) of vegetation plots, computed with presence/absence species data and down-weighting of rare species in each dataset using the *vegan* package (v. 1.17-9; Oksanen *et al*. 2019) in R (v. 3.4.2; R Core Team 2019).

3. **Results**

Diagnostic, constant and dominant species for each syntaxon are reported in Appendix 2. For *Pinus halepensis* woods, we interpreted the TWINSPAN clusters at the third hierarchical level of division (dendrogram not shown). The first division mainly separated the calcifuge and base-rich pine communities. The second division separated the communities growing on the island of San Pietro and the woods on sand dunes. At the third level, the woods growing on the Porto Pino promontory were separated from the others on the base of a substantial poverty of species of the Sardinian communities.

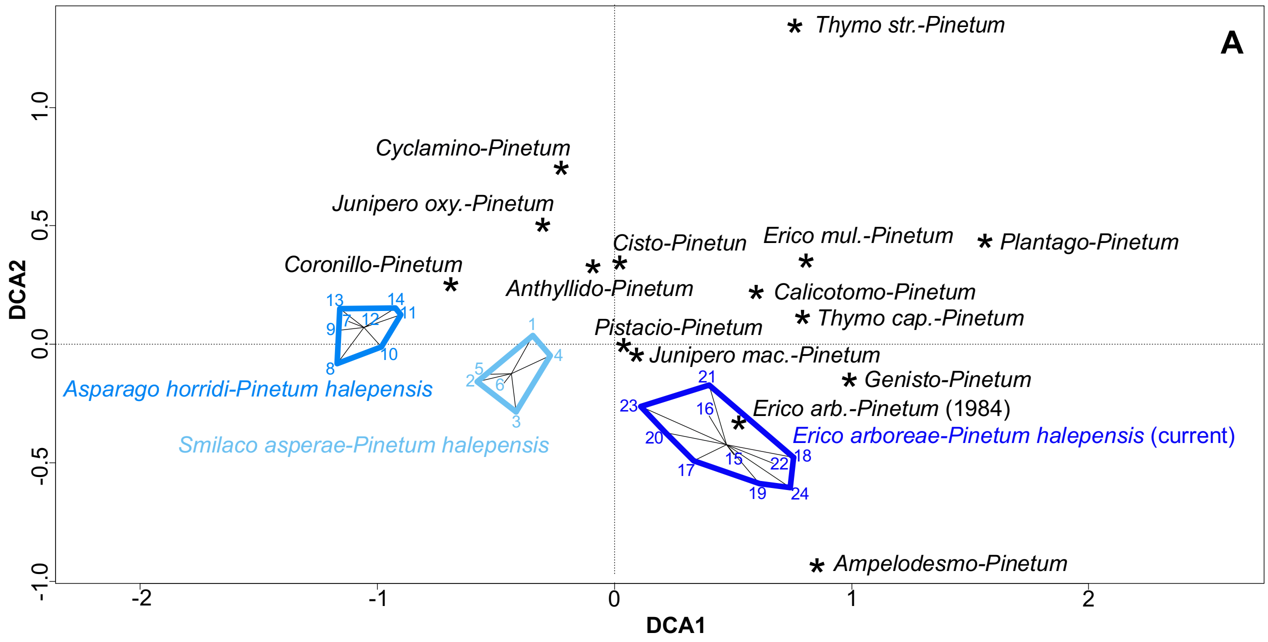
For *Pinus pinaster* subsp. *pinaster* woods, we interpreted TWINSPAN clusters at the third hierarchical level (dendrogram not shown). The first hierarchical division separated the sub-Mediterranean and Mediterranean *P. pinaster* subsp. *pinaster* types, suggesting the existence of two distinct alliances. The division at the second level separated the thermophilous and mesophilous Mediterranean communities. The third hierarchical level divided the Sardinian thermophilous communities from the Sicilian ones.

Finally, for *Pinus pinea* communities we interpreted TWINSPAN clusters at the first hierarchical level, where the Sardinian inland dune community and the Sicilian ones were separated (dendrogram not shown).

DCA ordinations, allowed us to show two vegetational communities clearly distinct from the previously described, a further four sub-associations, and a partial confirmation about one previously described association.

Pinus halepensis communities

The analysis of the 24 *P. halepensis* original relevés shows the presence of 3 groups, in agreement with the DCA, related to different ecological and edaphic conditions. The phytosociological table (Table 1) is reported in the Appendices. The clear floristic and ecological characterisation justify the presence of three associations, of which two are new.



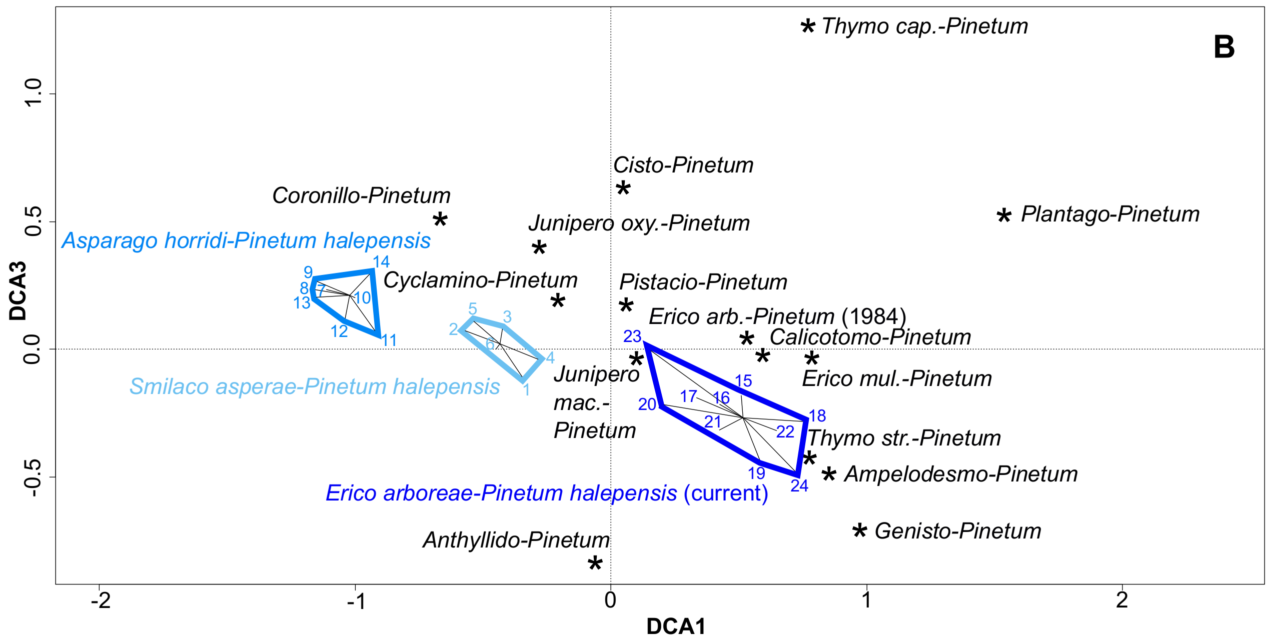


Figure 1 – Ordination diagram of the Italian Pinus halepensis *wood associations. The figure 1A of the ordination diagram represents the axes 1 and 2, while figure 1B represents the axes 1 and 3. Coloured relevés are new data from Sardinia. Asterisks represent type relevés of associations previously described. Full names of the syntaxa can be found in the Appendix 1. Current = This word refers to the current status of this vegetation type. See results and discussion for further explanation.*

Erico arboreae-Pinetum halepensis De Marco et Caneva 1984

Holotypus – Relevé no. 9 of table II in De Marco & Mossa (1980).

Diagnostic species – *Arbutus unedo*, *Cistus monspeliensis*, *Erica arborea*, *Lonicera implexa*, *Myrtus communis*, *Salvia rosmarinus* (Appendix 2).

Structure – Open to slightly open woods dominated by *Pinus halepensis*, from (4)8 to 10(14) m tall, with a dense understorey represented by sclerophyllous shrubs and a very poor herb layer, mainly with hemicryptophytes and geophytes. Moreover, there is a nearly total absence of those typical elements of garrigues (e.g. *Lotus dorycnium*, *Genista corsica* and *G. valsecchiae*) that were considered characteristic and differential of the association (De Marco & Mossa 1980). It is possible that these less evolved stages of vegetation are now present only as a variant in more degraded areas. The understorey of the community is rich in shrubs such as *Arbutus unedo*, *Erica arborea*, *Lonicera implexa*, *Myrtus communis*, *Phillyrea angustifolia*, *Pistacia lentiscus*. The presence of *Juniperus turbinata* is scarce. Other tree species, such as *Olea europaea* var. *sylvestris* and *Quercus ilex*, appear rarely in areas with deeper soil conditions and northern aspects.

Synecology – The geology of the Island of San Pietro, where this association occurs, is represented by Miocene volcanic formations such as ignimbrites, comendites, rhyolites, quartzites, and Quaternary sediments, like sands, arenites, travertine, and alluvial soils (Garbarino *et al.* 1985). Therefore, the association is calcifuge, typical of shallow soils and xeric conditions, and is present from the sea level up to 200 m a.s.l. Bioclimatically, it thrives in the Mediterranean Pluviseasonal Oceanic (hereafter MPO) bioclimate, from lower thermo-

Mediterranean to upper thermo-Mediterranean thermotypes, and from lower dry to upper dry ombrotypes (Bacchetta 2006; Canu *et al.* 2015).

Syndynamics – The community represents an evolved stage of the association *Erico arboreae-Pinetum halepensis* as it was previously described (De Marco *et al.* 1984; Pesaresi *et al.* 2017). Successional stages of the series are determined by shrubs belonging to the alliance *Oleo-Ceratonion siliquae* Br.-Bl. ex Guinochet et Drouineau 1944, garrigues of the class *Cisto-Lavanduletea stoechadis* Br.-Bl. in Br.-Bl., Molinier et Wagner 1940, and therophyte pastures of the alliance *Tuberarion guttatae* Br.-Bl. in Br.-Bl., Molinier et Wagner 1940 (Bacchetta *et al.* 2007). Our analyses did not allow to recognise the sub-associations *pinetosum halepensis*, *quercetosum ilicis* and *juniperetosum turbinatae*, which represent catenal contacts with more xeric formations (*Erico arboreae-Juniperetum turbinatae* Arrigoni, Bruno, De Marco et Veri 1985) and the mixed holm oak woods characterising the areas with a deeper soil.

Syntaxonomy – This association belongs to the order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014, the alliance *Pistacio lentisci-Pinion halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014, and the sub-alliance *Pistacio lentisci-Pinenion halepensis* Biondi et Pesaresi 2017 (Pesaresi *et al.* 2017).

Synchorology – This association spreads in many areas of the island of San Pietro (SW Sardinia), more specifically in the Sulcitano-Iglesiente biogeographic sector and Antioco-Carlofortino biogeographic sub-sector (Fenu *et al.* 2014), where it appears to be endemic (Pesaresi *et al.* 2017).

EUNIS code – T3A - Mediterranean lowland to submontane pine forests.

Habitats Directive code – 9540 - subtype no. 42.845.

Smilaco asperae-Pinetum halepensis Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. ass. nov.

Holotypus – Relevé n. 5 of Table 1.

Diagnostic species – *Arisarum vulgare*, *Quercus calliprinos*, *Smilax aspera*, *Stachys major* (Appendix 2).

Structure: Open woods, dominated by *Pinus halepensis*, from (2)10 to 12 m tall, represented by a dense understorey of sclerophyllous shrubs, with a rich presence of lianas and almost total absence of the herb layer. The understorey is mainly dominated by *Phillyrea angustifolia* and *Pistacia lentiscus*, with a relevant presence of *Juniperus turbinata* and *Quercus calliprinos*. Some geophytes are present in the herb layer, such as *Arisarum vulgare* and *Asparagus acutifolius*. Vines are diffused and often diagnostic and/or constant, such as *Rubia peregrina* and *Smilax aspera*.

Synecology – This association is found on coastal areas, mainly on base-rich substrates, from the sea level to 40 m a.s.l. They are the typical formations of Pleistocene conglomerates, mud deposits and limestones of Porto Pino promontory. Bioclimatically, they thrive in the MPO bioclimate, the lower thermo-Mediterranean thermotype, and lower dry ombrotype (Canu *et al.* 2015).

Syndynamics – This association is in series with the thermophilous shrub communities of the alliance *Oleo-Ceratonion siliquae*, and the garrigues of the class *Ononido-Rosmarinetea* Br. Bl. in A. Bolòs y Vayreda 1950 class (Bacchetta *et al.* 2007). Herb communities linked to the natural potential vegetation here described are the annual pioneer communities of the order *Brachypodietalia distachyi* Rivas-Mart. 1978. The association is in catenal contact with the associations *Rusco aculeati-Quercetum calliprini* Mossa 1990 and *Pistacio lentisci-Juniperetum macrocarpae* Caneva, De Marco et Mossa 1981 (Bacchetta *et al.* 2009).

Syntaxonomy: This new association belongs to the order *Pinetalia halepensis*, the alliance *Pistacio lentisci-Pinion halepensis*, and the sub-alliance *Pistacio lentisci-Pinenion halepensis*.

Synchorology – This association describes the endemic *P. halepensis* woods growing in coastal SW Sardinia, more specifically in the Sulcitano-Iglesiente biogeographic sector and Sulcitano biogeographic sub-sector (Fenu *et al.* 2014).

EUNIS code – T3A - Mediterranean lowland to submontane pine forests.

Habitats Directive code – 9540 - subtype no. 42.845.

Asparago horridi-Pinetum halepensis Calvia, Bonari, Angiolini, Farris, Fenu et Bacchetta ass. nov.

Holotypus – Relevé n. 11 of the Table 1.

Diagnostic species – *Asparagus horridus*, *Asphodelus ramosus*, *Juniperus macrocarpa*, *Pancratium maritimum*, *Silene canescens*, *Sixalix atropurpurea*, *Tolpis virgata* (Appendix 2).

Structure – Open woods dominated by *Pinus halepensis*, 5 to 10 m tall, often characterised by sparse patches of small pine trees with *Juniperus macrocarpa*. The understorey is represented by geophytes (i.e. *Pancratium maritimum*, *Sonchus bulbosus*) and shrubs (e.g. *Phillyrea angustifolia, Pistacia lentiscus*), with a rather dense presence of psammophilous hemicryptophytes and chamaephytes typical of the dunes, such as the species related to the alliance *Crucianellion maritimae* Rivas Goday et Rivas Mart. 1958 (i.e. *Crucianella maritima*, *Silene canescens*). *Asparagus horridus* often dominates the lower layer and is locally substituted by *A. acutifolius*, mainly in low-light conditions.

Synecology – This association grows in aeolian sand dunes. It is present both in foredune and in inner dune systems as long as 700 m from the seashore, from the MPO bioclimate, while the isobioclimate where the association thrives is a lower thermo-Mediterranean thermotype, lower dry ombrotype (Canu *et al.* 2015).

Syndynamics – The association is part of the Sardinian geosigmetum of coastal dune systems related to the association *Asparago acutifolii-Juniperetum macrocarpae* R. et R. Molinier ex O. Bolòs 1962 (Bacchetta *et al.* 2009). The chamaephyte communities are related to the association *Ephedro distachyae-Helichrysetum microphylli* Vals. et Bagella 1991, while the herbaceous layer is represented by aspects of the association *Sileno corsicae-Ammophiletum arenariae* Bartolo, Brullo, De Marco, Dinelli, Signorello et Spampinato 1992 and psammophilous therophytes belonging to the association *Sileno nummicae-Malcolmietum ramosissimae* Biondi et Bagella 2005. Locally, where these formations border the shores of the ponds, the association is in contact with the crassulent communities of the class *Salicornietea fruticosae* Br.-Bl. et Tx. ex A. Bolòs y Vaydera et O. Bolòs in A. Bolòs y Vayreda 1950.

Syntaxonomy – This new association belongs to the order *Pinetalia halepensis*, the alliance *Pistacio lentisci-Pinion halepensis*, and the sub-alliance *Pistacio lentisci-Pinenion halepensis*.

Synchorology: the association occurs exclusively in south-western Sardinia, on coastal dunes of the Gulf of Porto Pino (SW Sardinia), in the Sulcitano-Iglesiente biogeographic sector, and Sulcitano sub-sector (Fenu *et al.* 2014).

EUNIS code – T3A - Mediterranean lowland to submontane pine forests.

Habitats Directive code – 2270*.

***Pinus pinaster* subsp. *pinaster* communities**

The analysis of the 32 *P. pinaster* subsp. *pinaster* original relevés shows the presence of two groups, in agreement with the DCA, that related to different ecological conditions. The phytosociological table (Table S2) is reported in the Appendices. The floristic and ecological characterisation justify the presence of one new association, divided in two sub-associations.

Arbuto unedonis-Pinetum pinastri Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. ass. nov.

Holotypus – Relevé n. 4 of Table 2.

Diagnostic species – Arbutus unedo, *Bupleurum fruticosum*, *Erica arborea*, *Lonicera implexa*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Polypodium cambricum*, *Smilax aspera* (Appendix 2).

Structure: open to slightly open woods dominated by *Pinus pinaster* subsp. *pinaster*, (6)10 to 15(20) m tall, forming monospecific stands, sometimes with a lower tree layer characterised also by oaks (*Quercus ilex*, *Q. suber*). The understorey is dominated by sclerophyllous shrubs (e.g. *Arbutus unedo*, *Erica arborea*, *Myrtus communis*, *Phillyrea angustifolia*), and vines (e.g. *Lonicera implexa*, *Rubia peregrina*, *Smilax aspera*), while the herbaceous layer is not particularly rich neither in species (e.g. *Brachypodium retusum*, *Geranium purpureum*, *Pulicaria odora*, *Senecio lividus*, *Umbilicus rupestris*) nor in coverage.

Synecology: the association thrives on igneous intrusive substrates, where it normally occupies poor soil and rocky places, often with a steep slope. It is found along an elevation range from 90 to 1150 m a.s.l. The geology of the places where the association occurs is mostly related to equigranular monzogranites and equigranular leucogranites, which are the most common, while a very small portion of the northernmost locality (Costa Paradiso, Trinità d'Agultu) grows on sand and mud deposits of Pliocene-Pleistocene (Carmignani *et al.* 2001). The bioclimate is preferentially MPO, ranging from upper thermo-Mediterranean, upper dry in the most coastal zone, to lower supra-temperate (in sub-Mediterranean variant), lower humid in the central areas of Mount Limbara, where the highest formations grow (Canu *et al.* 2015).

Syndynamics – The association marks an edapho-xerophilous series, typical of areas characterised by poor and scarcely evolved soils, often in rocky and degraded places. Normally, the successional stages of these woods are related to shrub communities of the alliance *Ericion arboreae* (Rivas-Mart. ex Rivas-Mart. et al. 1986) Rivas-Mart. 1987, while the garrigue stage is mostly related to the alliance *Teucrion mari* (Gamisans et Muracciole 1984) Biondi et Mossa 1992. Finally, the herbaceous stage is connected to the communities of the alliance *Tuberarion guttatae* (Bacchetta *et al.* 2007). Locally, it has catenal contacts with some associations of the class *Quercetea ilicis*, such as *Galio scabri-Quercetum suberis* Rivas-Mart., Biondi, Costa et Mossa 2003, *Galio scabri-Quercetum ilicis* Gamisans (1977) 1986 and, only on the mountain areas, *Saniculo europaeae-Quercetum ilicis* Bacch., Bagella, Biondi, Farris, Filigheddu et Mossa 2004.

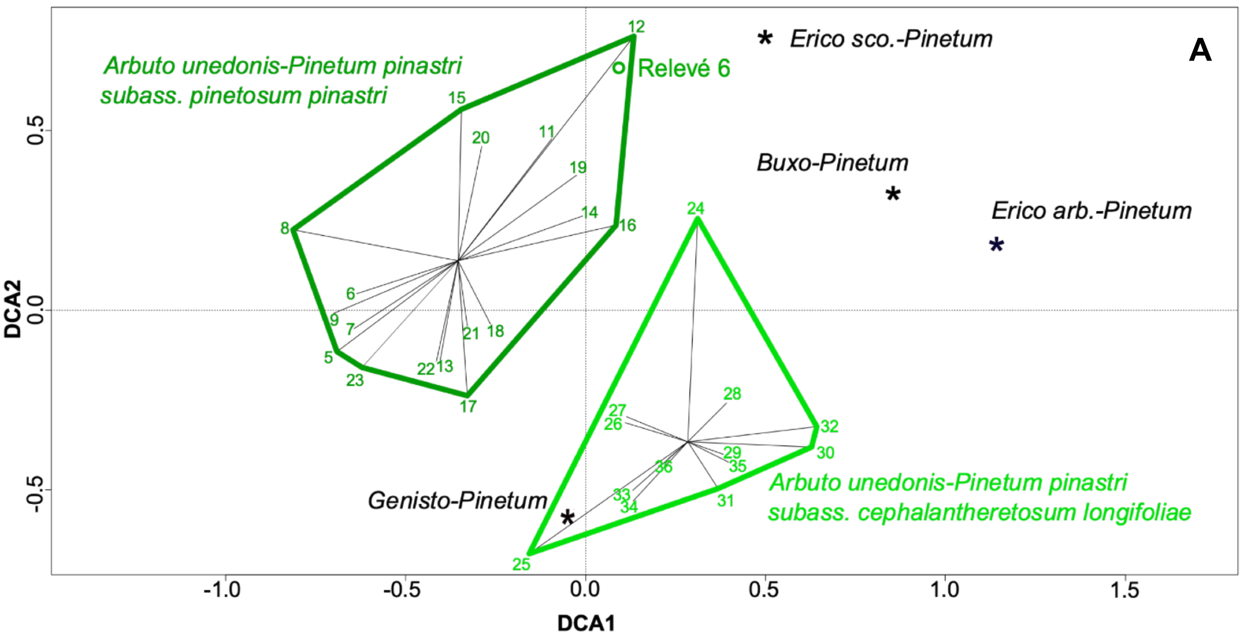
Syntaxonomy – The association is classified in the order *Pinetalia halepenis* and to the alliance *Genisto pilosae-Pinion pinastri* Biondi et Vagge 2015, although we found some differences in the species composition.

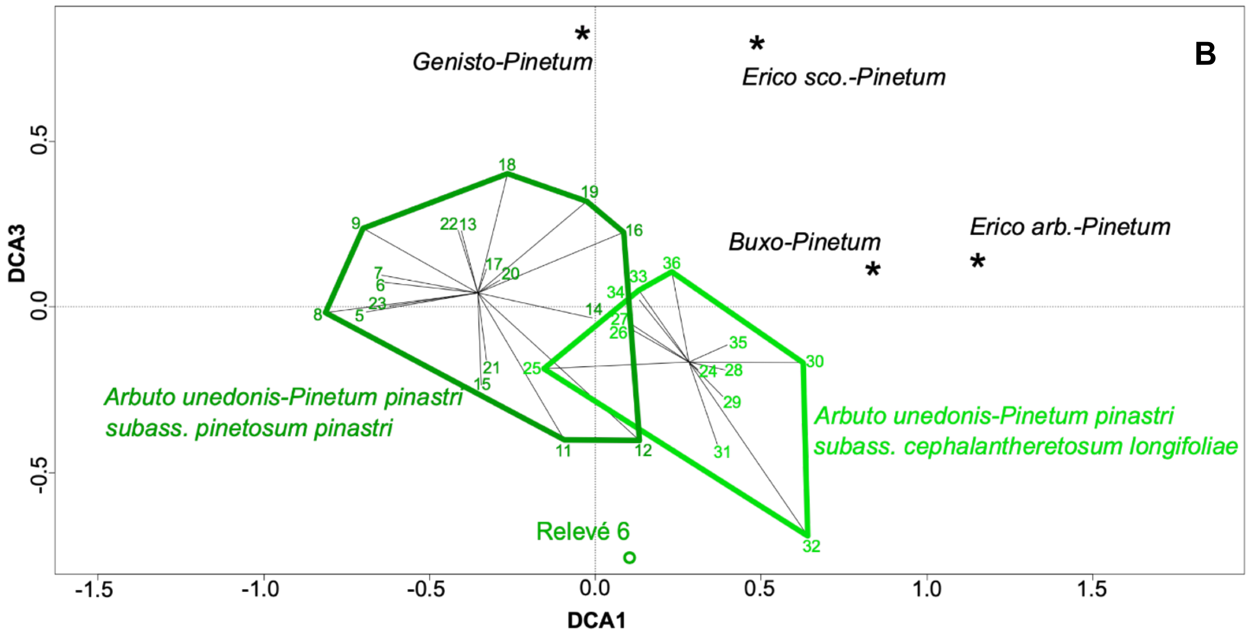
Synchorology: this association includes *P. pinaster* subsp. *pinaster* endemic woods growing on granitic substrates of north-eastern Sardinia, in the Goceano-Logudorese biogeographic sector and the Gallurese sub-sector (Fenu *et al*. 2014), from sub-coastal to mountain environments.

Variability: – Based on local bioclimatic differences, we distinguished two sub-associations that are characterised by a different species composition. The typical sub-association *pinetosum pinastri* is found in lowlands and hills with thermophilous and xerophilous species, e.g. *Bupleurum fruticosum*, *Lonicera implexa*, *Myrtus communis*, *Phillyrea angustifolia*, *Pistacia lentiscus*. The sub-association *cephalantheretosum longifoliae* is more related to mountain environments, with more mesophilous species, such as *Cephalanthera longifolia*, *Cytisus villosus*, *Fraxinus ornus* and *Viola alba* subsp. *dehnhardtii*. Our analyses evidenced one transitional plot relatively poor in diagnostic species, isolated from the others (Figure 2B, Table 2, rel. 6). It was recorded in an old-growth pine patch where the understorey shares a species composition belonging to both sub-associations.

EUNIS code – T3A - Mediterranean lowland to submontane pine forests.

Habitats Directive code – 9540 - subtype no. 42.825.





[Figure 2](#) – Ordination diagram of the Italian Pinus pinaster *subsp.* pinaster *woods. The figure 2A represents the axes 1 and 2, while figure 2B represents the axes 1 and 3. Coloured relevés are new data from Sardinia. Asterisks represent the type relevés of associations previously described. Circle indicates a single relevé placed at an intermediate position between the two sub-associations. Full names of the syntaxa can be found in the appendix 1.*

pinetosum pinastri Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. subass. nov. (Rel. 1-5; 7-19 in Table 2)

Holotypus – Relevé n. 4 of Table 2.

Diagnostic species – The same of the association (Appendix 2).

Structure – Open woods dominated by *Pinus pinaster* subsp. *pinaster*, (8)10 to 18(20) m tall, with a sparse to rather dense understorey, characterised by sclerophyllous shrubs, lianas and a scarce presence of sub-shrubs. Physiognomically, the understorey is characterised by woody sclerophyllous species, such as *Arbutus unedo*, *Erica arborea*, *Myrtus communis*, *Phillyrea angustifolia*, *Quercus ilex*, *Q. suber*, *Rhamnus alaternus*, and *Viburnum tinus*. The suffrutescent species and dwarf shrubs characteristic of the class *Cisto-Lavanduletea* are often limited to marginal areas in the open patches, where they appear as remnants of previous garrigues colonised by pines.

Synecology – This sub-association is found at lower elevations, on granitic hills, ranging from 90 to 650 m a.s.l. It thrives mainly on rocky places on southern aspect, while its bioclimatic range varies from the upper thermo-Mediterranean, upper dry, to the lower meso-Mediterranean, lower sub-humid (Canu *et al*. 2015).

Syndynamics – The sub-association represents the head series formation of the edapho-xerophilous and calcifuge sigmeta. It is sometimes in a catenal relation with the association *Galio scabri-Quercetum suberis*, and, locally, with the *Galio scabri-Quercetum ilicis*.

Synchorology – It has been recognised in the northern and central sides of Gallurese biogeographic sub-sector (Fenu *et al.* 2014), where it appears to be endemic, on the Monti Ultana chain, as well as in the restricted zone of Costa Paradiso (Trinità d'Agultu).

cephalantheretosum longifoliae Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. subass. nov. (Rel. 20-32 in Table 2)

Holotypus – Relevé n. 27 of Table 2.

Diagnostic species – *Cephalanthera longifolia*, *Cytisus villosus*, *Fraxinus ornus*, *Pteridium aquilinum*, *Rubus ulmifolius*, *Viola alba* subsp. *dehnhardtii* (Appendix 2).

Structure – Open woods dominated by *Pinus pinaster* subsp. *pinaster*, (8)10 to 15(18) m tall, with a rather thick understorey, represented by sclerophyllous shrubs and a scarce herbaceous layer, with rare therophytes and geophytes.

Synecology – This sub-association is found in mountain areas, mainly in the most edapho-xerophilous conditions, such as steep slopes and ridges, up to 1150 m a.s.l., thriving mainly on eastern aspects. In the mountain plateaus, it grows in very poor soils dominated by garrigue species, as a consequence of the past frequency of wildfires. However, locally it can be found also on deeper soils of the mountain slopes of Mount Limbara, between 500 and 700 m a.s.l.

Bioclimatically, this sub-association thrives on upper meso-Mediterranean, upper sub-humid, to lower supra-temperate, lower humid belts (Canu *et al.* 2015).

Syndynamics – In some of the most degraded areas, it represents the evolution of garrigues of the *Violo limbarae-Genistetum salzmannii* Vals. 1994. The sub-association is characterised by the presence of some species that are also part of the alliance *Genisto pilosae-Pinion pinastri*. Locally it appears to be in catenal contact with plant communities of the order *Quercetalia ilicis* Br. Bl. ex Molinier 1934. In particular, the *Galio scabri-Quercetum ilicis* in the lower part of its range, and the *Saniculo europaeae-Quercetum ilicis* at higher elevations (Bacchetta *et al.* 2009).

Synchorology – This sub-association is known in the inner part of Gallurese biogeographic sub-sector (Fenu *et al.* 2014), where it appears to be endemic and characterises the north-eastern side of the Limbara massif.

***Pinus pinea* communities**

The analysis of the 10 *P. pinea* original relevés shows a high affinity between them, therefore the presence of one group only, in agreement with the DCA. The floristic and ecological homogeneity justifies the existence of one association only. The phytosociological table (Table 3) is reported in the Appendices.

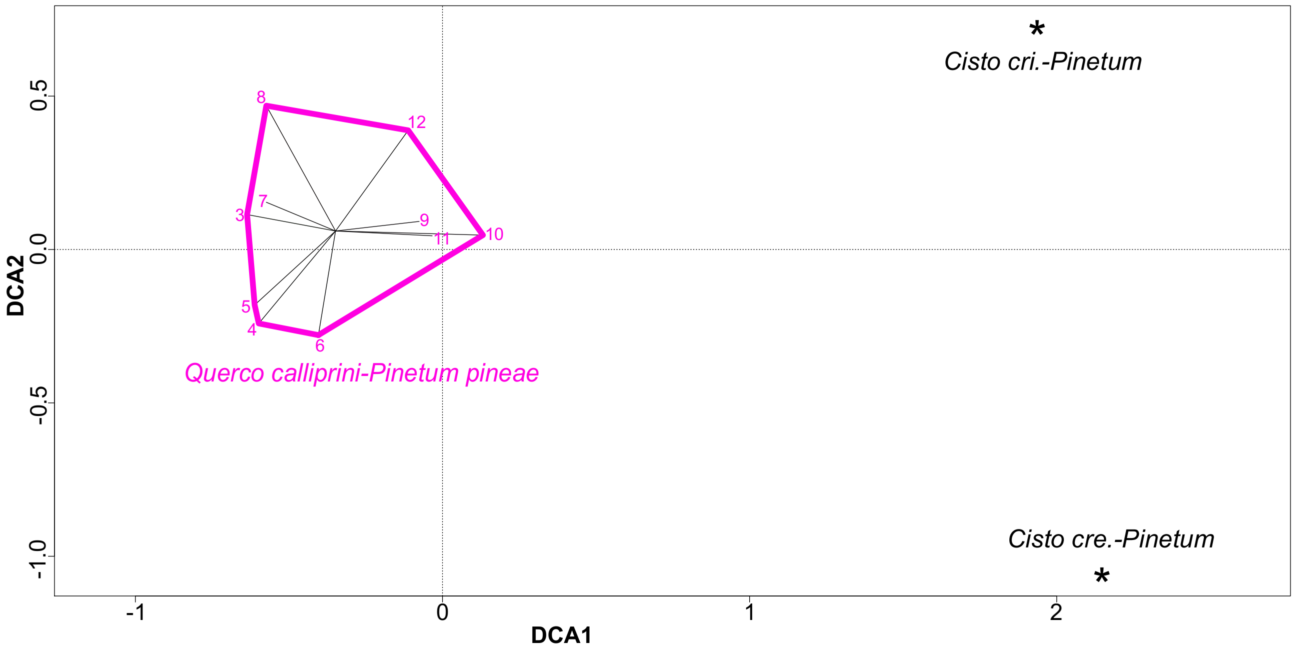


Figure 3 – *Ordination diagram of the Italian* Pinus pinea *woods. Figure 3 represents the axes 1 and 2. Coloured relevés are new data from Sardinia. Asterisks represent the type relevés of associations previously described. Full names of the syntaxa can be found in the appendix 1.*

Querco calliprini-Pinetum pineae Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. ass. nov.

Holotypus – Relevé n. 6 of Table 3.

Diagnostic species – *Juniperus macrocarpa*, *J. turbinata*, *Quercus calliprinos*, *Rubia peregrina* (Appendix 2).

Structure – Open woods dominated by *Pinus pinea*, (8)10 to 18(20) m tall. The tree layer is normally formed by pines, with a relatively sparse understorey of sclerophyllous shrubs. The herbaceous layer is often rich in therophytes, with rarer hemicryptophytes and geophytes. It is characterized by thermo-Mediterranean elements, with a relevant presence of psammophilous species, such as *Dianthus morisianus*, *Juniperus macrocarpa* and *Silene canescens*.

Synecology – The association thrives mainly on inner dune formations, between 10 and 200 m a.s.l. The natural *P. pinea* communities of Sardinia grow on Holocene sands, rarely extending on Ordovician meta-conglomerates. The bioclimate is MPO, with upper thermo-Mediterranean thermotype and upper dry ombrotype (Canu *et al*. 2015). The *P. pinea* formations grow mainly along ridges of the inner stabilised dunes, as well as on steep slopes facing both northern and southern exposures.

Syndynamic – The other stages related to this series are those of the associations *Pistacio lentisci-Juniperetum macrocarpae* Caneva, De Marco et Mossa 1981, *Crucianelletum maritimae* Br.-Bl. 1933 and *Rusco aculeati-Quercetum calliprini* Mossa 1990, of which it could represent a paraclimax (Mossa 1990).

Syntaxonomy – This new association is referred to the order *Pinetalia halepensis*, and to the informal group of Mediterranean *Pinus pinea* forests, in agreement with Bonari *et al*. (2021).

Synchorology – This association was detected only in the dune system of Portixeddu (Buggerru, SW Sardinia), in the Sulcitano-Iglesiente biogeographic sector and Iglesientino sub-sector (Fenu *et al*. 2014), where it appears to be endemic.

EUNIS code – T3A - Mediterranean lowland to submontane pine forests.

Habitats Directive code – 2270*.

4. **Discussion**

Our results allow us to describe six new syntaxa, including four associations and two sub-associations for the Sardinian pine woods.

The analyses of the vegetation plots dominated by *Pinus halepensis* evidenced a slight difference in composition with *Erico arboreae-Pinetum halepensis* described by De Marco *et al.* (1984). The understorey of the stands analysed in our study is richer in shrubs and poorer in chamaephytes, although in both cases the plots were species poor. Also, we did not find some of the diagnostic species highlighted by De Marco & Caneva (1984). This can be due to the fact that when the syntaxon was described the vegetation was not fully developed yet and perhaps rather related to the first phase of land abandonment (De Marco & Mossa 1980). For this reason, we believe there is no need to describe a new association. However, the floristic composition of our vegetation plots highlights the relation with the alliance *Pistacio lentisci-Pinion halepensis* (Pesaresi *et al.* 2017; Bonari *et al.* 2021).

The Porto Pino stands represent an association that, although is poor in species, deserves to be described as new, in contrast with former authors (De Marco *et al.* 1984; Pesaresi *et al.* 2017). The new association *Smilaco asperae-Pinetum halepensis* differentiates mostly in terms of synecologic, syndynamic, and synchorologic features. The species composition is similar to that of the *Pistacio lentisci-Pinetum halepensis*, although the DCA showed a certain distance between the two syntaxa. However, this association is represented mainly by shrubs and lianas, while the herb layer, including chamaephytes, abundant in the *Pistacio-Pinetum halepensis*, is here often nearly absent, as well as many differential species.

The composition of the new association *Asparago horridi-Pinetum halepensis* allows us to classify it within the alliance *Pistacio lentisci-Pinion halepensis*. It is differentiated from other psammophilous associations, like *Junipero macrocarpae-Pinetum halepensis* Biondi, Pesaresi et Vagge 2017 of Corsica, characterised by calcifuge species that totally lack in the Sardinian association. This finds support also in the fact that the dune system between Porto Pino and Capo Teulada has an aeolian nature where dunes are made up by the accumulation of sediments of organic origin and they are not made of intrusive and metamorphic rocks present in the catchment basin. The DCA showed a floristic similarity with the association *Cyclamino repandi-Pinetum halepensis* Biondi, Casavecchia, Guerra, Medagli, Beccarisi et Zuccarello 2004 from which it differs for a richer presence of psammophilous species. According to the DCA, the most closely related syntaxon to the new association would be *Coronillo emeroidis-Pinetum halepensis* Allegrezza, Felici et Biondi 2006. However, the ecology, as well as the species composition of the two syntaxa, are substantially different. The latter is characterised by the presence of species of the class *Querco roboris-Fagetea sylvaticae* Br.-Bl. et Vlieger 1937, which are absent in the Sardinian one.

Concerning the vegetation plots dominated by *Pinus pinaster* subsp. *pinaster*, we classified the new association *Arbuto unedonis-Pinetum pinastri* in the alliance *Genisto pilosae-Pinion pinastri*, described by Biondi & Vagge (2015), despite some differences in species composition. This alliance was described for the pine woods of *P. pinaster* subsp. *pinaster* growing on acid or decarbonated soils, rich in thermophilous evergreen species, diffuse along the Ligurian-Provençal sector. However, a broader analysis suggests that this alliance can grow on a variety of soils (Bonari *et al.* 2021). The higher presence, frequency and cover of West-Mediterranean and Circum-Mediterranean species of the Sardinian woods (e.g. *Brachypodium retusum*, *Myrtus communis*, *Phillyrea angustifolia*, *Quercus ilex*, *Q. suber*, *Rubia peregrina*), contrasts with the richer presence in Euro-Mediterranean species of the Ligurian-Provençal associations. From this point of view, *Arbuto unedonis-Pinetum pinastri* appears to be closer to the Sicilian association *Genisto aspalathoidis-Pinetum hamiltonii* Brullo, Di Martino et Marcenò 1977, from which, however, it differs for the higher presence of mesophilous elements. The Sicilian association is more xeric and differs from the Sardinian one in the characteristic species, as well as a remarkable presence of *Erica multiflora*, which in Sardinia is found on limestone rich soils only. *Pinus pinea* formations are included within the order *Pinetalia halepensis* and in the informal group of Mediterranean *P. pinea* forests. This informal group reflects the uncertainties at many Mediterranean sites about the origin of *P. pinea* stands (Bonari *et al.* 2021). Despite that, we speculate that the Sardinian association *Querco calliprini-Pinetum pineae* is probably the oldest *P. pinea* formation of Italy, known as a natural community since about 200 years (Moris 1827). On the basis of our analysis the new association *Querco calliprini-Pinetum pineae* is clearly separated from the previously described associations of Sicily (Brullo *et al.* 1977; Bartolo *et al.* 1994). The main difference is ecological, being the Sardinian formations characteristic of sand coastal dunes, while the Sicilian ones thriving inland and on rocky substrates (Gianguzzi et al. 2016). The floristic composition of Sardinian *P. pinea* woods is represented by several typical psammophilous species, which are lacking both in the *Cisto crispi-Pinetum pineae* Bartolo, Brullo et Pulvirenti 1994 and in the *Cisto cretici-Pinetum pineae* Brullo, Minissale, Siracusa, Scelsi et Spampinato 2002. The species belonging to the *Cisto-Lavanduletea* are nearly absent in the Sardinian *P. pinea* formations. Differently, Brullo *et al.* (2002) classified all the *P. pinea* associations described in Lebanon, Turkey and Sicily, within the class *Cisto-Lavanduletea*, the order *Lavanduletalia stoechadis* Br.-Bl. in Br.-Bl. *et al.* 1940 and the alliance *Pinion pineae* Feinbrun 1959. We should recall that classifying a forest syntaxon to an alliance of nanophanerophytes and chamaephytes is not optimal and might create problems in e.g. management. However, we followed the physiognomical approach for high ranks, in agreement with Bonari *et al.* (2021).

5. **Conclusions**

We provided the first updated and comprehensive vegetation knowledge of natural pine woods of Sardinia, with seven different syntaxa of Mediterranean pines, of which six are newly described. These syntaxa have an important chorological value within the Mediterranean context. Some of them have an extremely localized distribution range and have unique ecological features. Particularly, the limited distribution of native *Pinus halepensis* and *P. pinea* stands in Sardinia has a high phytogeographic importance. The conservation value of these communities is also relevant. For example, some of the syntaxa presented in this study are part of the priority habitat 2270* and they deserve to be protected, especially considering that they often grow in coastal environments threatened by human activities. This study provides the description and classification of the natural pine formations of Sardinia, allowing a better understanding of their ecology, floristic composition and differences with other Mediterranean pine woods.

Syntaxonomic scheme

PINETEA HALEPENSIS Bonari et Chytrý 2021
  - *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014
    - *Pistacio lentisci-Pinion halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014
      - *Pistacio lentisci-Pinenion halepensis* Pesaresi, Vagge, Galdenzi et Casavecchia 2017
        - *Erico arboreae-Pinetum halepensis* De Marco et Caneva 1984
        - *Smilaco asperae-Pinetum halepensis* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021
        - *Asparago horridi-Pinetum halepensis* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021
    - (?)*Genisto pilosae-Pinion pinastri* Biondi et Vagge 2015
        - *Arbuto unedonis-Pinetum pinastri* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021
          - *pinetosum pinastri* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021
          - *cephalantheretosum longifoliae* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021
    - Mediterranean *Pinus pinea* forests (informal group)
        - *Querco calliprini-Pinetum pineae* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2021

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Data availability

The data presented in this article are available in the *CircumMed Database* (GIVD code: EU-00026).

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7. **Appendices**

Table 1 – Smilaco asperae-Pinetum halepensis *ass. nova (holotypus: rel. n. 5);* Asparago horridi-Pinetum halepensis *ass. nova (holotypus: rel. n. 11);* Erico arboreae-Pinetum halepensis *De Marco et Caneva 1984.*

			1	2	3	4	5*	6	7	8	9	10	11**	12	13	14	15	16	17	18	19	20	21	22	23	24	Occurrences
			Smilaco asperae-Pinetum halepensis						***Asparago horridi-Pinetum halepensis***								***Erico arboreae-Pinetum halepensis***										
		Elevation (m a.s.l.)	41	38	31	30	29	33	4	4	5	5	4	3	14	15	27	26	151	152	154	133	132	83	81	82	
		Aspect	NE	NE		NNE	NE	NE	NE	NE	NE	NE	NE	NE	NW	NW					E	NE	ENE	SW	SW	ENE	
		Slope (°)	2	2		3	2	2	3	3	3	3	3	3	12	5					8	6	5	12	10	20	
		Substrate	Dolo	Dolo	Dolo	Dolo	Dolo	Dolo	Dune	Dune	Dune	Dune	Dune	Dune	Dune	Dune	Ryo	Ryo	Ryo	Ryo	Ryo	Ryo	Ryo	Ryo	Ryo	Ryo	
		Rockiness (%)															8	5			10			20	10	25	
		Stoniness (%)															2	2	5	5	5	2		5	10	2	
		Area (sq. m)	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	
		Canopy cover (%)	95	90	90	90	100	85	80	90	95	90	95	95	85	90	85	90	95	85	80	100	100	90	90	85	
		Mosses-lichens cover (%)	3	2	2	5	2	5											2		20	15	15			10	
		Average height of vegetation (m)	10	10	10	10	12	12	6	5	7	6	5	6	4,5	6	6,5	7	8	9	9	10	8	4,5	10	12	
		Number of species	10	9	10	11	12	10	15	13	15	14	15	15	10	11	10	8	10	12	14	11	12	10	10	10	
Chorotype	Bio form																										
		Ch. and diff. of ass. *Smilaco asperae-Pinetum halepensis*																									
Circum-Medit.	NP	*Prasium majus* L.	+	+	.	+	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	7
Circum-Medit.	P lian	*Smilax aspera* L.	+	+	+	2	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Circum-Medit.	G rhiz	*Arisarum vulgare* L.	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	5
E-Medit.	P caesp	*Quercus calliprinos* Webb	.	.	2	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
		Ch. ass. *Asparago horridi-Pinetum halepensis*																									
Circum-Medit.	P caesp	*Juniperus macrocarpa* Sm.	.	.	.	.	.	.	2	3	2	3	2	3	3	3	.	.	.	.	.	.	.	.	.	.	8
Circum-Medit.	H scap	*Tolpis virgata* (Desf.) Bertol.	.	.	.	.	.	.	+	1	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	7
Circum-Medit.	G rhiz	*Asphodelus ramosus* L.	.	+	.	.	+	.	+	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	7
Circum-Medit.	G rhiz	*Asparagus horridus* L.	.	.	.	.	.	.	1	+	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	6
Circum-Medit.	G bulb	*Pancratium maritimum* L.	.	.	.	.	.	.	.	+	+	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	5
Circum-Medit.	T scap	*Silene canescens* Ten.	.	.	.	.	.	.	+	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	5
Circum-Medit.	H bienn	*Sixalix atropurpurea* (L.) Greuter & Burdet	.	.	.	.	.	.	+	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	4
		Ch. ass. *Erico arboreae-Pinetum halepensis*																									
Circum-Medit.	P caesp	*Erica arborea* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	3	2	1	2	3	1	2	10
Circum-Medit.	NP	*Salvia rosmarinus* Spenn.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	1	+	+	+	+	.	+	1	+	.	10
Circum-Medit.	P caesp	*Myrtus communis* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	2	1	1	1	2	1	.	8
Circum-Medit.	P lian	*Lonicera implexa* Aiton	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	1	+	+	.	.	.	7
Circum-Medit.	P caesp	*Arbutus unedo* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	1	3	1	.	1	.	2	7
Circum-Medit.	NP	*Cistus monspeliensis* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+	+	4
		Ch. *Pistacio-Pinion halepensis*: *Pinenion halepensis*																									
Circum-Medit.	P caesp	*Phillyrea angustifolia* L.	1	2	2	3	2	1	.	+	.	+	.	1	.	+	3	2	3	2	1	4	2	2	3	1	20
Circum-Medit.	P caesp	*Rhamnus alaternus* L.	.	.	.	.	+	.	.	.	+	.	.	1	+	1	.	.	.	.	.	+	.	.	+	.	7
		Ch. and diff. *Pinetalia halepensis*																									
Circum-Medit.	P scap	*Pinus halepensis* L.	5	5	4	5	4	5	5	4	4	4	5	4	3	4	5	5	5	5	4	5	4	5	5	4	24
Circum-Medit.	P caesp	*Pistacia lentiscus* L.	4	2	2	3	2	2	+	1	1	+	2	1	+	1	2	2	2	1	2	1	3	1	2	2	24
Circum-Medit.	G rhiz	*Asparagus acutifolius* L.	+	1	+	+	+	1	+	1	2	+	1	+	+	+	.	.	+	+	+	+	+	.	.	.	19
Circum-Medit.	P lian	*Rubia peregrina* L.	+	+	+	+	1	+	+	1	1	+	+	1	+	1	.	.	+	.	+	+	.	.	+	.	18
Circum-Medit.	P caesp	*Juniperus turbinata* Guss.	2	3	2	+	2	3	.	2	3	2	1	2	+	.	1	1	.	.	.	.	1	+	2	.	17
Medit-Turan.	NP	*Cistus salviifolius* L.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	+	4
Circum-Medit.	P scap	*Olea europaea* L. var. *sylvestris* Brot.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1
		Ch. *Quercetea ilicis*																									
Circum-Medit.	P scap	*Quercus ilex* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	2	2
Circum-Medit.	H caesp	*Carex distachya* Desf.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
		Others																									
Medit-Turan.	H caesp	*Piptatherum miliaceum* (L.) Coss ssp. *thomasii* (Duby) Freitag	+	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
SW-Medit.	G bulb	*Romulea ligustica* Parl.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	3
Subendem. Sa Co AT HI Bl	Ch suffr	*Teucrium marum* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	2
Circum-Medit.	Ch suffr	*Crucianella maritima* L.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Circum-Medit.	H scap	*Lobularia maritima* (L.) Desv.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	2
Circum-Medit.	G bulb	*Sonchus bulbosus* (L.) N.Kilian & Greuter	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	2
Circum-Medit.	H scap	*Reichardia picroides* (L.) Roth	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	2
Subendem. Sa Co Bl	G bulb	*Brimeura fastigiata* (Viv.) Chouard	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	2
		Accidental taxa: 12	.	.	.	1	.	1	2	1	2	.	.	.	1	1	.	.	.	.	1	.	.	2	.	.	

Date and locality of the relevés

Table 1: 1-3, 5-6, Pineta Candiani, Sant'Anna Arresi, 31-05-2018; 4, Pineta Candiani, Sant'Anna Arresi, 04-06-2019; 7-12, Porto Pino, Sant'Anna Arresi, 31-05-2018; 13-14, Porto Pinetto, Sant'Anna Arresi, 04-06-2019; 15-24, Island of San Pietro, Carloforte, 26-03-2019.

Sporadic taxa

4: *Brachypodium retusum* (Pers.) P.Beauv. +; 6: *Calicotome villosa* (Poir.) Link +; 7: *Euphorbia segetalis* L. 1, *Plantago crassifolia* Forssk. 1; 8: *Leontodon tuberosus* L. +; 9: *Carex flacca* Schreb. +, *Schoenus nigricans* L. +; 13: *Lagurus ovatus* L. +; 14: *Pulicaria odora* (L.) Rchb. +; 19: *Stachys glutinosa* L. +; 22: *Anacamptis papilionacea* (L.) R.M.Bateman, Pidgeon et M.W.Chase +, *Genista sardoa* Vals. +.

Table 2 – Arbuto unedonis-Pinetum pinastri *ass. nova (holotypus: rel. n. 4);* pinetosum pinastri *subass. nova (holotypus: rel. n. 4);* cephalantheretosum longifoliae *subass. nova (holotypus: rel. n. 27).*

			1	2	3	4*	5	7	8	9	10	11	12	13	14	15	16	17	18	19	6	20	21	22	23	24	25	26	27*	28	29	30	31	32	Occurrences
		Elevation (m a.s.l.)	220	228	230	210	187	415	380	420	310	280	299	290	425	102	574	666	613	562	426	765	1010	835	1010	930	1001	965	918	1140	1023	995	1010	957	
		Aspect	SW	NW	NNW	S	S	NW	NE	SE	NE	SE	WSW	S	ENE	W	SSW	SE	SW	SW	NW	SSE	WSW	SSE	SE	SE	NNW	NE	ENE	E	NE	WSW	WSW	NW	
		Slope (°)	15	8	15	18	25	10	10	28	12	33	12	10	30	6	12	17	20	30	18	15	7	17	10	14	5	10	22	10	15	3	5	5	
		Rockiness (%)	25	37	45	35	20	5	2	50	8	20	40	55	65		10	30		25	30	20	45	25	2	18	12	5	40		65	10	5	5	
		Stoniness (%)	10	12	5	5	10	5	5	5	5	15	20	20	10	5	25	25	20	60	5	10	5	10	20	10	8	10	20	40	25	8	2	25	
		Mosses-lichens cover (%)	15	30	35	15	30	10		45	5	3	30	20	50		5	20	1	15	20	5	45	35	5		2	5	35	20	50	5	2	10	
		Forest litter (%)	20	60	40	45	40	50	95	30	50	90	70	50	30	90	70	70	85	80	60	80	35	35	60	80	75	40	45	90	50	80	85	55	
		Bare soil (%)	15	10	5	10	7	5	1	2	2	5	1	5	5	5	12	2	5	5	2	1	18	12	3		3	5	8			1			
		Canopy cover (%)	75	90	80	80	90	98	80	75	90	90	85	80	90	95	90	95	75	75	80	90	90	90	80	90	95	85	90	100	80	80	75	85	
		Average height of vegetation (m)	6	6	7	6,5	7,5	9	8	7	9,5	13	9	10	7,5	13	9	12	10	8	18	10	10	8	7	9	10	8	13	15	12	10	12	7	
		Substrate	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	Granites	
		Area (sq. m)	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	
		Number of species	16	16	15	16	21	15	16	20	14	15	13	12	19	19	14	13	14	12	16	15	14	13	14	15	11	17	18	18	7	13	12	13	
Chorotype	Bio form																																		
		Ch. and diff. of ass. and subass. *pinetosum pinastri*																																	
W-Medit. Atl.	P scap	*Pinus pinaster* Aiton	5	4	4	4	4	4	3	4	5	5	5	5	4	5	5	5	5	5	5	5	5	4	5	5	5	5	5	5	5	5	5	4	32
Circum-Medit.	P caesp	*Erica arborea* L.	2	3	3	2	2	3	3	3	2	1	2	1	2	3	+	3	3	2	.	2	2	3	3	3	2	3	1	3	3	3	3	4	31
Circum-Medit.	P scap	*Arbutus unedo* L.	2	3	3	2	2	2	2	2	2	1	2	1	2	1	3	1	2	3	2	1	.	2	1	2	.	2	2	+	2	3	1	3	30
Subtrop.	P lian	*Smilax aspera* L.	.	1	1	2	1	+	1	.	1	1	+	.	.	.	2	.	+	.	2	+	.	.	.	+	.	.	.	.	.	.	.	.	14
W-Medit.	P caesp	*Phillirea angustifolia* L.	1	1	+	1	1	1	1	1	.	.	.	.	.	1	2	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
Circum-Medit.	P lian	*Lonicera implexa* Aiton	+	2	1	1	1	+	+	.	+	+	.	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	11
Circum-Medit.	P caesp	*Pistacia lentiscus* L.	.	1	1	2	+	.	.	+	.	2	+	.	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
Circum-Medit.	NP	*Bupleurum fruticosum* L.	1	1	1	1	1	.	.	1	.	.	.	+	.	.	.	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
Euri-Medit.	H ros	*Polypodium cambricum* L.	.	+	+	+	+	+	.	+	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
		Diff. of subass. *cephalantheretosum longifoliae*																																	
Euri-Medit.	NP	*Rubus ulmifolius* Schott	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	1	+	+	+	.	+	1	2	+	+	.	.	.	+	13
Eurasiat.	G rhiz	*Cephalanthera longifolia* (L.) R.M.Fritsch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	+	+	+	+	+	+	+	+	12
W-Medit.	P caesp	*Cytisus villosus* Pourr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	+	+	2	1	.	1	+	+	1	11
S-Europ.	P scap	*Fraxinus ornus* L.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.	1	2	1	.	.	.	+	8
Circum-Medit.	H ros	*Viola alba* Besser *dehnhardtii* (Ten.) W.Becker	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	+	+	.	7
Cosmop.	G rhiz	*Pteridium aquilinum* (L.) Kuhn	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	+	+	+	.	.	.	.	5
		Ch. *Pinetea halepensis*																																	
Steno-Medit. M	P lian	*Rubia peregrina* L.	1	1	+	+	+	+	+	+	1	+	+	+	+	+	1	1	+	+	1	+	+	1	1	+	1	1	+	1	+	+	1	1	32
Circum-Medit.	P scap	*Quercus ilex* L.	2	2	2	3	2	2	1	.	1	2	2	1	2	2	1	2	+	1	2	+	2	2	2	1	2	2	2	+	2	2	1	2	31
W-Medit.	H caesp	*Brachypodium retusum* (Pers.) P.Beauv.	.	+	.	.	+	.	.	1	1	+	+	.	+	+	+	+	+	+	.	+	+	.	1	+	+	.	+	.	.	+	.	+	20
W-Medit.	P caesp	*Juniperus oxycedrus* L.	.	.	.	.	.	.	2	.	1	.	2	1	3	+	1	.	.	.	.	.	.	.	1	1	1	1	1	.	.	.	+	.	13
Euri-Medit.	H scap	*Pulicaria odora* (L.) Rchb.	.	.	.	.	.	+	+	.	.	.	+	.	.	+	.	+	.	.	.	+	.	+	.	+	.	+	.	.	.	+	+	.	11
Circum-Medit.	G bulb	*Cyclamen repandum* Sibth. & Sm.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	4
Circum-Medit.	NP	*Salvia rosmarinus* Spenn.	.	+	.	+	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Circum-Medit.	NP	*Cistus creticus* L. ssp. *eriocephalus* (Viv.) Greuter & Burdet	1	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
		Ch. and diff. *Galio scabri-Quercetum suberis*																																	
W-Medit.	P scap	*Quercus suber* L.	.	.	.	.	.	2	3	2	+	2	.	.	.	.	1	.	.	1	1	+	.	1	1	.	.	.	.	.	.	.	.	.	11
Circum-Medit.	P caesp	*Myrtus communis* L.	.	.	.	.	.	1	2	1	2	+	2	.	.	3	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	10
Circum-Medit.	G rhiz	*Arisarum vulgare* Targ.-Tozz.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Circum-Medit.	P caesp	*Phillirea latifolia* L.	.	.	1	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Circum-Medit.	P caesp	*Viburnum tinus* L.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Circum-Medit.	P caesp	*Rhamnus alaternus* L.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Circum-Medit.	H scap	*Galium scabrum* L.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	2
		Ch. *Saniculo europeae-Quercetum ilicis*																																	
Subatl.	P scap	*Ilex aquifolium* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1
Eurosib.	P caesp	*Crataegus monogyna* Jacq.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
		Ch. *Querco-fagetea*																																	
Paleotemp.	P scap	*Taxus baccata* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	2
Euri-Medit.	P lian	*Hedera helix* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	2
		Ch. upper units																																	
Circum-Medit.	T scap	*Senecio lividus* L.	+	.	.	+	+	.	.	+	+	.	.	.	+	+	.	.	.	+	.	.	+	.	.	.	.	.	+	.	.	.	.	.	10
Circum-Medit.	NP	*Cistus salviifolius* L.	.	.	.	.	1	.	.	+	.	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	7
Circum-Medit.	NP	*Lavandula stoechas* L.	.	.	.	.	1	.	.	+	.	.	.	+	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	6
Euri-Medit.	T scap	*Geranium purpureum* Vill.	.	.	+	.	.	.	.	+	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	5
Circum-Medit.	G rhiz	*Asphodelus ramosus* L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	3
Circum-Medit.	P caesp	*Juniperus turbinata* Guss.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Paleotrop.	H ros	*Asplenium onopteris* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1
		Others																																	
Medit-Atl.	G bulb	*Umbilicus rupestris* (Salisb.) Dandy	.	+	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	7
Endem. Sa Co	NP	*Genista corsica* (Loisel.) DC.	1	.	+	+	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	6
Circum-Medit.	P caesp	*Daphne gnidium* L.	1	.	.	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	6
Endem. Sa Co A	Ch frut	*Stachys glutinosa* L.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Euri-Medit.	T scap	*Stellaria pallida* (Dumort.) Piré	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	3
Endem. Sa Co E	G bulb	*Brimeura fastigiata* (Viv.) Chouard	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.	3
Endem. Sa	H scap	*Hieracium bernardii* Rouy ssp. *gallurense* (Arrig.) Greuter	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	2
Eurasiat. Orof.	H scap	*Galium rotundifolium* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	2
Euri-Medit.	NP	*Osyris alba* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2
Endem. Sa Co A	H bienn	*Ptilostemon casabonae* (L.) Greuter	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2
Circum-Medit.	H scap	*Ferula communis* L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
		Accidental taxa: 31	4	1	.	1	2	.	2	.	.	2	1	.	1	2	1	2	1	.	.	2	2	1	3	1	.	1	.	1	.	.	.	.	

Date and locality of the relevés

Table 2: 1-5, M. Lu Pinu, Trinità d'Agultu, 16-05-2018; 6-7, Tarrabinu/Vaccileddu, Sant'Antonio di Gallura, 21-05-2018; 8, Capriuneddu, Sant'Antonio di Gallura, 01-06-2018; 9, Sarra Littu Petrosu, Sant'Antonio di Gallura, 21-V-2018; 9, Macchia di Scopa, Sant'Antonio di Gallura, 21-05-2018; 10, Monti Santu, Sant'Antonio di Gallura, 21-05-2018; 11-14, Sarra di Monti Santu, Sant'Antonio di Gallura, 02-06-2018; 15, between Stazzo Alto and Rio San Giovanni, Olbia, 21-07-2018; 16-19, Monte Pino, Olbia/Telti, 31-05-2019; 20, Mount Limbara, Canale Arcanzelu, Berchidda, 17-05-2018; 21, Mount Limbara, M Sa Pira west, Berchidda,17-05-2018; 22, Mount Limbara, Su Furrighesu, Berchidda, 17-05-2018; 23, Mount Limbara, Sa Punziuda, Berchidda, 09-06-2018; 24, Mount Limbara, Scala di Lu Lioni, Calangianus, 09-06-2018; 25, Mount Limbara, Monte Sa Pira north, Calangianus, 09-06-2018; 26, Mount Limbara, Scala di Li Pini, Calangianus, 19-05-2018; 27, Mount Limbara, Carracana, Berchidda, 21-05-2018; 28, Mount Limbara, M. Niiddoni, Calangianus, 23-08-2018; 29, Mount Limbara, M. Niiddoni, Calangianus, 22-07-2018; 30-31, Mount Limbara, Pianu 'e Iscoba, Berchidda, 17-06-2018; 32: Mount Limbara, La Pira-Lu Pulcili, Calangianus, 30-06-2018.

Sporadic taxa

1: *Cistus monspeliensis* L. 1, *Lysimachia arvensis* (L.) U.Manns et Anderb. subsp. *arvensis* +, *Odontites luteus* (L.) Clairv. +, *Hypochaeris achyrophorus* L. +; 2: *Calicotome villosa* (Poir.) Link +; 4: *Raphanus raphanistrum* L. +; 5: *Asparagus acutifolius* L. +, *Halimium halimifolium* (L.) Willk. +; 8: *Rosa sempervirens* L. +, *Lathyrus ochrus* (L.) DC. +; 11: *Ficus carica* L. 1, *Bituminaria bituminosa* (L.) C.H.Stirt. +; 12: *Urospermum dalechampii* (L.) F.W.Schmidt +; 14: *Allium subhirsutum* L. +; 15: *Teline monspessulana* (L.) K.Koch +, *Lathyrus cicera* L. +; 16: *Briza maxima* L. +; 17: *Teucrium flavum* L. subsp. *glaucum* (Jord. et Four.) Ronniger +, *Leontodon tuberosus* L. +; 18: *Vicia lathyroides* L. +; 20: *Erica scoparia* L. 1, *Salix atrocinerea* Brot. +; 21: *Hypochaeris robertia* (Sch. Bip.) Fiori +, *Geranium columbinum* L. +; 22: *Melica minuta* L. +; 23: *Teucrium marum* L. +, *Viola riviniana* Rchb. +, *Carlina gummifera* (L.) Less. +; 24: *Melica arrecta* Kuntze +; 26: *Dactylorhiza insularis* (Sommier) Ó.Sánchez et Herrero +; 28: *Polypodium vulgare* L. +.

Table 3 – Querco calliprini-Pinetum pineae *ass. nova (holotypus: rel. n. 6).*

			1	2	3	4	5	6*	7	8	9	10	Occurrences
		Elevation (m a.s.l.)	76	47	58	69	74	148	78	94	101	115	
		Aspect	NE	SW	NE	NE	NE	N	SW	SW	S	SE	
		Slope (°)	25	5	30	40	45	25	15	20	40	20	
		Substrate	Dune	Dune	Dune	Dune	Dune	Dune	Dune	Dune-schist	Dune	Dune	
		Stoniness (%)								55			
		Area (sq. m)	500	200	1000	500	1000	200	200	200	200	200	
		Canopy cover (%)	100	90	100	100	95	95	95	90	90	100	
		Mosses-lichens cover (%)	5		60	20	10	5	5				
		Average height of vegetation (m)	16	13	16	14	18	12	14	15	15	14	
		Number of species	23	23	25	25	22	12	16	15	15	12	
Chorotype	Bio form												
		Ch. of the association *Querco calliprini-Pinetum pineae*											
Euri-Medit.	P scap	*Pinus pinea* L.	5	5	5	4	5	5	5	5	5	5	10
Circum-Medit.	P caesp	*Quercus calliprinos* Webb	2	1	2	2	2	2	2	2	1	2	10
		Ch. and diff. *Pinetalia halepensis*											
Circum-Medit.	P caesp	*Pistacia lentiscus* L.	3	+	1	+	2	1	1	+	1	2	10
Circum-Medit. Macaror	P lian	*Rubia peregrina* L.	2	1	1	+	1	2	+	+	+	+	10
Circum-Medit.	P caesp	*Juniperus turbinata* Guss.	1	.	+	1	.	1	3	3	2	3	8
Circum-Medit.	P lian	*Smilax aspera* L.	3	2	1	1	2	+	.	.	.	.	6
Circum-Medit.	NP	*Cistus creticus* L. subsp. *eriocephalus* (Viv.) Greuter & Burdet	+	+	+	+	.	.	+	+	.	.	6
Circum-Medit.	P caesp	*Cistus salviifolius* L.	.	+	.	+	.	.	.	1	+	1	5
Circum-Medit.	G rhiz	*Asparagus acutifolius* L.	1	+	+	.	1	+	.	.	.	.	5
Circum-Medit.	P lian	*Lonicera implexa* L.	+	+	.	.	.	.	.	.	.	.	2
		Ch. *Pinetea halepensis*											
Circum-Medit.	P caesp	*Juniperus macrocarpa* Sm.	2	3	3	2	1	3	1	.	1	2	9
Circum-Medit.	P caesp	*Phillyrea angustifolia* L.	1	1	1	+	.	.	1	1	+	+	8
Circum-Medit.	P caesp	*Rhamnus alaternus* L.	+	+	+	1	1	1	.	.	.	.	6
Circum-Medit.	P caesp	*Arbutus unedo* L.	1	1	+	.	.	2	.	.	.	.	4
Circum-Medit.	NP	*Prasium majus* L.	.	1	1	+	.	.	.	.	.	.	3
Circum-Medit.	NP	*Salvia rosmarinus* Spenn.	.	.	.	.	.	.	.	1	1	.	2
Circum-Medit.	P caesp	*Calicotome villosa* (Poir.) Link	.	.	.	.	+	.	.	.	.	.	1
Circum-Medit.	NP	*Daphne gnidium* L.	.	.	+	.	.	.	.	.	.	.	1
W-Medit.	NP	*Chamaerops humilis* L.	.	.	.	+	.	.	.	.	.	.	1
		Others											
Euri-Medit.	T scap	*Geranium purpureum* L.	+	+	1	+	+	.	1	+	.	2	8
Euri-Medit.	T scap	*Lagurus ovatus* L.	.	+	+	+	.	.	+	.	+	+	6
Circum-Medit.	H caesp	*Dactylis glomerata* L. subsp. *hispanica* (Roth) Nyman	+	.	+	+	.	.	+	+	.	.	5
Circum-Medit.	G bulb	*Sonchus bulbosus* (L.) N.Kilian & Greuter	.	.	.	.	.	+	2	+	1	1	5
Euri-Medit.	G rhiz	*Ruscus aculeatus* L.	.	+	+	+	1	.	.	.	.	.	4
Circum-Medit.	T scap	*Rumex bucephalophorus* L.	.	.	.	+	.	.	+	+	+	.	4
Euri-Medit.	G rad	*Dioscorea communis* (L.) Caddick & Wilkin	.	+	+	+	1	.	.	.	.	.	4
Subcosmop.	T scap	*Torilis arvensis* (Link) Huds.	.	+	+	+	+	.	.	.	.	.	4
Circum-Medit.	Ch suffr	*Lobularia maritima* (L.) Desv.	.	+	.	.	.	.	+	+	.	.	3
Paleotrop.	H ros	*Asplenium onopteris* L.	+	+	1	.	.	.	.	.	.	.	3
Circum-Medit.	T scap	*Silene canescens* Ten.	.	.	.	+	.	.	+	.	+	.	3
Circum-Medit.	T scap	*Senecio leucanthemifolius* Poir.	.	.	.	+	.	.	+	.	+	.	3
Endem. Sa	G rtb	*Ophrys chestermanii* (J.J.Wood) Gölz & H.R.Reinhard	+	+	+	.	.	.	.	.	.	.	3
Endem. Sa	Ch suffr	*Dianthus morisianus* Vals.	.	.	.	+	+	+	.	.	.	.	3
Circum-Medit.	H bienn	*Sixalix atropurpurea* (L.) Greuter & Burdet	.	.	+	+	+	.	.	.	.	.	3
Euri-Medit.	H ros	*Polypodium cambricum* L.	+	.	+	.		.	.	.	.	.	2
Euri-Medit.	NP	*Osyris alba* L.	+	.	.	+	.	.	.	.	.	.	2
Euri-Medit.	H caesp	*Carex halleriana* Asso	1	1	.	.	.	.	.	.	.	.	2
Circum-Medit.	G rhiz	*Arisarum vulgare* L.	+	.	.	.	+	.	.	.	.	.	2
		Accidental taxa: 12	2	.	1	.	6	.	.	1	1	1	

Date and locality of the relevés

Table 3: 1-5, Portixeddu dunes north, Buggerru, 12-05-2008; 6-10, Portixeddu dunes south, Buggerru, 10-03-2019.

Sporadic species

1: *Charybdis pancration* (Steinh.) Speta +, *Cruciata glabra* (L.) Ehrend. +; 3: *Cynosurus effusus* Link +; 5: *Asperula laevigata* L. +, *Allium triquetrum* L. +, *Galium aparine* L. +, *Geranium molle* L. +, *Arum pictum* L.f. +, *Bryonia marmorata* E.Petit +; 8: *Arenaria leptoclados* (Rchb.) Guss. 1; 9: *Malcolmia ramosissima* (Desf.) Al-Shehbaz +; 10: *Brachypodium retusum* (Pers.) P.Beauv. +.

Appendix 1. List of associations

Pinus halepensis syntaxa (Brullo *et al*., 1977; De Marco *et al*., 1984; De Marco et Caneva, 1984; Pesaresi *et al*., 2017)

Erico arboreae-Pinetum halepensis De Marco et Caneva 1984
Thymo capitati-Pinetum halepensis De Marco et Caneva 1984
Pistacio lentisci-Pinetum halepensis De Marco, Veri et Caneva 1984
Plantago albicantis-Pinetum halepensis Bartolo, Brullo, Minissale et Spampinato 1985
Junipero oxycedri-Pinetum halepensis Vagge 2000
Anthyllido barba-jovis-Pinetum halepensis Biondi, Casavecchia, Guerra, Medagli, Beccarisi et Zuccarello 2004
Cyclamino hederifolii-Pinetum halepensis Biondi, Casavecchia, Guerra, Medagli, Beccarisi et Zuccarello 2004
Coronillo emeroidis-Pinetum halepensis Allegrezza, Biondi et Felici 2006
Ampelodesmo mauritanici-Pinetum halepensis Biondi et Pesaresi 2017
Calicotomo infestae-Pinetum halepensis Biondi et Pesaresi 2017
Genisto tyrrhenae-Pinetum halepensis Biondi et Pesaresi 2017
Thymo striati-Pinetum halepensis Biondi et Pesaresi 2017
Junipero macrocarpae-Pinetum halepensis Biondi, Pesaresi et Vagge 2017
Erico multiflorae-Pinetum halepensis (Brullo, Di Martino et Marcenò 1977) Biondi et Pesaresi 2017
Cisto albidi-Pinetum halepensis Vagge, Biondi et Pesaresi 2017

Pinus pinaster subsp. *pinaster* syntaxa (Brullo *et al*., 1977; Biondi et Vagge, 2015)

Genisto aspalathoidis-Pinetum pinastri Brullo, Di Martino et Marcenò 1977
Buxo sempervirentis-Pinetum pinastri Biondi et Vagge 2015
Erico arboreae-Pinetum pinastri Biondi et Vagge 2015
Erico scopariae-Pinetum pinastri Biondi et Vagge 2015

Pinus pinea syntaxa (Bartolo *et al*., 1994; Brullo *et al*., 2002)

Cisto crispi-Pinetum pineae Bartolo, Brullo et Pulvirenti 1994
Cisto cretici-Pinetum pineae Brullo, Minissale, Siracusa, Scelsi et Spampinato 2002

Appendix 2. Analysis of synoptic table reporting Diagnostic (Dg), Constant (C) and Dominant (Dm) species of clusters resulting from the TWINSPAN analysis. The name of the syntaxon to which a cluster corresponds is reported, along with the number of plots assigned to the cluster. The numbers reported for diagnostic species are fidelities (phi values multiplied by 100), those for constant species are percentage frequencies (constancy), and those for dominant species are percentage frequencies of occurrences with a cover higher than 20%. Species with $\Phi \geq 0.2$ and p-value < 0.05 (based on Fisher's exact test), were considered as diagnostic. Constant species were defined as those with percentage occurrence frequency >20%. Species are sorted in decreasing order.

Erico arboreae-Pinetum halepensis De Marco et Caneva 1984
Number of relevés: 10

Diagnostic species:

Erica arborea	(C, Dm)	100.0
Myrtus communis	(C)	85.3
Arbutus unedo	(C, Dm)	78.0
Lonicera implexa	(C)	78.0
Salvia rosmarinus	(C)	66.7
Cistus monspeliensis	(C)	55.5

Constant species:

Pinus halepensis	(Dm)	100
Phillyrea angustifolia	(Dm)	100
Pistacia lentiscus	(Dm)	100
Erica arborea	(Dg, Dm)	100
Myrtus communis	(Dg)	80
Salvia rosmarinus	(Dg)	80
Arbutus unedo	(Dg, Dm)	70
Lonicera implexa	(Dg)	70
Juniperus turbinata		50
Asparagus acutifolius		50
Cistus monspeliensis	(Dg)	40
Rubia peregrina		40

Dominant species:

Pinus halepensis	(C)	100
Phillyrea angustifolia	(C)	40
Erica arborea	(Dg, C)	20
Arbutus unedo	(Dg, C)	10
Pistacia lentiscus	(C)	10
Quercus ilex		10

Smilaco asperae-Pinetum halepensis *ass. nova*
Number of relevés: 6

Diagnostic species:

Smilax aspera	(C)	100.0
Arisarum vulgare	(C)	66.6
Quercus calliprinos	(C)	63.2
Stachys major	(C)	47.4

Constant species:

Pinus halepensis	(Dm)	100
Pistacia lentiscus	(Dm)	100
Juniperus turbinata	(Dm)	100
Phillyrea angustifolia	(Dm)	100
Asparagus acutifolius		100
Rubia peregrina		100
Smilax aspera	(Dg)	100
Arisarum vulgare	(Dg)	67
Stachys major	(Dg)	67
Quercus calliprinos	(Dg)	50

Carex distachya		33
Asphodelus ramosus		33
Piptatherum miliaceum		33

Dominant species:

Pinus halepensis	(C)	100
Juniperus turbinata	(C)	33
Pistacia lentiscus	(C)	33
Phillyrea angustifolia	(C)	17

Asparago horridi-Pinetum halepensis *ass. nova*
Number of relevés: 8

Diagnostic species:

Juniperus macrocarpa	(C, Dm)	100.0
Tolpis virgata	(C)	90.7
Asparagus horridus	(C)	81.6
Pancratium maritimum	(C)	75.0
Silene canescens	(C)	72.5
Sixalix atropurpurea ssp. *maritima*	(C)	63.2
Asphodelus ramosus	(C)	46.3

Constant species:

Pinus halepensis	(Dm)	100
Juniperus macrocarpa	(Dg, Dm)	100
Asparagus acutifolius		100
Pistacia lentiscus		100
Rubia peregrina		100
Juniperus turbinata	(Dm)	75
Asparagus horridus	(Dg)	75
Tolpis virgata	(Dg)	88
Pancratium maritimum	(Dg)	62
Silene canescens	(Dg)	62
Asphodelus ramosus	(Dg)	62
Phillyrea angustifolia		50
Rhamnus alaternus		50
Sixalix atropurpurea ssp. *maritima*	(Dg)	50
Stachys major		38
Cistus salviifolius		25
Crucianella maritima		25
Lobularia maritima		25
Piptatherum miliaceum		25
Salvia rosmarinus		25
Romulea ligustica		25

Dominant species:

Pinus halepensis	(C)	100
Juniperus macrocarpa	(Dg, C)	62
Juniperus turbinata	(C)	12

Arbuto unedonis-Pinetum pinastri *ass. nova*
cephalantheretosum longifoliae *subass. nova*
Number of relevés: 13

Diagnostic species:

Cephalanthera longifolia	(C)	92.6
Cytisus villosus	(C)	85.6

Viola alba ssp. *dehnhardtii*	(C)	60.7
Rubus ulmifolius	(C)	53.1
Fraxinus ornus	(C)	46.4
Pteridium aquilinum	(C)	42.6

Constant species:

Pinus pinaster subsp. *pinaster*	(Dm)	100
Erica arborea	(Dm)	100
Quercus ilex		100
Rubia peregrina		100
Cephalanthera longifolia	(Dg)	92
Arbutus unedo	(Dm)	85
Cytisus villosus	(Dg)	85
Rubus ulmifolius	(Dg)	69
Brachypodium retusum		62
Viola alba ssp. *dehnhardtii*	(Dg)	54
Fraxinus ornus	(Dg)	46
Juniperus oxycedrus		46
Pulicaria odora		46
Pteridium aquilinum	(Dg)	31
Quercus suber		23
Brimeura fastigiata		23
Melica minuta		23

Dominant species:

Pinus pinaster subsp. *pinaster*	(C)	100
Erica arborea	(C)	69
Arbutus unedo	(C)	15

Arbuto unedonis-Pinetum pinastri *ass. nova*
pinetosum pinastri *subass. nova*
Number of relevés: 18

Diagnostic species:

Phillyrea angustifolia	(C)	70.7
Bupleurum fruticosum	(C)	62.0
Lonicera implexa	(C)	62.0
Pistacia lentiscus	(C)	57.7
Smilax aspera	(C)	52.1
Polypodium cambricum	(C)	49.1

Constant species:

Pinus pinaster subsp. *pinaster*	(Dm)	100
Arbutus unedo	(Dm)	100
Erica arborea	(Dm)	100
Quercus ilex	(Dm)	100
Rubia peregrina		100
Phillyrea angustifolia	(Dg)	67
Smilax aspera	(Dg)	67
Brachypodium retusum	(Dm)	67
Lonicera implexa	(Dg)	56
Bupleurum fruticosum	(Dg)	56
Pistacia lentiscus	(Dg)	50
Juniperus oxycedrus	(Dm)	39
Myrtus communis	(Dm)	39
Senecio lividus		39
Polypodium cambricum	(Dg)	39

Quercus suber	(Dm)	33
Lavandula stoechas		28
Pulicaria odora		28
Cistus salviifolius		22
Daphne gnidium		22
Genista corsica		22
Salvia rosmarinus		22
Umbilicus rupestris		22

Dominant species:

Pinus pinaster subsp. *pinaster*	(C)	100
Erica arborea	(C)	44
Arbutus unedo	(C)	22
Juniperus oxycedrus	(C)	6
Myrtus communis	(C)	6
Quercus ilex	(C)	6
Quercus suber	(C)	6
Brachypodium retusum	(C)	6

Querco calliprini-Pinetum pineae *ass. nova*

Number of relevés: 10

Diagnostic species:

Quercus calliprinos	(C)	100.0
Rubia peregrina	(C)	100.0
Juniperus macrocarpa	(C, Dm)	90.5

Constant species:

Pinus pinea	(Dm)	100
Pistacia lentiscus	(Dm)	100
Quercus calliprinos	(Dg)	100
Rubia peregrina	(Dg)	100
Juniperus macrocarpa	(Dg, Dm)	90
Juniperus turbinata	(Dm)	80
Phillyrea angustifolia		80
Geranium purpureum		80
Rhamnus alaternus		60
Smilax aspera	(Dm)	60
Cistus creticus		60
Lagurus ovatus		60
Cistus salviifolius		50
Dactylis glomerata		50
Aetheorhiza bulbosa		50
Asparagus acutifolius		50
Arbutus unedo		40
Dioscorea communis		40
Rumex bucephalophorus		40
Ruscus aculeatus		40
Torilis arvensis		40
Lobularia maritima		30
Ophrys fuciflora ssp. *chestermanii*		30
Dianthus morisianus		30
Asplenium onopteris		30
Prasium majus		30
Senecio leucanthemifolius		30
Silene canescens		30
Sixalix atropurpurea ssp. *maritima*		30

Dominant species:

Pinus pinea	(C)	100
Juniperus macrocarpa	(Dg, C)	30
Juniperus turbinata	(C)	30
Pistacia lentiscus	(C)	10

Chapter 2

Temporal increase in the extent of pine stands in Sardinia (Italy)

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Contribution to the project – I collected the data, organised and analysed the dataset. I realised all the figures. I leaded the preparation of the manuscript, which was implemented and reviewed by the contributions of the co-authors.

Abstract – Knowledge of temporal changes in the distribution of habitats is often lacking. In this research, we investigated the changes in the distribution of the two Natura2000 habitats (codes 2270 and 9540) structurally characterized by the three Mediterranean pines native or putative native to Sardinia, namely *Pinus halepensis*, *P. pinaster* subsp. *pinaster*, and *P. pinea*. We analysed aerial photographs to prepare detailed maps of the past and current distribution of natural pine woods, as well as pine-related toponymy maps. We calculated the current amount of natural pine woods included within each Natura2000 habitat and found a high rate of recovery during the last decades. This rate is double when compared to the average extent of other Sardinian woody habitats in the same period. Among the three pine species, *P. pinaster* subsp. *pinaster* and *P. halepensis* woods showed the highest increase in extension. However, the study of pine-related toponyms indicated that the pine stands might have been more extended in the far past, especially *P. pinaster* subsp. *pinaster* woods, thus suggesting that the present distribution has not however reached the ancient extent. Currently, 135 ha of natural pine woods are included in the priority habitat 2270, while 1,100 ha are included in habitat 9540. From the conservation perspective, we found that about 90% of pine woods fall within protected areas. Our study provides a complete survey of natural Sardinian pine woods and related habitat distribution, together with the quantification of their increase in the last decades, highlighting the importance of diachronic analyses for monitoring habitat changes through time.

Keywords: *Cartography, EU Habitat, Land-use change, LEK, Mediterranean forest, Pinus, Phytotoponym, Vegetation map*.

1. **Introduction**

The Mediterranean Basin has a historical relationship between the environment and human activities (Thompson 2020). Humans modelled this region since the beginning of agriculture, nearly 10,000 years ago (Quézel *et al*. 1999; Blondel *et al*. 2010; Marignani *et al*. 2017). Mediterranean woods represented a crucial resource for human activities (Di Pasquale *et al*. 2004; Blondel *et al*. 2010; Puddu *et al*. 2012; Broodbank 2013). In this context, pine tree species represent an important part of the woody component of this geographical area, where 10 pine species are considered native (Barbéro *et al*. 1998; Médail *et al*. 2019; Euro+Med 2020). However, the pine species that can be considered strictly Mediterranean in terms of ecological requirements and distribution are four: *Pinus brutia, P. halepensis*, *P. pinaster*, and *P. pinea* (Barbéro *et al*. 1998; Bonari *et al*. 2021). These species characterise two habitats of community importance, according to the Habitats Directive 92/43/EEC (European Commission 1992): i) the priority habitat 2270 "Wooded dunes with *Pinus pinea* and/or *P. pinaster* subsp. *pinaster*, including old-established pine plantations on dune contexts" (Biondi *et al*. 2010), and ii) the habitat 9540 "Mediterranean pine forests with endemic mesogean pines" (Biondi *et al*. 2010). In the EUNIS system, Mediterranean pine woods have been classified under the codes T3A (Mediterranean lowland to submontane *Pinus* forests) and N1G (Mediterranean coniferous dune forests), respectively (Chytrý *et al*. 2020).

Detailed knowledge of the distribution of habitats is crucial to understand land-use changes at the local and at the broader scales as well as to inform conservation (Puddu *et al*. 2012; Vila-Cabrera *et al*. 2012; Bonari *et al*. 2020). Manifolds are the tools that can support, implement or refine the understanding of species distribution. For example, aerial photographs can help in understanding temporal changes in canopy cover as a proxy for wood extent and its relation to the land-use change (e.g. Kozak *et al*. 2006; Wezyk *et al*. 2018). Further, also local people can bring valuable information on different aspects (Davis & Wagner 2003; Aswani *et al*. 2018), that is why the role of Local Ecological Knowledge (LEK) is more and more considered in ecological studies (Charnley *et al*. 2007; Joa *et al*. 2018). Besides, a valuable tool for understanding the changes in species distribution across time is related to the study of phytotoponyms (Fegúndez & Izco 2016; Signorini *et al*. 2016). This type of information has proven to be important for understanding distributional traits and changes of different species (Bacchetta *et al*. 2000, 2007; Pinna et al. 2017).

In Sardinia, three of the four Mediterranean pine species occur with an indigenous status (Bacchetta *et al*. 2009; Pignatti 2017-2019), while *P. brutia* occurs only as planted in reforestation (Arrigoni 2006). Historical data suggest a broader diffusion of the pine natural stands on the island (e.g., Angius 1851; De Marco & Mossa 1980). Cuttings and wildfires caused a significant reduction of their distribution during the 19th century and in the first 60 years of the 20th century (Desole 1960, 1964; Arrigoni 1967; De Marco & Mossa 1980; Camarda & Valsecchi 2008). Because of habitat depletion, reforestation has been carried out, typically to contrast soil erosion and strengthen dune stability (Pavari 1935; D'Autilia *et al*. 1967a). Additionally, thousands of hectares of pine afforestation in many areas of the island have been planted, rarely using indigenous material (D'Autilia *et al*. 1967b; Brigaglia 1994; Calvia & Ruggero 2020). During the 20th century, research on the distribution (Desole 1960, 1964; Arrigoni 1967; Mossa 1990) and phytosociology (De Marco & Mossa 1980) of Sardinian pine formations were published. These works often described landscapes affected by decades of harvesting and fire (Desole 1960; De Marco & Mossa 1980), whereas the distributional trends consequent to land-use change that occurred during the last decades have not been investigated yet. Accordingly, the creation of detailed maps of the present distribution of Sardinian native pine woods and habitats, and the quantification of their temporal variation is needed.

With this study, we aim at defining the present and past distribution of Sardinian pine stands where they are supposed to be native. We aimed at: i) creating the first detailed distribution maps of natural pine habitats of Sardinia; ii) quantifying their distribution changes across the second half of the 20th century and the first two decades of the 21st century; iii) quantifying the pine woods included in the two recognized habitats of the Habitats Directive and protected areas.

2. **Material and methods**

2.1 Study area

Sardinia has an area of 24,090 km², including smaller islands and islets. Sardinian coasts are about 1,900 km long, three-quarters of which are rocky and the remaining sandy (Bacchetta *et al.* 2009). From a geological point of view, Sardinia is very diversified. The granitic rocks dominate the outcrops of the eastern half of the island, while effusive rocks predominate on the western side. Metamorphic rocks and sedimentary carbonate reliefs are in turn present in many parts of Sardinia (Carmignani *et al.* 2001).

The climate of Sardinia is prevalently Mediterranean, only locally temperate, with a sub-Mediterranean variant, in mountain areas of the northern and eastern parts of the island. It is characterised by a typical seasonality, with mild-wet winters and dry-hot summers (Bacchetta *et al.* 2009; Canu *et al.* 2015).

Biogeographically, Sardinia falls in the Italo-Tyrrhenian Superprovince (Ladero Álvarez 1987; Bacchetta *et al.* 2013), of which it represents the Sardinian-Corsican province together with the Tuscan Archipelago (Bacchetta *et al.* 2012, 2013). The island is divided into six biogeographic sectors and 22 subsectors (Fenu *et al.* 2014).

2.2 Pine species

Pinus halepensis (Aleppo pine) is a circum-Mediterranean species (Tutin *et al.* 1993; Barbéro *et al.* 1998; Fady *et al.* 2003; Blondel *et al.* 2010; Farjon 2017; Pesaresi *et al.* 2017; Pignatti 2017-2019; Bonari *et al.* 2021). Its elevation range is from sea level up to 1,700 m a.s.l. in Morocco (Farjon 2017). It is indifferent to substrates, although it is often reported with preference to marls and limestones (Barbéro *et al.* 1998; Mauri *et al.* 2016; Farjon 2017). It is a thermophilous and xerophilous plant, growing in areas with an annual average rainfall comprised between 350 and 700 mm (Barbéro *et al.* 1998; Mauri *et al.* 2016). In the Mediterranean Basin, the woods dominated by this species cover more than 3.5 million ha, and they are concentrated mainly in the western part of the basin, while they are more scattered in the eastern (Pesaresi *et al.* 2017). In Italy, *P. halepensis* is considered a native species in many administrative regions, including the islands of Sicily and Sardinia (Bartolucci *et al.* 2018, 2020).

Pinus pinaster subsp. *pinaster* (Maritime pine) is a western Mediterranean and Atlantic species (Farjon 2017). It grows from the sea level to 1,600 m a.s.l. in Spain and Corsica, reaching 2,000 m a.s.l. in Morocco (Abad Viñas *et al.* 2016a; Farjon 2017). It is a heliophilous and xerophilous species, that requires a climate with oceanic influence and a minimum annual average rainfall of about 600 mm, being water stress a limiting factor for its growth (Mazza *et al.* 2014). Geologically, it thrives mostly on siliceous substrates (Barbéro *et al.* 1998; Abad Viñas *et al.* 2016a). In Italy, *P. pinaster* subsp. *pinaster* is native to the administrative regions of Liguria, Tuscany, Sicily and Sardinia (Bartolucci *et al.* 2018).

Pinus pinea (Stone pine) is a Mediterranean species, though it is unclear its native distribution due to human plantations over wide areas of the Mediterranean Basin for a long time (Bonari *et al.* 2017). It grows on coastal areas or inland, reaching elevations up to 600 m a.s.l. (Farjon 2017). It is a heliophilous, xerophilous, and thermophilous plant, with optimum rainfall of 600 mm per year, and prefers sandy, siliceous substrates (Abad Viñas *et al.* 2016b; Bonari *et al.* 2020). In Italy, it grows in the peninsular administrative regions, Sicily and Sardinia, but it is often cultivated (Pignatti 2017-2019).

2.3 Current distribution of native pine habitats of Sardinia

To define the present distribution of natural Sardinian pine species and habitats, delimiting their extension, and updating the data available, we collected information from cartographic and bibliographic sources (Arrigoni 1967 and De Marco & Mossa 1980 for *P. halepensis*; Desole 1960, 1964 and Veri & Bruno 1974 for *P. pinaster* subsp. *pinaster*; Arrigoni 1967 and Mossa 1990 for *P. pinea*). We used the maps issued by the Italian Military Geographic Institution (IGM, scale 1:25,000 maps) integrated with data deriving from local people interviews that represent the Local Ecological Knowledge (LEK). This information included old toponyms, pine stands extant and confirmation of extinct ones. In addition, to refine the data, we accomplished 60 field excursions on the whole island of Sardinia in the years 2017-2019. These surveys concerned the previously reported localities and the new ones we retrieved. Each pine stand area was delimited using ©Garmin GPS62st.

To define and map the present distribution of each pine species and the habitats they form, we considered three canopy cover categories, defined as follows: i) areas where the species had a <1% of the total canopy cover (including isolated trees, used for defining the presence of the species); ii) areas where the species had a higher canopy threshold, i.e., 1-35% of the total canopy cover; iii) areas where the species had a canopy threshold >35% of the total canopy cover. Then, we calculated the area of extent of each species, also considering their presence in protected areas (areas managed by the Forestry Agency of Sardinia, Special Areas of Conservation - SAC) and areas where these stands were recognised as habitats by the Habitats Directive.

We prepared the distribution maps using the Open-Source Geographic Information System Quantum GIS (QGIS 3.18).

2.4 Diachronic analysis of the distribution of the pine species in Sardinia

To understand the changes in the distribution of the pine habitats during the last decades, we used direct and indirect references as cartographic data, literature, toponymic information and LEK. The historical digitalised aerial photographs, referred to four different years of aerial surveys (1954, 1977, 1998 and 2016), allowed us to create a multitemporal series of cartographic data. We retrieved these data from the Sardegna geoportale website (2019). After aerial photograph interpretation, we delimited all polygons undoubtedly referred to each pine species for the different years examined. Then, we calculated the area of extent of different pine woods for each available year and compared these measures with the current distribution maps obtained before (see the method described in paragraph 2.3). We prepared the diachronic distribution maps using the Open-Source Geographic Information System Quantum GIS (QGIS 3.18).

2.5 Collection and interpretation of the pine-related toponyms of Sardinia

To better understand a likely past distribution of the pines, we searched for toponyms recalling their mention. To do so, we primarily inspected all the maps of Sardinia issued by the Italian Military Geographic Institute (IGM, scale 1:25,000 maps), and consulted the Sardegna Geoportale website (2019). Then, we searched for localities reported in literature (e.g., Angius 1851; Desole 1960; Bacchetta 2006). Lastly, we added LEK information about local pine-related toponyms through interviews with local people, i.e., landowners, forestry workers, elders. Biogeographical as well as historical information helped in attributing every toponym to each pine species.

We created a table containing all the pine-related toponyms we found from different sources. The table reports the list of phytotoponyms, their translation into English, municipality, biogeographical sector and subsector, coordinates, elevation, current status (extant or extinct), the referred pine species and sources (literature, website of the Autonomous Region of Sardinia; IGM maps, LEK). Then, we prepared a distribution map with all phytotoponyms found and compared them with the current Sardinian pine species distribution. We geo-referenced the phytotoponyms by using the Open-Source Geographic Information System Quantum GIS (QGIS 3.18).

All the toponyms that we recognised as referring to undoubtedly planted pines as well as personal names (in the Italian and Sardinian languages “Pino” is used as an abbreviation of the name Giuseppe - Joseph) were not included in the map nor considered in our analyses. In this case, LEK was often important to discern the actual meaning of the toponyms.

3. **Results**

3.1 Current distribution of the pine species and habitats in Sardinia

The distribution of the three pine species and they associated habitats is reported in Figure 1. *Pinus halepensis* is currently distributed in an area of about 4,864 ha in south-western Sardinia (Figures 1, S1A). Scattered trees (<1% of the total pine canopy) represent about 20.4%. Intermediate canopy cover distribution areas (1-35% of the total pine canopy cover) are 63.7%. Finally, the areas where *P. halepensis* cover is >35% of the total canopy cover are 15.9%.

Pinus pinaster subsp. *pinaster* is currently distributed in north-eastern Sardinia over an area of approximately 5,894 ha. The area with scattered pines is 49.2% of the total cover (Figures 1, S1B, Table 1). Mixed woods with intermediate *P. pinaster* subsp. *pinaster* cover (canopy cover 1-35%) are 43%. Then, dense *P. pinaster* subsp. *pinaster* woods (estimated canopy cover >35%) occupy 7.8%.

The *Pinus pinea* distribution is about 582 ha in the south-western part of the region (Figures 1, S1C). The area with scattered pines is 79.7%, while that of intermediate cover woods (canopy cover 1-35%) is 10.3%. Finally, the woods of *P. pinea* with high cover (canopy cover >35%) are found in an area of about 10% (Table 1).

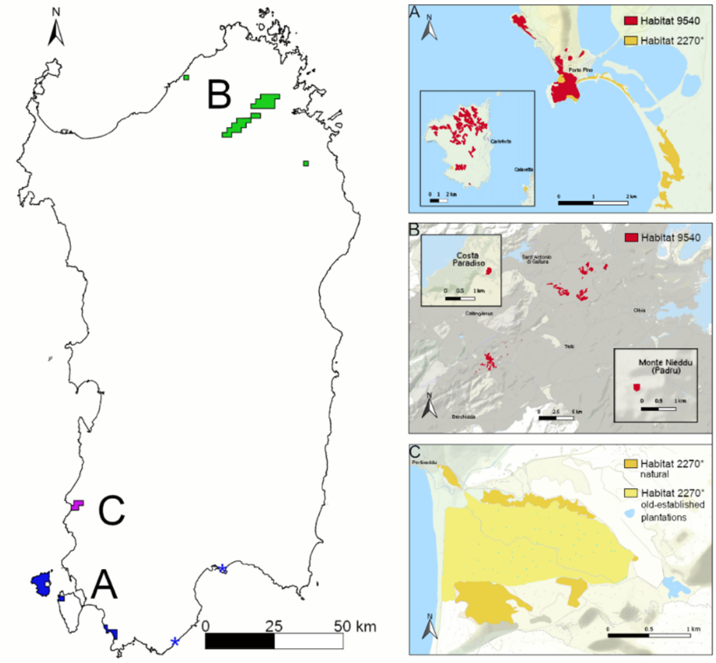

Figure 1 – Map of Sardinia showing the distribution of the three pine species structurally dominating the two Natura2000 habitats 2270 and 9540 considered native in the island. A (blue) =* Pinus halepensis *area; B (green) =* P. pinaster *subsp.* pinaster *area; C (purple) =* P. pinea *area. Blue asterisks show the doubtful P. halepensis stands. The corresponding frames (A-C) show the distribution of the habitats.*

Table 1 – Comparison of the extents in hectares of different canopy covers across the three wood canopy categories of the different pine species. Aerial photographs were taken from RAS (2019).

Species	**Canopy cover (ha)**		
	<1%	1-35%	>35%
Pinus halepensis	994	3,100	770
Pinus pinaster	2,903	2,537	454
Pinus pinea	464	60	58

A high percentage of Sardinian pine stands falls within protected areas (Table 2). *Pinus halepensis* natural habitats are almost totally included in SACs, while about 20% of *P. pinaster* subsp. *pinaster* stands are not included in protected areas (SACs and State Forests). On the contrary, only 34% of the *P. pinea* stands fall within a protected area, though all the natural woods are included there and recognised as priority habitat 2270*.

Table 2 – Comparison of the extents in hectares of the three pine species distribution within protected areas (SACs, Forestry Agency managed areas), matching the two habitats 2270 and 9540 of the Habitats Directive. PA = Protected areas. Past data refer to standard data forms or management plans of the SACs.*

Species	**Stands included in PA % (ha)**	**Out of PA % (ha)**	**Habitat 2270* (ha) (past data)**	**Habitat 2270* (ha) (our study)**	**Habitat 9540 (ha) (past data)**	**Habitat 9540 (ha) (our study)**
Pinus halepensis	99.7 (4,848)	0.3 (16)	28.8	77	710.2	666
Pinus pinaster	80.3 (4,732)	19.7 (1,162)	0	0	166.2	454
Pinus pinea	33 (193)	67 (389)	167.7	58	0	0

3.2: Diachronic analysis of the distribution of natural pine woods in Sardinia (1954-2016)

We recorded a significant expansion of the three pine wood types of Sardinia during the last 60 years. This increase is divided as follows: +1,043% *Pinus pinaster* subsp. *pinaster*, +235% *P. halepensis*, +27% *P. pinea*. *Pinus halepensis* woods showed a minimum occupancy in 1954 (Figure 2), with an area of about 222 ha. The first increase was reached in 1977, with 288 ha. In 1998 there was a further increase, reaching 438 ha. In 2016 the canopy cover was 770 ha (Supplementary material I: Figure S2).

Pinus pinaster subsp. *pinaster* woods were at their minimum in 1954 (Figure 2) when their occupied area was 39.5 ha. In 1977 the total *P. pinaster* subsp. *pinaster* extension in Sardinia slightly grew to 55 ha. A further increase of the extent was in 1998 when *P. pinaster* subsp. *pinaster* woods reached 127.5 ha. The current extension of *P. pinaster* subsp. *pinaster* woods reaches 454 ha (Supplementary material I: Figure S3).

Pinus pinea woods occupancy is rather constant during the last decades (Figure 2), slightly fluctuating from 43 ha in 1954 to a minimum of 42.5 ha in 1977, then increasing to 45.5 ha in 1998, and finally reaching the current 58 ha (Supplementary material I: Figure S4).

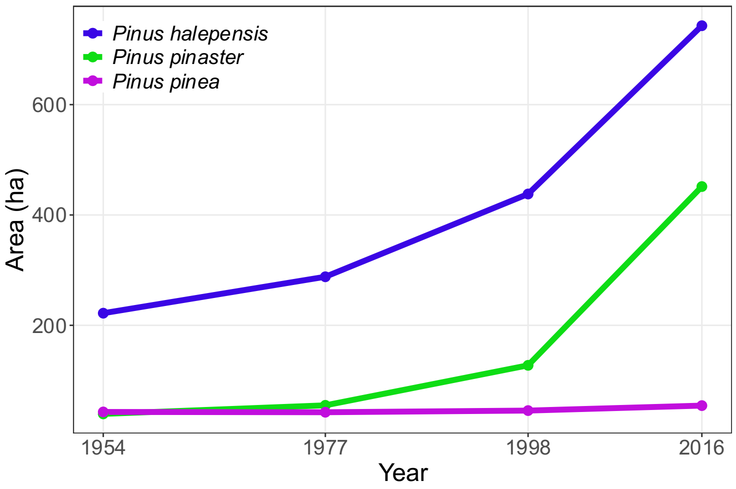

Figure 2. Variations in hectares of native Sardinian Pinus *woods during the period between 1954 and 2016, according to the interpretation of aerial photographs at intervals of about 20 years. Aerial photographs of*

1954, 1977, 1998 and 2016 were taken from RAS (2019).

3.3 Pine-related toponyms

We found a total of 36 toponyms attributable to native stands of the three pine species (Figure 3; the full list is reported in Table S1, while the doubtful toponyms are reported in Table S2). Seven toponyms are related to *Pinus halepensis*. They are all concentrated in four municipalities of south-western Sardinia. Five toponyms fall in extant stands. We found 26 toponyms referred to as *P. pinaster* subsp. *pinaster*, located in 15 municipalities, that are concentrated in the north-eastern part of the island. Another toponym exists on the central-eastern part of Sardinia. Five out of 27 toponyms fall in the current native pine distribution, while the others are long extinct. Finally, we found two toponyms that are referred to as *P. pinea*. Both are in south-western Sardinia, where this species still thrives.

We found also 11 toponyms that were not referred to as native pine stands. Nine were recognised as related to planted pines since they indicate farms, private houses, reforestation occurred in the 20th century, while two were referred to personal names.

4. **Discussion**

4.1 Distribution of the three pine species in Sardinia: an update

We found an overall increase in the extent of all Sardinian pine species investigated and of their associated habitats. From 1954 to the present, they show an expansion of +310%. Noteworthy is *Pinus pinaster* subsp. *pinaster*, which covers at present an area more than 10 times larger than in 1954, as well as *P. halepensis*, which is widespread in an area that is currently about three times larger than in 1954. These trends mirror the description of Puddu *et al.* (2012). They reported an increase in the Sardinian total woody habitats from less than 2,000 km² in 1965, to 4,927 km² in 2007, their extent passing from a minimum of 7.9% to 20% of the Sardinian area. This means a general wood expansion of +146% in 42 years, for the whole of Sardinia.

Sardinian *P. halepensis* native stands grow on different substrates and in some of the most arid zones of Sardinia, in thermomediterranean thermotype. Since the 19th century, these stands were reported in the areas of the south-western Sardinia where the species is currently present: the Island of San Pietro and the Gulf of Porto Pino (Moris 1827; Angius 1851). In this study, we add another stand that was found on the Island of Sant'Antioco. Previous authors did not quantify the total cover of the species but depicted mostly sparse groves, small trees scattered between garrigues and scrublands (Arrigoni 1967; De Marco & Mossa 1980). All the reported areas fall in the Sulcitano-Iglesiente sector and Antioco-Carlofortino sub-sector (Fenu *et al.* 2014). However, in Sardinia some doubtful stands exist. One is represented by several scattered pines and some groves growing on the calcareous hills surrounding the city of Cagliari (Turritano-Campidanese sector and Campidanese sub-sector, Fenu *et al.* 2014). In this case, a possible spread due to planted trees for ornamental purpose is likely. Another it is located in a small coastal area of about 2.1 ha close to Santa Margherita di Pula, on the southern part of the island (Sulcitano-Iglesiente sector and Sulcitano subsector, Fenu *et al.* 2014). This area is surrounded by wide pine plantations that mostly occurred since the beginnings of the 20th century

(D'Autilia *et al.* 1967a). Only future genetic analyses could shed light on the origin of these trees.

Sardinian *P. pinaster* subsp. *pinaster* stands are related to granitic rocks, ranging from 90 m up to about 1,250 m a.s.l. in Mount Limbara, where the species reaches the temperate bioclimate in the sub-Mediterranean variant (Calvia & Ruggero 2020). Historical data, referring to the 19th century, showed a past distribution of *P. pinaster* subsp. *pinaster* wider than today, since Angius (1851) reported the species in three different Sardinian sub-sectors (Fenu *et al.* 2014): Gallurese, Baronico and Ogliastrino. Nowadays, of the 27 toponyms mentioning *P. pinaster* subsp. *pinaster*, only five preserve pine stands. However, the current species distribution is generally larger, if compared to what was depicted by Desole (1960, 1964). This author reported *P. pinaster* subsp. *pinaster* in four areas of Gallura. We refined the current distribution of *P. pinaster* subsp. *pinaster* in Sardinia, which currently grows in the same four areas cited above, but in 56 stands. Biogeographically, all the extant stands fall within the Goceano-Logudorese sector and the Gallurese sub-sector (Fenu *et al.* 2014).

Sardinian native *Pinus pinea* stands are located at only one area (Arrigoni 1967; Mossa 1990; Bacchetta *et al.* 2009). These stands, already cited by Moris (1827; 1858-59) and Angius (1851), can be considered the only natural *P. pinea* woods on dunes in Italy (Pignatti 2017-2019). They grow mainly on Holocene sands of the wide dune system that, from Portixeddu, extends towards inland for about 3 km, reaching a maximum height of 202 m a.s.l., in the upper thermomediterranean thermotype. Some more isolated trees grow until 6 km inland, at the extreme border of the alluvial deposits. Our research showed the increased area covered by these stands. We detected five main stands, while several scattered trees grow elsewhere and are mostly isolated in low dunes and scrublands. The total area of the *P. pinea* stands is about 582 ha. It is confined in the south-western coast between Fluminimaggiore and Buggerru, in the Sulcitano-Iglesiente sector and Iglesiente sub-sector (Fenu *et al.* 2014).

The *P. pinea* natural woods today are often in contact with an extensive old-established plantation of *P. pinea* trees, which was planted starting from 1958 (Arrigoni 1967), along with the invasive *Acacia saligna*. Planted pine trees currently cover approximatively 224.5 ha, while *A. saligna* is colonising the understorey and the open areas of the dune system.

For what concerns the conservation status of the Sardinian pine stands, they mostly fall within protected areas. All *P. halepensis* stands on the Island of San Pietro fall within the SAC ITB040027, (Isola di San Pietro) while almost all the stands of the coastal areas of south-western Sardinia are included in the SAC ITB0400025, (Promontorio, dune e zona umida di Porto Pino). Only the small portion present on the Island of Sant'Antioco and the southernmost fragment of the stand of Porto Pino is not included in any protected area. Moreover, this latter is part of the military polygon of Capo Teulada and was partly damaged by the military activities in the past. Among Sardinian native pines, *P. halepensis* is the only species whose woods fall in both habitat 2270* and habitat 9540 (Table 2).

About *P. pinaster* subsp. *pinaster* stands, the northernmost is included in the SAC ITB012211, (Isola Rossa - Costa Paradiso). The stands of Monte Limbara are part of the SAC ITB011109. At both sites, *P. pinaster* subsp. *pinaster* woods are within the community habitat 9450. On the other hand, the *P. pinaster* subsp. *pinaster* stands of Monti Ultana and Monte Nieddu are not inserted in any protected area but can be also classified within habitat 9540. Finally, *P. pinea* woods are included in the SAC ITB042247, (Is Compinxius - Campo dunale di Buggerru - Portixeddu). These natural pine stands are within the priority habitat 2270*, although without a clear distinction with pine plantations. Recent studies have clarified some ecological aspects about the priority habitat 2270*, mainly considering *P. pinea* stands of the Tyrrhenian shores of central Italy and partly those of the North Adriatic coast (Bonari *et al.* 2017, 2018; Sarmati *et al.* 2019). However, further studies considering the old-established plantations are needed for this habitat in Sardinia, where only natural woods have been in the spotlight (Calvia *et al.* 2021). In line with this, it is worth recalling that determining whether a pine stand is of native or planted origin was not always straightforward. However, in our study, this effort was necessary for a reliable accounting of the forest surface (see Chiarucci & Piovesan 2020). In Sardinia, pines were planted in vast areas of the island during the 20th century (D'Autilia *et al.* 1967a). In this paper therefore, we have considered as native not only those stands whose ancient presence in the island was confirmed by historical documents, but also those stands whose presence was supported by LEK, and those which developed spontaneously by means of natural seed dispersal from strictly native trees.

4.2 Pine wood changes between the 20th and 21st centuries reflect the land-use change

The results of our study shed light on the landscape transformations observed in Sardinia for over 60 years. The total distribution of native pine woods in Sardinia, as for other species, has been affected during the last centuries by strong human pressure (Angius 1851, Spano 1958; Desole 1960, 1964; Arrigoni 1967). The interpretation of the aerial photographs has allowed us to confirm that the pine species were at their minimum in post-World war II, and to estimate the increase in canopy cover that occurred during the last decades. This is in line with the increasing trend of forest areas in Sardinia, Italy and other European regions (Poyatos *et al.* 2003; Falcucci *et al.* 2007; Gehrig-Fasel *et al.* 2007; Puddu *et al.* 2012; Barbati *et al.* 2013; Smiraglia *et al.* 2015; Ferretti et al. 2018). The recent expansion of the pine stands can be explained by the fact that they are pioneer species, especially *Pinus halepensis* and *P. pinaster* subsp. *pinaster*, and can therefore rapidly recolonise degraded lands (Barbéro *et al.* 1998).

The first mention of *P. halepensis* in Sardinia dates to 1737 and specifically refers to the Island of San Pietro, which was described as rich in pine woods (Arrigoni 1967). Since then, in a short time frame, this surface was greatly reduced, mostly as a consequence of frequent wildfires (De Marco & Mossa 1980). The constant increase of these pine woods has led to reach the current 770 ha.

Historical data reported *P. pinaster* subsp. *pinaster* at some places where it no longer grows (Angius 1851; Desole 1960). The many toponyms found in north-eastern Sardinia, as well as some confirmation by LEK and literature, helped in depicting a former distribution of *P. pinaster* subsp. *pinaster* with a larger extent, if compared to the current one. Conversely, the constant increase in *P. pinaster* subsp. *pinaster* woods cover is primarily due to the reduction of agropastoral activities such as ploughing, cutting of Mediterranean scrubland and, especially, the annual burning of scrublands for obtaining cattle and goat pastures (Desole 1960; Piussi 2005; Mancino *et al.* 2014; Camarretta *et al.* 2017). The creation of vast protected areas allowed the recovery of more natural conditions. However, several non-native species were also planted in reforestation, such as *Abies cephalonica*, *Cedrus atlantica*, *P. nigra* subsp. *laricio* (Calvia & Ruggero 2020).

P. pinea is the only species that, during the examined decades, maintained in Sardinia a rather constant distribution area. This is due to its extremely limited distribution on the island. Moreover, these stands remained isolated in some portions of the dune system that did not differ much, except for the afforestation started in 1958 around the historical natural stand (Arrigoni 1967). A very small decrease was observed between 1955 and 1977. Since then, the main stands had a small increase, mainly in the innermost parts of the dune, i.e., those not reached by any intervention of afforestation.

Despite the native pine wood extent increase, these woods are often invaded by alien species. Specifically, the current invasion by *Acacia saligna*, in the long term, could affect the natural wood patches referred to in the EU priority habitat 2270*, as already shown both in Sardinia and in other Italian regions (e.g., Del Vecchio *et al*. 2013; Lozano *et al*. 2020). Similarly, the diffusion of alien conifers spreading from reforestation affects the habitat 9540 in mountain and hill contexts (Calvia & Ruggero 2020). The other two factors limiting the expansion and quality of pine stands, are related to urbanisation, as well as to the pressure of agropastoral activities.

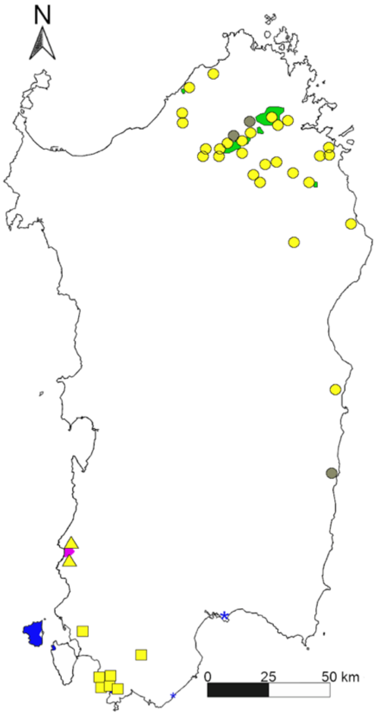

Figure 3 – Map of toponyms referred to natural pine stations found in Sardinia (toponyms related to planted pines were not mapped). Blue, green and magenta areas represent the current extent of Pinus halepensis*,* P. pinaster *subsp.* pinaster *and* P. pinea*, respectively. Yellow squares, circles and triangles indicate the toponyms related to each pine species (*P. halepensis*,* P. pinaster *subsp.* pinaster*,* P. pinea*, respectively) found in our study; grey circles identify the* P. pinaster *subsp.* pinaster *sites reported in the literature but currently extinct.*

5. **Conclusions**

Our study contributes to better understand the past and present distribution of *Pinus halepensis*, *P. pinaster* subsp. *pinaster* and *P. pinea* in Sardinia and their associated habitats 2270* and 9540.

The three species grow in the same areas where they were historically mentioned. However, there is a trend of expansion that is occurring in the pine wood habitats of Sardinia during the last decades, with a recovery pattern two times faster than the average forest recovery of Sardinia. In particular, *P. halepensis* and *P. pinaster* subsp. *pinaster* native woods are facing an important increase in their distribution, while *P. pinea* is rather stable. Nevertheless, especially *P. halepensis* and *P. pinaster* subsp. *pinaster* woods are still far from reaching the distribution range. The search of toponyms highlighted an important loss of pine woods area, presumably occurred between the 19th and the first half of 20th century, that affected *P. pinaster* subsp. *pinaster* stands and, to a lesser extent, *P. halepensis*.

This study informs about the distribution of the two EU habitats structurally characterised by Mediterranean pines in Sardinia, i.e., 2270* and 9540, including problematic aspects such as the identification of old-established plantations that are frequently difficult to be recognised if not with local knowledge, thus strengthening the importance of LEK in ecological studies. From the conservation perspective, large parts of the native pine wood habitats are currently protected.

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Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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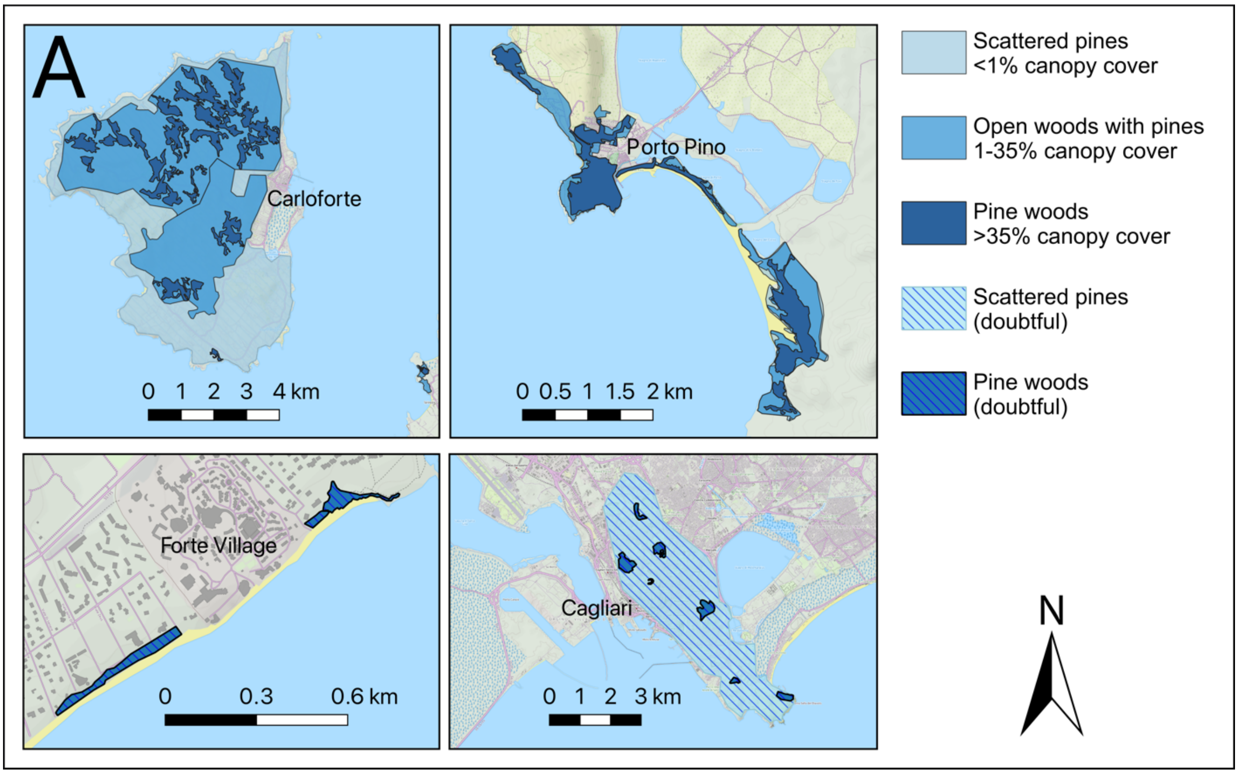
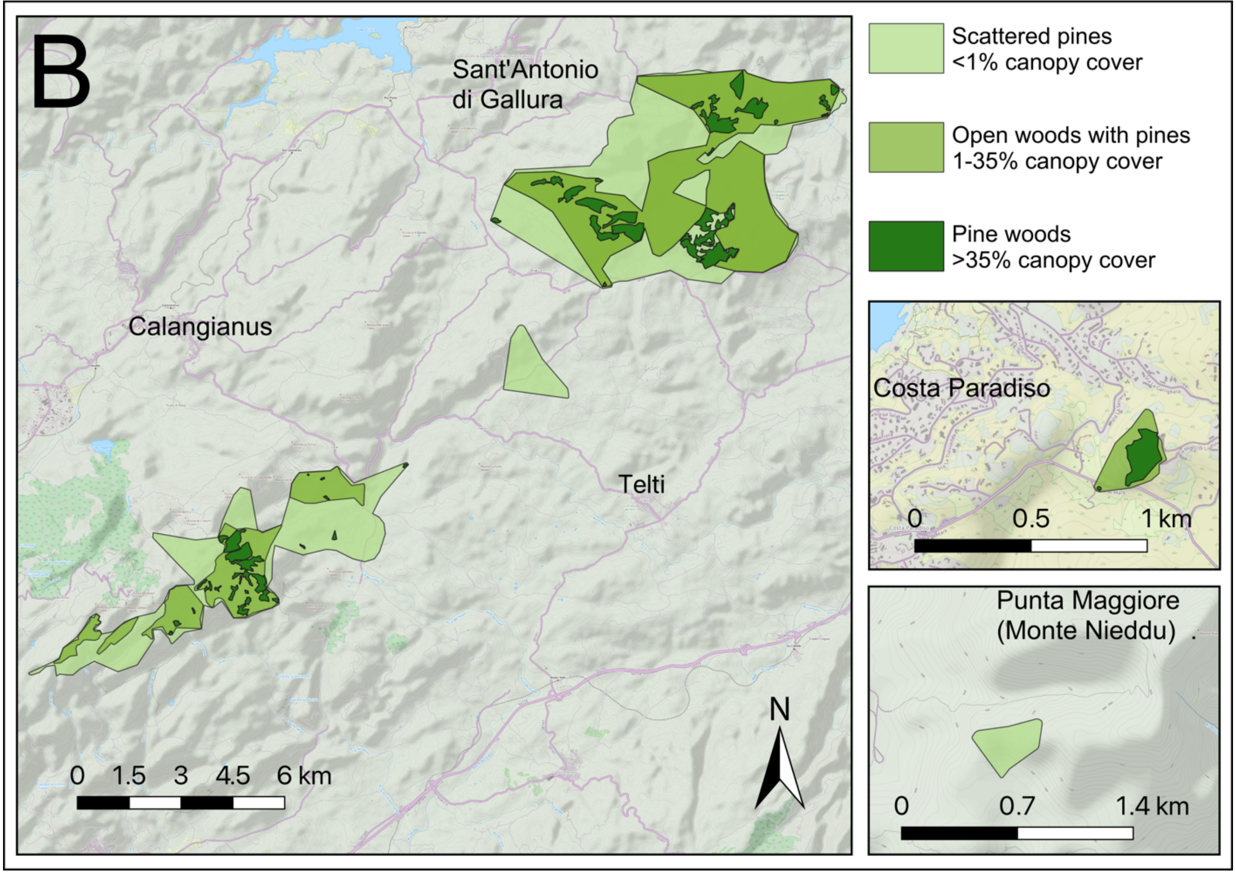
7. Appendices





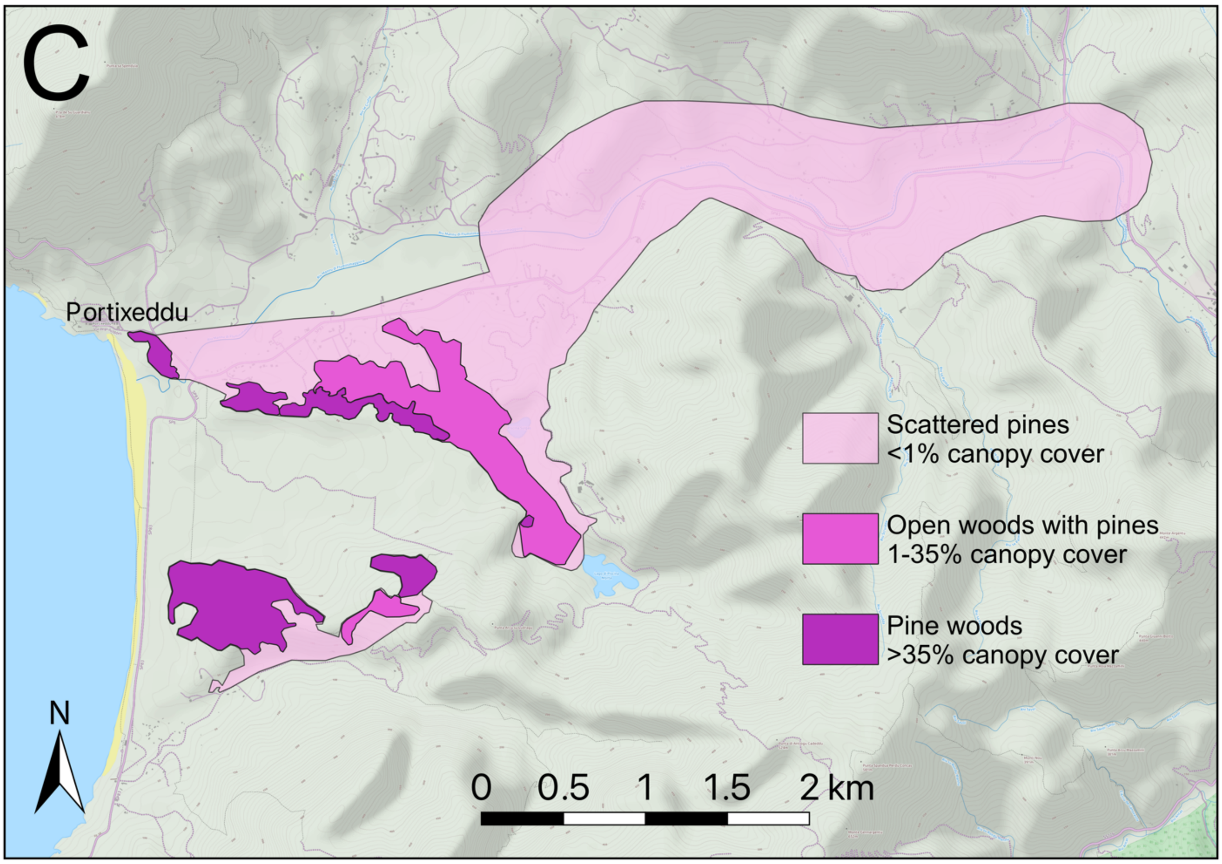


Figure S1 – Maps of the current distribution for the three pine species in Sardinia (Italy). A = Pinus halepensis *stands; B =* Pinus pinaster *subsp.* pinaster *stands; C =* Pinus pinea *stands. Shades of colour refer to different canopy covers. Aerial photographs from 2016 were taken from RAS (2019).*

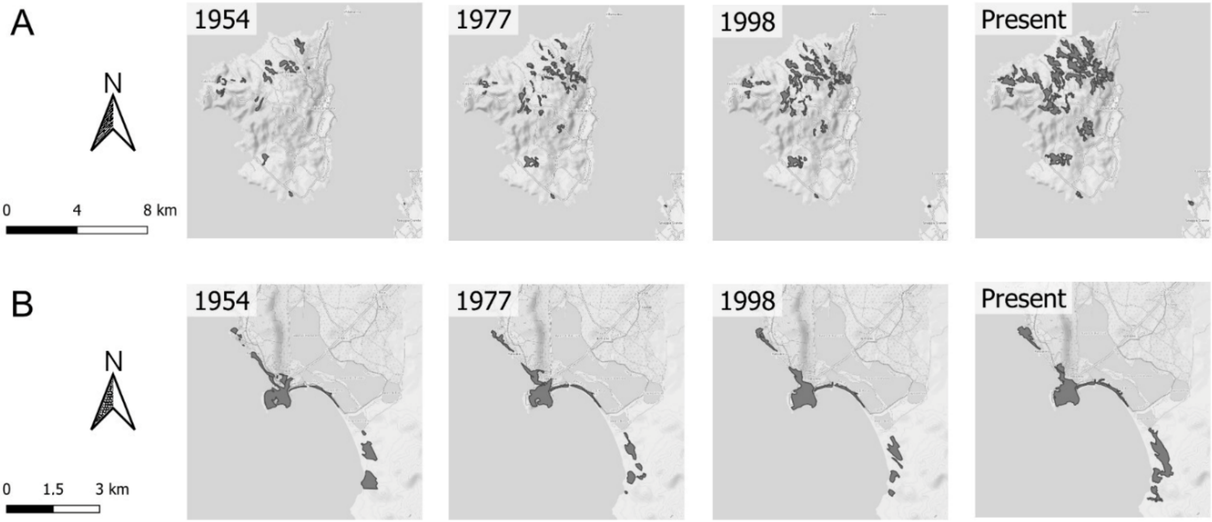


Figure S2 – Pinus halepensis *wood changes from 1954 to 2016. A = Island of San Pietro and Calasetta (Carloforte, Calasetta; Sud Sardegna); B = Porto Pino zone (Sant'Anna Arresi, Teulada; Sud Sardegna).*

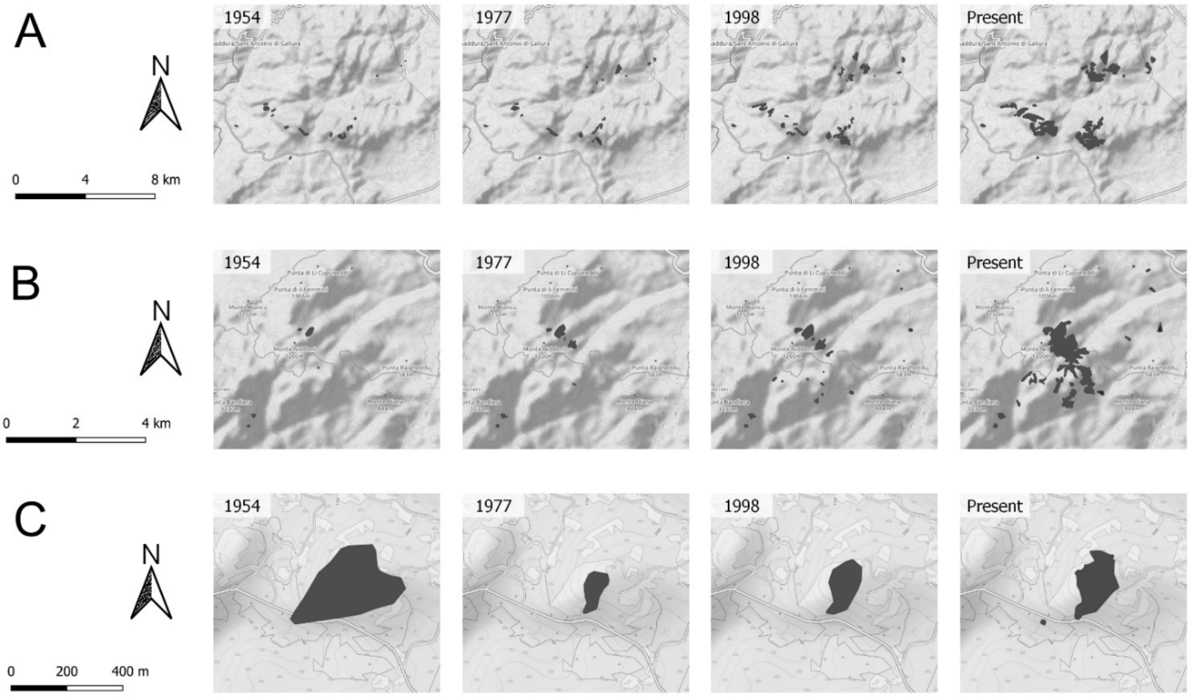


Figure S3 – Pinus pinaster *wood changes from 1954 to 2016. A = Mounts Ultana chain (Olbia, Sant'Antonio di Gallura, Telti; Sassari); B = Mount Limbara (Berchidda, Calangianus; Sassari); C = Costa Paradiso (Trinità d'Agultu; Sassari).*

Figure S4 – Pinus pinea *wood changes from 1954 to 2016. A = Portixeddu dune system (Buggerru; Sud Sardegna).*

Table S1 – List of the pine-related toponyms found during this research referring to natural stands.

Toponym	Municipality	Biogeographic sector	Biogeographic subsector	Coordinates (UTM)	Elevation range (m a.s.l.)	Current status	Species	Sources
Pinuitteddu (Small Pine)	Aglientu	Goceano-Logudorese	Gallurese	507811.18 E – 4551455.05 N	90-125	Extinct	*P. pinaster*	6
Monti di Lu Pinu (Mount of the Pine)	Trinità d'Agultu	Goceano-Logudorese	Gallurese	496840.07 E – 4544773.58 N	150-230	Extant	*P. pinaster*	5, 6
Punta di Pinu (Peak of Pine)	Trinità d'Agultu	Goceano-Logudorese	Gallurese	496189.56 E – 4534338.47 N	490-500	Extinct	*P. pinaster*	6
Li Pini (The Pines)	Viddalba	Goceano-Logudorese	Gallurese	496243.61 E – 4533587.15 N	400-460	Extinct	*P. pinaster*	6
Pinu Toltu (Bent Pine)	Calangianus	Goceano-Logudorese	Gallurese	522898.17 E – 4532341.02 N	500-550	Extinct	*P. pinaster*	6
Monte Pino (Mount of Pine)	Telti/Olbia	Goceano-Logudorese	Gallurese	531484.94 E – 4532820.26 N	500-720	Extant	*P. pinaster*	1, 3, 6
Sarra di Monte Pino (Ridge of Pine's Mount)	Olbia	Goceano-Logudorese	Gallurese	532273.49 E – 4532301.38 N	400-600	Extant	*P. pinaster*	4, 6
Campo di Pino (Field of Pine)	Olbia	Goceano-Logudorese	Gallurese	536515.28 E – 4532546.76 N	120-150	Extinct	*P. pinaster*	6
Rio Lu Pinu (Stream of the Pine)	Tempio Pausania	Goceano-Logudorese	Gallurese	504775.14 E – 4519989.89 N	350-500	Extinct	*P. pinaster*	6
Contra di Lu Pinu (Crest of the Pine)	Tempio Pausania	Goceano-Logudorese	Gallurese	504726.77 E – 4519796.85 N	500-550	Extinct	*P. pinaster*	6
Monte Lu Pinu (Mount of the Pine)	Berchidda	Goceano-Logudorese	Gallurese	511968.57 E – 4520229.00 N	1050-1100	Extinct	*P. pinaster*	6
Funtana 'e Su Pinu (Fountain of the Pine)	Berchidda	Goceano-Logudorese	Gallurese	512213.36 E – 4520442.13 N	1050	Extinct	*P. pinaster*	7, 8
La Pineta (The Pinewood)	Tempio Pausania	Goceano-Logudorese	Gallurese	515197.84 E – 4523136.06 N	1150-1200	Extinct	*P. pinaster*	6
Canale Su Pinazzu (Creek of the Ruined Pine)	Berchidda	Goceano-Logudorese	Gallurese	519106.93 E – 4520893.44 N	530-580	Extinct	*P. pinaster*	6, 7
Scala di Li Pini (Passageway of the Pines)	Calangianus	Goceano-Logudorese	Gallurese	517996.41 E – 4523517.07 N	900-1050	Extant	*P. pinaster*	7
Pinitteddi (Small Pines)	San Teodoro	Goceano-Logudorese	Gallurese	553755.25 E – 4520988.62 N	170-200	Extinct	*P. pinaster*	6
Sarra di Lu Pinu (Ridge of the Pine)	San Teodoro	Goceano-Logudorese	Gallurese	551270.12 E – 4519626.26 N	170-220	Extinct	*P. pinaster*	6
Punta di Lu Pinu (Peak of the Pine)	San Teodoro	Goceano-Logudorese	Gallurese	552286.30 E – 4519440.47 N	350-390	Extinct	*P. pinaster*	6
Su Pinu (The Pine)	Berchidda	Goceano-Logudorese	Gallurese	525291.64 E – 4510700.08 N	540-560	Extinct	*P. pinaster*	6
Rio Su Pinu (Stream of the Pine)	Monti	Goceano-Logudorese	Gallurese	525632.90 E – 4510268.78 N	500-550	Extinct	*P. pinaster*	6
Punta Matta 'e Pinu (Peak of the Pines' Grove)	Monti	Goceano-Logudorese	Gallurese	528992.55 E – 4515598.71 N	580-600	Extinct	*P. pinaster*	6, 7
Monte Pinigheddu (Mount of the Small Pine)	Monti	Goceano-Logudorese	Gallurese	531681.67 E – 4516615.02 N	480-520	Extinct	*P. pinaster*	6
Monte di Pinu (Mount of Pine)	Olbia	Goceano-Logudorese	Gallurese	539021.05 E – 4512550.83 N	480-700	Extinct	*P. pinaster*	6
Punta Sos Pinos (Peak of the Pines)	Padru	Goceano-Logudorese	Gallurese	547564.29 E – 4508395.73 N	680-800	Extant	*P. pinaster*	5, 6
Cuccuru 'e Pinu (Peak of Pine)	Onanì	Goceano-Logudorese	Nuorese	539839.43 E – 4485901.58 N	340-350	Extinct	*P. pinaster*	6
Su Pinu (The Pine)	Siniscola	Supramontano	Baronico	562551.72 E – 4493515.92 N	5-10	Extinct	*P. pinaster*	1, 6
Su Oppinu (The Pine)	Triei	Turritano-Campidanese	Ogliastrino	556805.65 E – 4428984.82 N	200-300	Extinct	*P. pinaster*	6
Is Compinxius (The Pines)	Buggerru	Sulcitano-Iglesiente	Iglesiente	450397.78 E – 4365485.89 N	10-80	Extant	*P. pinea*	1, 6
Is Compinxeddus (The Small Pines)	Buggerru	Sulcitano-Iglesiente	Iglesiente	450144.11 E – 4364345.41 N	40-120	Extant	*P. pinea*	7
Punta Su Pineddu (peak of the small pine)	Santadi	Sulcitano-Iglesiente	Sulcitano	480530.03 E – 4324465.12 N	489	Extinct	*P. halepensis*	2, 7
Bau Cumpingiu (Ford of Pine)	San Giovanni Suergiu	Sulcitano-Iglesiente	Antioco-Carlofortino	455534.93 E – 4333591.54 N	40-50	Extinct	*P. halepensis*	7, 9
Porto Pino (Pine's Harbour)	Sant'Anna Arresi	Sulcitano-Iglesiente	Antioco-Carlofortino	464771.31 E – 4312964.64 N	2-30	Extant	*P. halepensis*	1, 6
Porto Pinetto (Harbour of the Small Pine)	Sant'Anna Arresi	Sulcitano-Iglesiente	Antioco-Carlofortino	463844.29 E – 4313736.99 N	5-30	Extant	*P. halepensis*	2, 6
Punta Su Pineddu (Peak of the Small Pine)	Sant'Anna Arresi	Sulcitano-Iglesiente	Antioco-Carlofortino	464460.30 E – 4313696.03 N	30-50	Extant	*P. halepensis*	2, 6
Porto Pineddu (Harbour of the Small Pine)	Sant'Anna Arresi	Sulcitano-Iglesiente	Antioco-Carlofortino	464597.06 E – 4312422.41 N	1-30	Extant	*P. halepensis*	2, 6
Funtana de is Opinos (Fountain of the Pines)	Teulada	Sulcitano-Iglesiente	Antioco-Carlofortino	467510.84 E – 4310891.39 N	15-20	Extant	*P. halepensis*	6

Table S2 – List of the pine-related toponyms found during this research referring to planted pines or personal names.

Toponym	Municipality	Biogeographic sector	Biogeographic subsector	Coordinates (UTM)	Elevation range (m a.s.l.)	Current status	Species	Sources
Stazzo di Lu Pinu (the farm of the pine)	Arzachena	Goceano-Logudorese	Gallurese	530234.18 E – 4548892.05 N	140-150	Planted	*P. pinea*	6, 7
Lu Pinu (the Pine)	Calangianus	Goceano-Logudorese	Gallurese	516183.07 E – 4529653.58 N	500	Planted	*P. pinea*	7
Tanca Su Pinu (acreage of the Pine)	Sassari	Turritano-Campidanese	Turritano	467124.56 E – 4511322.47 N	250	Planted	Uncertain	6
Punta di Lu Pinu (peak of the pine)	Loiri - Porto San Paolo	Goceano-Logudorese	Gallurese	540834.23 E – 4521884.89 N	43	Planted	Uncertain	7, 9
Rio Pretu e Pinu (stream of Peter and Joseph)	Lodè	Goceano-Logudorese	Nuorese	548694.32 E – 4490085.09 N	220-390	Personal name		6, 7
Riviera dei Pini (coast of the pines)	Budoni	Supramontano	Baronico	563336.09 E – 4502053.19 N	5	Planted	*P. pinea*	6
Mulino Su Pinu (Mill of the pine)	Mamoiada	Goceano-Logudorese	Nuorese	525309.34 E – 4452559.54 N	640	Planted	Uncertain	9
Casa Pineddu (Pineddu's house	Cardedu	Campidanese-Turritano	Ogliastrino	552658.17 E – 4404486.40 N	37	Surname		6, 7
Poggio dei Pini (hill of the pines)	Capoterra	Campidanese-Turritano	Campidanese	496868.39 E – 4332969.52 N	75-110	Planted	*P. pinaster*	2
Su Pineddu (the small pine)	Capoterra	Campidanese-Turritano	Campidanese	494471.65 E – 4332337.64 N	308	Planted	*P. pinaster*	9
Riva dei Pini (seashore of the pines)	Pula	Sulcitano-Iglesiente	Sulcitano	493012.58 E – 4308520.49 N	5	Planted	*P. pinea*	2, 6
Pinus Village	Pula	Sulcitano-Iglesiente	Sulcitano	492107.16 E – 4307783,55 N	10-60	Planted	*Pinus* spp.	2, 9

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Chapter 3

From real to potential distribution: the case of study of *Taxus baccata* L. in Sardinia

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Contribution to the project – I participated to the collection of the data and organised the dataset. I leaded the preparation of the manuscript, which was implemented and reviewed by the contributions of the co-authors.

Abstract – *Taxus baccata* L. is a relic species declining in many areas of its range, especially in Mediterranean areas. In the Island of Sardinia, which is close to the southern border of the species range, it is still present in many mountain areas. In this study we found 234 growing stations of the species, mostly distributed in the northern and central mountains. In the island the species is indifferent to substrata and prefers moist sites with northern aspects. The average elevation range of the species is from 695 to 1225 m a.s.l. In this study, to predict the current potential distribution of this species, we applied the maximum entropy algorithm (MaxEnt), together with the collection of data from literature and field. In total, 202 field-based sites and 19 bioclimatic variables were used to model the potential distribution area under the climatic current conditions. Annual precipitation, together with mean temperature of the warmest month and isothermality were the key drivers for the distribution of *T. baccata*. If considering permutation importance, mean diurnal range and precipitation of the warmest quarter were the main environmental variables. The response curves showed that this species prefers habitats with annual mean temperature ranging from 8.65 to 12.55 °C and annual mean precipitation from 770 to 1085 mm. Most of the potential current suitable conditions were found in the northern and central parts of the island, as confirmed by field findings. Currently, the majority of Sardinian *T. baccata* populations have an unbalanced structure, being mostly composed of mature to old trees, with a scarce or absent renewal. Moreover, we highlighted the high number of dead trees found during this research. This loss of samples appears to be related to climate change and poses an increasing concern about the future of the species and the priority habitat in many parts of Sardinia.

1. **Introduction**

Taxus baccata L. (yew) is an evergreen, non-resinous gymnosperm tree, with a fragmented Eurasian distribution, extending northwards to Great Britain, Norway, Sweden and Estonia, southwards to Spain, Italy, Greece and North Africa, westwards to Azores and Madeira archipelagos, and eastwards to Ukraine, Anatolia, Caucasus, and Iranian mountains (Thomas & Polwart 2003; Charco 2007; Schirone *et al*. 2010; Vessella *et al*. 2013; Romo *et al*. 2017; Ahmadi *et al*. 2020). *T. baccata* is considered a relic species of Tertiary origin, often threatened within its natural range, being locally extinct or progressively decreasing over the past millennia in many parts of Europe (Hulme 1996; García *et al*. 2000; Dhar *et al*. 2006; Linares 2013; Iszkuło *et al*. 2016). The main causes of yew decline are climatic factors, human pressure, grazing, poor competitive ability, changes in rain distribution, droughts, fungal infections, dioecy related problems (Svenning & Magärd 1999; Iszkuło 2001; Thomas & Polwart 2003; Kassioumis *et al*. 2004; Mysterud & Østbye 2004; Farris & Filigheddu 2008; Iszkuło 2011; Linares 2013; Iszkuło *et al*. 2014; Devaney *et al*. 2015; Garbarino *et al*. 2015). In southern Europe and North-Africa, yew decline was often attributed to climate change (Anzalone *et. al*. 1997; Thomas & García-Martí 2015; Romo *et al*. 2017). In the southern areas of Europe, a local increase in yew populations has been observed, where more suitable climatical conditions exist (Carvalho *et al*. 1999; Cortes *et al*. 2000; Kassioumis *et al*. 2004; Fernandez-Manso *et al*. 2011; Serra & García-Martí 2011). Anyway, natural regeneration of *T. baccata* is often scarce (Iszkuło & Boratyński 2006; Ruprecht *et al*. 2010), in general because of intensive human land-use (O'Connell & Molloy 2001; Thomas & Polwart 2003) and forest management, which changed the vegetation structure and species composition since the Neolithic Age (Jahn 1991; Svenning & Magård 1999; Thomas & Polwart 2003). As a result of this regression, yew occurrence is often scattered, normally limited to mountain areas and on shady northern slopes (García *et al*. 2000; Thomas & Polwart 2003).

The critical conditions of yew populations across their range have led to many concerns over its long-term future (Dhar *et al*. 2006; Iszkuło et al. 2009; Linares 2013). This species is now legally protected in a number of European countries (Hageneder 2007) and has priority status under the EU Habitats Directive (European Commission 2013), because its habitats (Mediterranean *Taxus baccata* woods 9580* and Apennine beech forests with *Taxus* and *Ilex* 9210*) are listed with priority rank in the European Habitat Directive 92/43/EEC (European Commission 1992), established to conserve its natural distribution (Svenning & Magärd 1999; Thomas & Polwart 2003; Mysterud & Østbye 2004; Iszkuło *et al*. 2016).

In Italy, *T. baccata* is diffuse in all the administrative regions, although rare in many of them (Pignatti 2017-2019). In recent years, some studies have been carried out to explain different features concerning yew ecology and its regeneration (e.g., Piovesan *et al*. 2009; Scarnati *et al*. 2009; Salis 2011). Some of them interested specifically Sardinian yew populations (Bacchetta & Farris 2007; Farris & Filigheddu 2008; Farris *et al*. 2012).

Species Distribution Models (SDMs), and Ecological Niche Models (ENM) are statistical tools that correlate the observed occurrence of species and a combination of environmental abiotic factors allowing it to survive, persist and preserve durable populations (Guisan & Zimmermann 2000; Peterson *et al*. 2011). For their use in estimates of the current, past and predicted future potential distribution of species, they represent important tools of study (Scoble & Lowe 2010; Svenning *et al.* 2011). Moreover, ENMs allow a comparison between theoretical and real species distributions, thus involving or suggesting concerns about biogeography, evolutionary ecology, conservation and restoration measurements, as well as in species invasion monitoring (Anderson *et al.* 2003; Peterson 2006). Normally, three groups of explanatory variables are used: climatic or bioclimatic (temperature, rainfall and evapotranspiration), topographical (e.g., elevation, slope, aspect) and geological (e.g., lithology, pedology). This information can be set in a grid of points by means of Geographic Information Systems (GIS) allowing to determine the suitability of the presence for the studied species at each point. Then, the information is frequently expressed as values between zero (meaning no suitability) and one (high suitability). The resulting data, based on the species' niches, identified as fundamental niches by Hutchinson (1957), is described by a map that reflects the potential distribution of the target species (Anderson *et al.* 2003). Among the many applications of these models, the prediction of potential distributions of plant species under climate changes are more and more used in ecological studies (Vessella & Schirone 2013; López-Tirado & Hidalgo 2014; Abdelaal *et al.* 2019; Ahmadi *et al.* 2020).

Few studies have been done on modelling the distribution of *T. baccata* during the last years (Harrison et al. 2001; Svenning & Skov 2004; Ahmadi *et al.* 2020). While in the UK and Ireland the effect of climate change suggests little change on *T. baccata* distribution (Harrison *et al.* 2001), at a general European level it was shown that yew currently only occurs in half of the potentially suitable areas from a bioclimatic point of view, because of range contractions due to human overexploitation and management practices (Svenning & Skov 2004). Finally, it was predicted a strong reduction of suitable sites for the species during the 21st century in the Hyrcanian mountains in Iran (Ahmadi *et al.* 2020).

To better understand the climatic factors influencing the yew's present distribution in the Mediterranean context, we embarked in the first study aiming at modelling and quantifying its present distribution in a large Mediterranean island, Sardinia (Italy).

Specific main aims of this study were to: i) identify and describe the current distribution of *T. baccata* in Sardinia from a climatic point of view; ii) recognise the general state of health of these communities; iii) obtain a high-resolution potential distribution map of the species in Sardinia.

2. **Material and methods**

2.1 Study area

Sardinia has an area of 24,090 km², including smaller islands and islets (Figure 1). From a geological point of view, granitic substrates dominate mostly the eastern half of the island, while effusive rocks predominate in the western part. Nonetheless, sedimentary carbonate reliefs and metamorphic ones as well are diffuse in several parts of Sardinia, from north to south (Carmignani *et al.* 2001). The climate of Sardinia is prevalently Mediterranean and has a characteristic seasonality, with mild-wet winters and dry-hot summers (Bacchetta *et al.* 2009; Canu *et al.* 2015). Two macro-bioclimates, seven thermometric belts, and 43 isobioclimates have been recently recognised (Canu *et al.* 2015).

Biogeographically, Sardinia is part of the Italo-Tyrrhenian Superprovince (Ladero-Alvarez 1987; Bacchetta *et al*. 2013). More specifically, it represents the Sardinian-Corsican province together with Corsica and Tuscan Archipelago (Bacchetta *et al*. 2012; Bacchetta *et al*. 2013). The island has been recently divided in 6 sectors and 22 subsectors by Fenu *et al*. (2014).

The human activities, during the 19th century and the first half of the 20th one, have strongly affected the island, mainly due to intense land-use, often in the form of wildfires, cuttings, agriculture, pastoralism, industry, mining, and coastal exploitation for touristic purposes (e.g., Zucca *et al*. 2010; Caterini 2013).

2.2 Target species

Taxus baccata is a small tree, sometimes capable of reaching a height up to 20(-28) m (Thomas & Polwart 2003). It is slow growing, and usually reaches sexual maturity at ca. 70 years, though in particular conditions female samples generate seeds at 30-35 years (Thomas & Polwart 2003). Yew is one of the few conifers capable of regenerating through vegetative reproduction (Benham *et al*. 2016) thus is often multi-stemmed (Piovesan *et al*. 2009). It is considered one of the longest-lived of all European trees, with estimated maximum ages of over 1,000, or even 5,000 years (Mitchell 1990; Pridnya 2002; Thomas & Polwart 2003).

This species can grow on almost all substrata (Thomas & Polwart 2003; Bacchetta & Farris 2007; Benham *et al*. 2016). Root system of yew is mostly shallow, but it is capable of penetrating the most compressed soils, meaning that it is able to grow under extreme conditions such as rocks and vertical cliffs (Benham *et al*. 2016).

Yews are dioecious, although single monoecious individuals are reported in literature (Pridnya 1984; Thomas & Polwart 2003; Iszkuło & Jasińska 2004). After wind pollination, they generate berry-like pseudo-fruits, constituted by a red fleshy aril surrounding the central seed (Stützel & Röwekamp 1999). The main yew-seed dispersers are frugivorous birds (e.g., *Turdus merula*, *T. philomelos*, *T. viscivorus*, rarely *Garrulus glandarius* and *Erithacus rubecula*) and mammals such as *Vulpes vulpes* and *Martes martes* (Farris & Filigheddu 2008). Seedlings emerge in the second spring after seed fall (Melzak & Watts 1982; Thomas & Polwart 2003).

Within its distributional area, *T. baccata* normally occupies the mid to lower layers of the forest, under the canopy of taller species (Król & Gołąb 1996). Nonetheless, pure yew stands can be found across many parts of its range (Farris *et al*. 2012; Thomas & García-Martí 2015).

2.3 Data collection and analysis

Occurrence and ecological data of *Taxus baccata* in Sardinia were assembled from different sources. We collected distributional information about *T. baccata* firstly from the literature (e.g., Desole 1948, 1966; Bacchetta & Farris 2007; Farris *et al*. 2012). Then, we found further information through the interviews to local people (landowners, forestry workers, elder of villages, environmental guides). Furthermore, we checked and updated all the information found by accomplishing several field excursions in the whole island of Sardinia, during the last 6 years (2015-2020), using ©Garmin GPS62st. A census of yews with stem Diameter at Breast Height (DBH) ≥ 4 cm has been performed in the whole Sardinia; diameter and sex determination have been recorded for adult trees. DBH for multi-stemmed trees has been recorded as average of diameters of all trunks (Vessella *et al*. 2015). We distinguished five classes of DBH: 4-10 cm (young fertile trees); 10.1-25 cm (adult trees); 25.1-50 cm (mature trees); 50.1-100 cm (old trees); >100 cm (senescent trees). Regeneration abundance (juveniles/hectare) was also estimated (in larger sites, where it was impossible to check entirely the areas, they were based on 20 × 20 m grid cells), then subdivided in 5 classes: absent; scarce (<1/ha); sporadic (1-2/ha); frequent (2-10/ha); abundant (>10/ha). Finally, we performed a census of dead samples, by counting all the individuals encountered (both long died stumps/fallen trees and recently dried up ones). On the base of dead trees per site, we calculated the ratio of dead yews in relation to living ones. We believe the number of polygons collected in this investigation significantly approximates the yew distribution in Sardinia.

To create the potential distribution of *Taxus baccata* in Sardinia, we worked with a final resolution of ca. 1 × 1 km, in order to facilitating analysis and subsequent models. Therefore, raster and shape files were transformed into a grid of points, each point being located in the centre of each pixel. We used 202 presence records for training, 67 for testing and 10,140 (background and presence) points to determine the MaxEnt distribution (background points and presence points), then the current distribution of *T. baccata* in the study area and to generate SDM. Then, 19 climate variables were considered for predicting potential occurrence of *T. baccata* and establish its distribution model under the current climate conditions (~1970-2000) (Table S1). Among them, 11 explanatory variables were related to temperatures, and eight to precipitations. These 19 variables were BIOCLIM climatic factors downloaded from WorldClim 2.1 project (Fick & Hijmans et al. 2017) at a spatial resolution of 30 arc-second (ca. 1 × 1 km).

To determine the accuracy of the resulting models, we computed the Area Under the Curve (AUC) of the Receiver Operating characteristic Curve (ROC). AUC score is the prevailing tool to measure the model performance, mainly due to its independence by threshold choices (Bosso *et al.* 2013; Fois *et al.* 2018). A higher value of AUC (closer to 1) means a better the performance of the model (Fielding & Bell 1997; Phillips *et al.* 2006). The generated AUC graph is obtained by plotting the true positive predictions (sensitivity) against the false positive predictions (1-specificity) (Fielding & Bell 1997).

The resulting logistic output of MaxEnt application is a map, indexing the environmental suitability of *T. baccata* with values ranging from 0 (unsuitable) to 1 (optimal). The MaxEnt results, imported into ArcGIS 10.4.1, allowed to obtain four classes of potential habitats: unsuitable (0-0.23), low potential (0.24-0.46), moderate potential (0.47-0.77) and high potential 0.78-1).

3. **Results**

3.1 Yew distribution in Sardinia

To realise this work, we mapped and georeferenced 234 Sardinian yew localities, referred to 16 mountain ranges (Table 1). The growing stations of yews found in this research are mostly concentrated in the northern and central part of Sardinia (Figure 1a), while in the southern one they are very rare. The richest sector of the island, *sensu* Fenu *et al.* (2014), is the Goceano-Logudorese, where 82 localities are known in seven different mountain systems. The total extent of the yew populations in this sector covers about 550 ha. The Supramontano sector follows with 78 localities, in two mountain massifs. Yews are there sparsely spread in 157 ha of surface. The Gennargenteo sector has 35 localities and 33 ha of surface, while the Barbaricino one has 34 sites with a surface of 105 ha. Finally, in the Sulcitano-Iglesiente sector there are five growing stations of yews, divided in two mountain chains and with a total area of 2.4 ha (Table 1). Though the elevation of yew populations in Sardinia extends from 45 m a.s.l. to 1,650 m a.s.l., the average elevation range is from 645 to 1,225 m a.s.l.

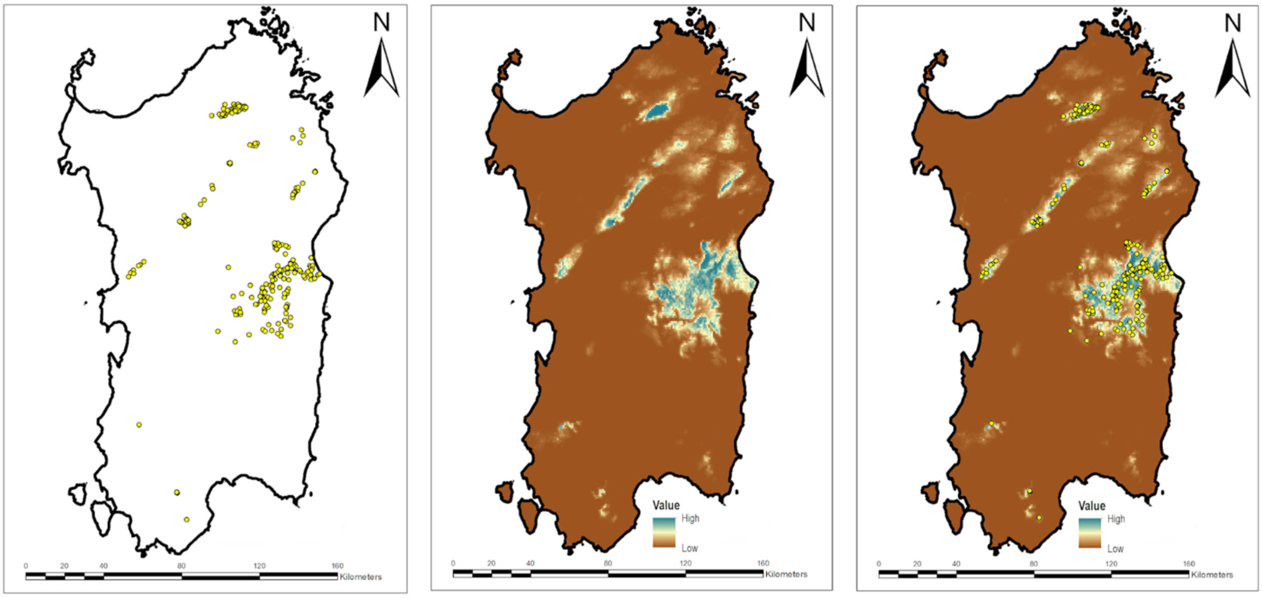

Figure 1 – Current Taxus baccata *distribution due to our findings (A); current potential distribution of* T. baccata *(B); comparison of current and potential distribution of* T. baccata *in Sardinia (C).*

Table 1 – Distribution of yews in Sardinia. All the sectors follow Fenu et al. (2014) and are abbreviated as follows: Barbar. = Barbaricino; Gennar. = Gennargenteo; Goc-Log. = Goceano-Logudorese; Sul-Igl. = Sulcitano-Iglesiente; Supram. = Supramontano.

Mountain area	Sector	Total area (ha)	Number of sites	Elevation range	Number of yews	Mean DBH (cm)
Monte Limbara	Goc-Log.	368	50	450-1350	ca. 2500	17.2
Monte Nieddu	Goc-Log.	11	4	260-700	133	44.4
Monti di Alà	Goc-Log.	90	5	725-1070	68	33
Monte Lerno	Goc-Log.	15	2	850-975	31	23.2
Montalbo	Supram.	18	17	650-1100	ca. 350	38.3
Goceano	Goc-Log.	41	5	950-1100	ca. 1000	28.1
Marghine	Goc-Log.	20	9	925-1180	ca. 450	50
Montiferru	Goc-Log.	6	7	620-900	41	38.3
Supramontes	Supram.	139	61	45-1450	ca. 800	60.8
M. San Basilio	Gennar.	5	1	955-1100	26	44.5
Gennargentu	Gennar.	30	34	890-1650	ca. 600	73.6
Ogliastra	Barbar.	65	31	750-1120	ca. 780	51.4
Sarcidano	Barbar.	22	1	650-750	122	18.2
Barbagia di Seulo	Barbar.	23	2	700-900	125	32
Monte Linas	Sul-Igl.	0.4	1	875-925	17	49

Monti del Sulcis	Sul-Igl.	2	4	535-900	45	25

The majority of the yew populations are represented by a small number of samples (Figure 2). The sites where the species was reported in the past but where it is now locally extinct represent 2% of the total. The presence of *Taxus baccata* is today limited to isolated trees in 16% of the total. The number of adult yews is limited to 2-10 samples in another 34% of the entire contingent of the yew sites in the island. Moreover, the species is present with a number of trees comprised between 11 and 50, in 32% of the sites. The number of localities with *T. baccata* having from 51 to 100 samples equals to 7% of the total. Finally, the sites where we counted more than 100 adult yew trees correspond to 9% of all the Sardinian populations.

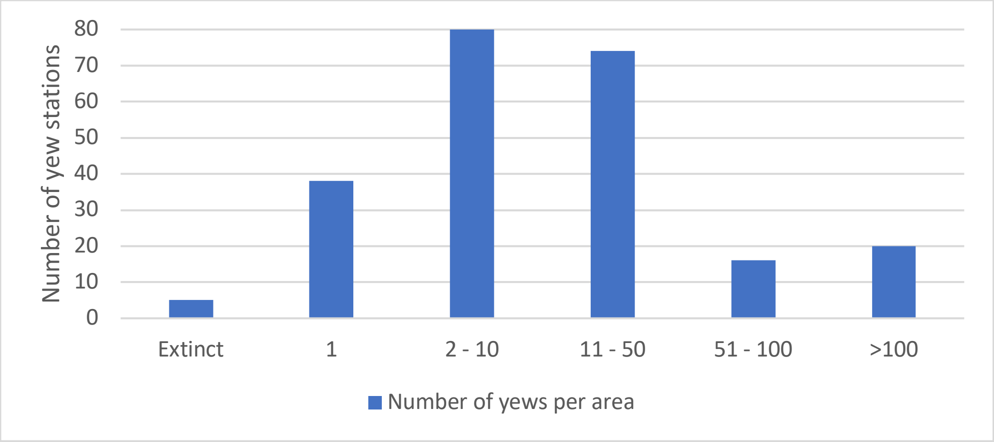

Figure 2 – Diagram showing the number of adult yew trees found during this study.

In terms of population structure, male trees prevail, being 2,330, corresponding to a total percentage of 56%. Female trees are 1,835 (44%) (Figure 3).

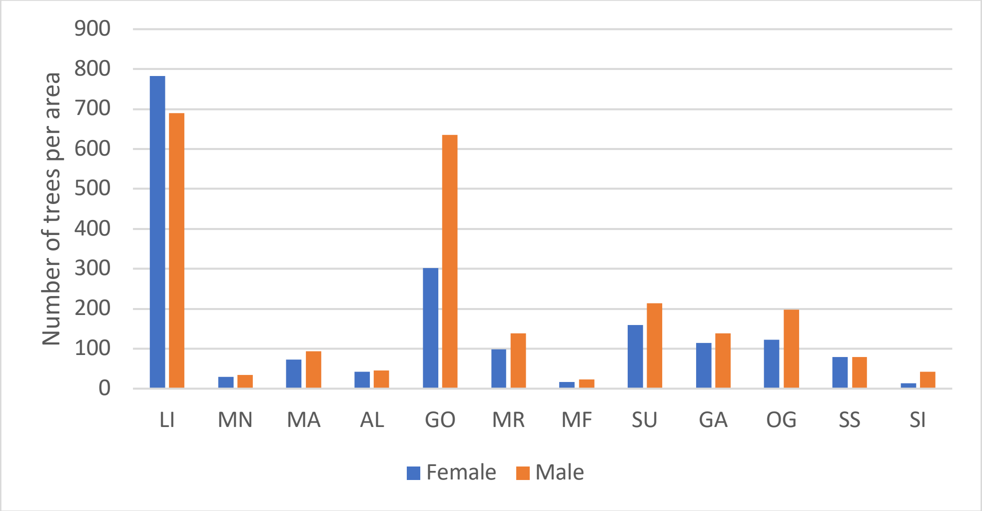

Figure 3 – Sex ratio of the Sardinian yew populations, divided for mountain areas: LI = Limbara; MN = Monte Nieddu; MA = Montalbo; AL = Monti di Alà/Lerno; GO = Goceano; MR = Marghine; MF =

Montiferru; SU = Supramontes; GA = Gennargentu; OG = Ogliastra; SS = Sarcidano/Seulo; SI = Sulcis-Iglesiente.

The yew populations of Sardinia are mostly represented by full grown trees (Figure 4). In particular, 27% of the total extent are young trees already capable of reproduction, 20% are adult trees, 30% are mature trees, 20% old growth trees, 3% senescent trees. Among the young fertile trees, we found that 86% of all the samples censused were located on Mount Limbara (northern Sardinia). On the contrary, the majority of areas are dominated by mature trees. Specifically, 41% of all mature trees is concentrated on the Montalbo and Supramonte massifs (eastern Sardinia). Finally, senescent trees are mostly concentrated on the Gennargentu massif (central Sardinia), where 55% of the total samples having a DBH >1 m was found.

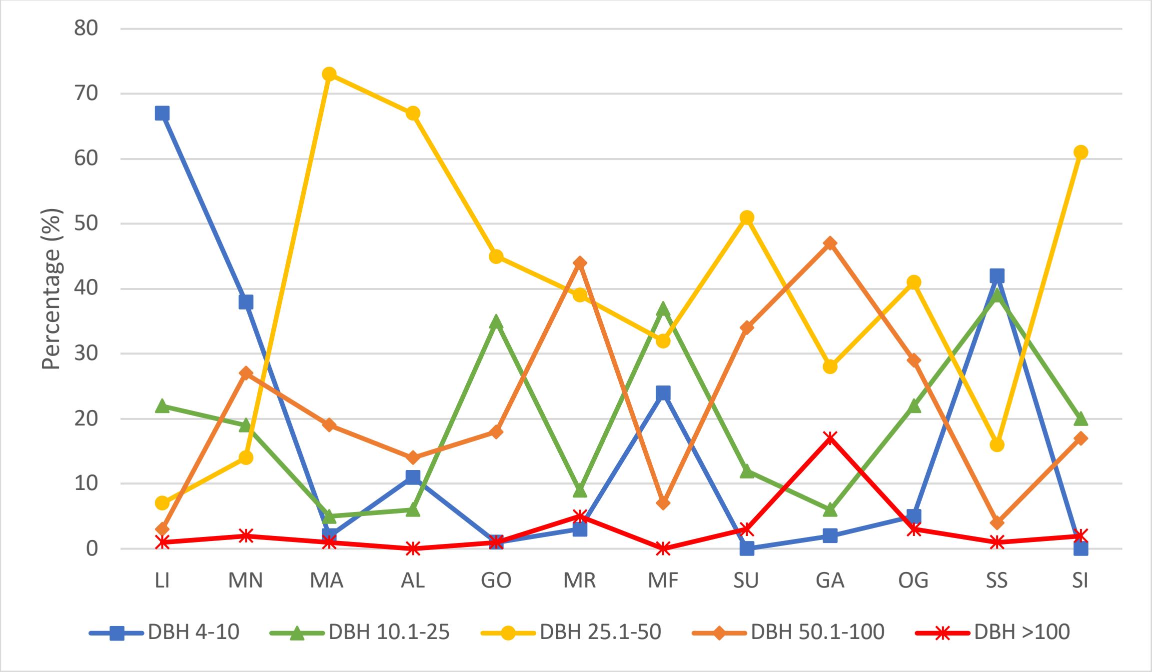

Figure 4 – Percentages of yew categories based on DBH (expressed in cm). Abbreviations are as in Figure 3.

For what concerns regeneration, Sardinian *Taxus baccata* populations are rather poor in recruitment (Figure 5). In fact, recruitment was abundant in only 3% of the sites. In 9% of sites, it was >10 plants per hectare. A lower presence of recruitment (from 2 to 10 plants per hectare) was observed in 16% of sites. On the other hand, in 12% of sites the regeneration was comprised between 1 and 2 plants per hectare. A further 8% showed a really scarce presence of recruitment (>1/ha). Finally, 55% of Sardinian yew populations showed an absence of both seedlings and saplings during our research. A total 127 sites had no recruitment among 234. While 37% of all the populations where recruitment was absent are located on the Supramontes, 57% of the populations with more abundant regeneration were found on the Limbara massif.

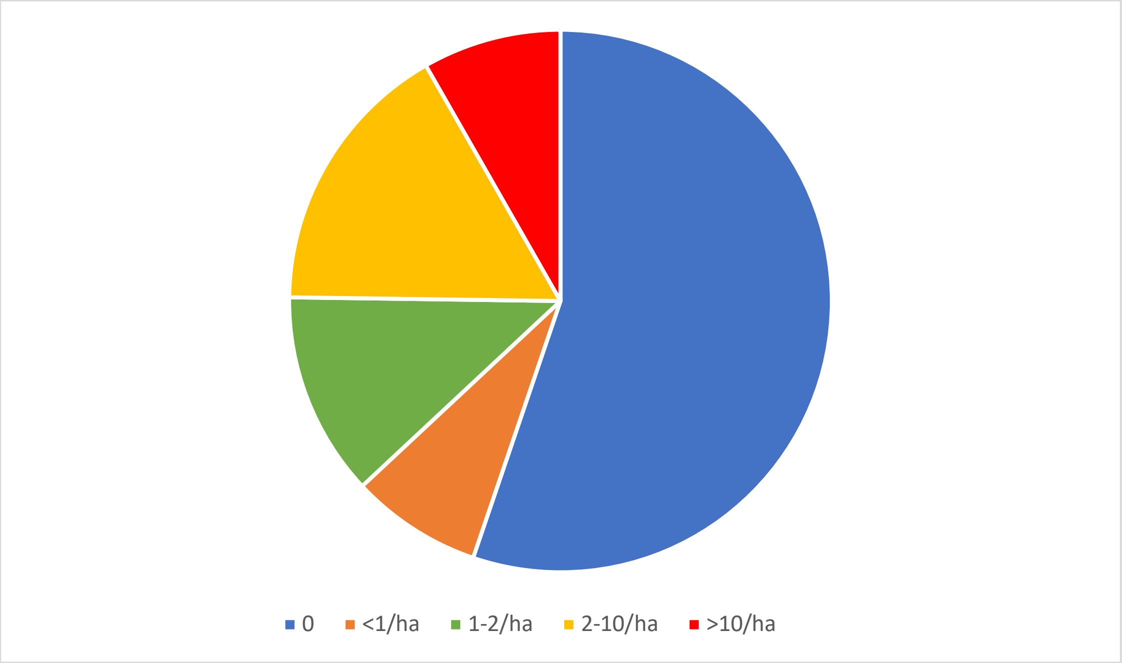

Figure 5 – Distribution of renewal in the Sardinian yew populations.

In the Sardinian yew populations, the declinate rate is often rather low: we found an abundant presence of dead trees in 3.4% of sites. In 4.3% of the sites dead yews were frequent. In another 7.3% of the sites there is a sporadic presence of dead yews. The presence of dead yew samples is scarce in 39% of sites, while in other 46% dead yews were absent (Figure 6).

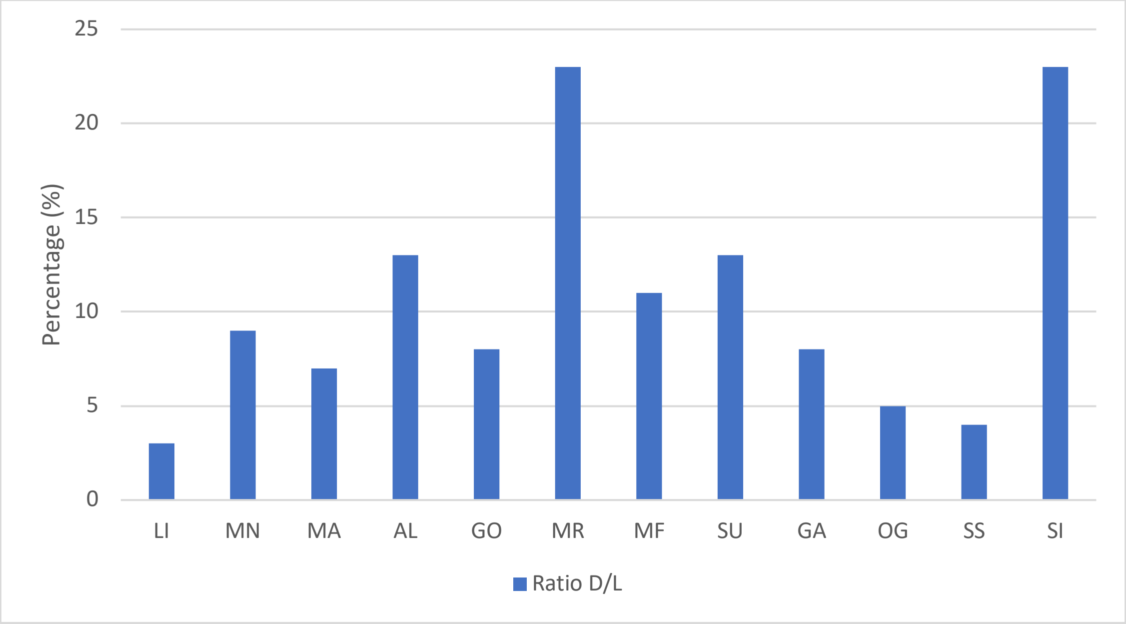

Figure 6 – Ratio of dead/living yews in the different areas of Sardinia (abbreviations are as in Figure 3).

3.2 Yew potential distribution in Sardinia

Our model showed high levels of predictive performances with significative values of AUC (training, 0.962; test, 0.963). Environmental predictors that exhibited the highest mean contributions to the definition of the yew's climatic niche were annual precipitation (Bio1, 23.6), mean temperature of the warmest month (Bio5, 22.6) and isothermality (Bio3, 20.2). Among the others, Bio10, Bio2, Bio14, Bio9, Bio7, Bio6, and Bio11 provided gains >2 to the model, when used individually (Figure 7; Table S1). Considering permutation importance only, Bio2 (mean diurnal range) and Bio18 (precipitation of the warmest quarter) were the main environmental variables influencing the potential distribution of *T. baccata* (Figure 7; Table S1).

While considering probabilities of temperature variables, the mean annual temperature range (Bio1) of *T. baccata* was 8.65-12.55 °C, while the mean diurnal range temperature (Bio2) ranged from 4.57 °C to 6.5 °C. Moreover, the range of isothermality (Bio3) varied from 23.8 to 29.5. The mean temperature of the warmest quarter (Bio10) varied from 16.6 to 20 °C. The range of annual precipitation (Bio12) was 770 to 1085 mm per year. Suitable habitat conditions occur also with a precipitation seasonality (Bio15) of 45.6-49.7. The highest suitability for *T. baccata* resulted at an annual temperature of 11.4 °C, 900 mm annual precipitation. On the other hand, areas with an annual temperature higher than 13 °C were the less suitable for *T. baccata*.

In Sardinia, *T. baccata* had the following potential distribution (Figure 8). Out of 24,090 km² of the total Sardinian area, 18,837 km² was unsuitable for *T. baccata* (≤0.10); 3,281 km² had a low potential distribution, 1,519 km² showed a moderate potential and 853 km² were identified as the portion with the highest probability of suitable ecological conditions (3.54% of the island area). The majority of suitable habitats (≥0.71) was located in the northern and central part of Sardinia.

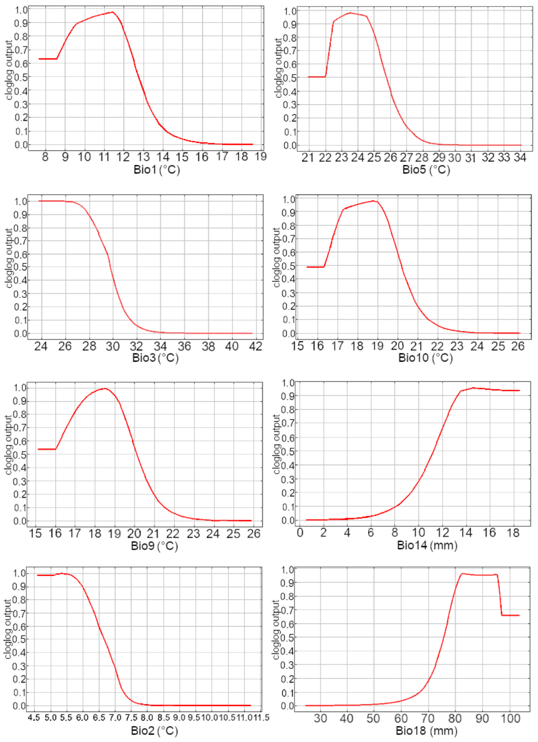

Figure 7 – Response curves of the eight main environmental predictors used in the ecological niche model for Taxus baccata*.*

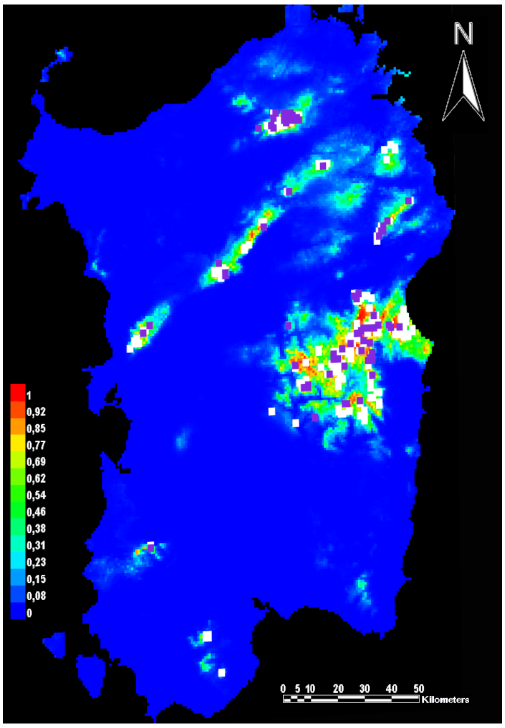

Figure 8 – Map of Sardinia with current potential habitat suitability of Taxus baccata*, according to occurrence records: unsuitable (0-0.23), low potential (0.24-0.46), moderate potential (0.47-0.77) and high potential (0.78-1.0).*

4. **Discussion**

The low percentage of very small fertile trees (i.e., having a DBH of 4-10 cm) is influenced by the high rate of disturbed sites, while in areas such Mount Limbara and the Sarcidano zone their percentages raise even to 69%. On the other hand, mature trees (DBH 25.1-50 cm) are often dominating in other mountains, with a general 40.6% that is even corresponding to ¾ of the entire yew populations in areas such as Monti di Alà and Montalbo. The number of old yews (DBH 50.1-100 cm) is high as well, equalling to 22% that in some areas (i.e., Supramontes, Marghine and Gennargentu) grows to 34, 44 and 49%. Finally, the percentage of senescent trees (DBH >100 m) is attested in 2.8%, of which the majority are concentrated in the Gennargentu Massif, reaching a considerable 17%.

The sex ratio recorded on the entire island shows a male prevalence. Overall, the percentage of female samples is 45.5%, while 55.5% are male. This data is in line with previous results from other populations (Iszkuło *et al*. 2009; Vessella *et al*. 2013). In Sardinia, the difference in the sex distribution varies depending on the areas analysed. We observed a female predominance in the Limbara massif, where 53% of the censused 1473 samples were females. This area is also one of the richest in young formations. On the other hand, mountain massifs where old yews prevail show a male dominance, reaching even to 68% of the 968 adult yews counted on the Goceano localities. This data well fit with previous records, which relate a male predominance with the old-growth status of many localities or by the Mediterranean climate, generally less favourable for certain species than northern ones (Klinkhamer & de Jong 1997; Gauquelin *et al*. 2002; Vessella *et al*. 2013).

For what concerns the recruitment, it is generally low or absent. We hypothesize that grazing, summer drought, low humidity, high temperatures and light availability affect yew regeneration, seedling survival and growth, as previously demonstrated elsewhere (García *et al*. 2000; Iszkuło & Boratyński 2005; Farris & Filigheddu 2008; Mendoza *et al*. 2009; Iszkuło 2010; Perrin & Mitchel 2013; Linares 2013).
Taxus baccata is known to be browsed by vertebrate herbivores, although its foliage being poisonous (García *et al*. 2000; García & Obeso 2003; Thomas & Polwart 2003; Mysterud & Østbye 2004; Perrin *et al*. 2006; Farris & Filigheddu 2008). In this respect, 16 of the 19 localities where we found a renewal higher than 10 plants per hectare, corresponding to 7% of the total studied sites, were located in areas no longer affected by livestock grazing.

Our data highlighted for *Taxus baccata* in Sardinia an average elevation range from 645 to 1225 m, with an optimal elevation at around 928 m a.s.l., a temperature range of 8.65-12.55 °C and an annual precipitation range of 770-1085 mm as the main species' requirements in Sardinia. Consequently, areas with an elevation higher than 1650 m a.s.l. as well as warmer and dryer sites with elevation <500 m a.s.l. and southern aspects are not suitable for *T. baccata*. Under the current climatic conditions, the highest environmental suitability of *T. baccata* in Sardinia can be recognised in the mountain areas, especially in the northern and central parts of the island, covering 3.54% only of the island surface. Moderate suitability was found on small mountain areas on the southern part of the island. Low and no suitability was found on the north-western part of Sardinia as well as in the plains and coastal zones. This data fits with the previous information known from literature (e.g. Bacchetta & Farris 2007) and observations in the field.
Overall, the general distribution of yew in Sardinia, as well its potential range, is represented by areas where the Mediterranean bioclimate interacts with the Temperate one. Generally, these areas show a humid ombrotype, accounting to ca. 4.5% of the island surface (Canu *et al*. 2015). These data are in accordance with previous studies on the yew's global range, demonstrating that water availability seems to be limiting yew regeneration to a greater extent than that of herbivory at its range's southern margin (Linares 2013). In this study, for the first time, we highlighted that annual precipitation (Bio1) and mean temperature of the warmest month (Bio5) were the environmental predictors that exhibited the highest mean contributions to the definition of the yew's climatic niche in Sardinia, both being implicated in the discrimination of Mediterranean vs. Temperate bioclimates. Furthermore, our analyses showed that Bio18 (precipitation of the warmest quarter) was one of the main environmental variables influencing the potential distribution of *T. baccata* considering permutation importance: this is another key climatic parameter useful to distinguish Mediterranean from Temperate areas.
The only Sardinian area with a local moderate suitability for yew, but where the species is not currently known, is represented by the south-eastern massifs. However, it appears that *T. baccata* was present there, although rare, until the first half of the 19th century (Angius 1851). This local disappearance could be related to overexploitation, since the southern mountains of the island were among the most deforested during the XIX century (Beccu 2000).

Contrarily, ca. 9% of all the sites we censused for this research do not reflect elevation requirement, compensating it by growing preferentially on wet sites (streams, gorges) and northern aspects when at lower elevations, as it was previously observed for other Mediterranean areas (García *et al.* 2000; Thomas & Polwart 2003; Hageneder 2007).

The populations of *T. baccata* in Sardinia are scattered and are often constituted by few mature to senescent individuals growing within small areas. This implies that these localities have a relict character, due to the contraction of the species' range resulting from multiple factors: increasing drought effects (Thomas & Garcia-Marti 2015), which often restricted the areas with suitable conditions for the species to moist niche refugia (Romo *et al.* 2017); human pressure, firstly as a result of deforestation during the last centuries (Zucca et al. 2010), cutting of trees to protect livestock against intoxication (Gianguzzi & La Mantia 2004; Mazzola & Domina 2006) and intensive browsing by livestock, which is capable of eliminating yew seedlings (Charco 2007; Farris & Filigheddu 2008).

Considering the major role recognised by previous studies (Linares 2013), to water availability with respect to browsing or other human-induced disturbances in conditioning the presence and recruitment of yew, it is therefore of utmost importance to recognise those areas characterised by suitable environmental conditions and in particular climatic, bioclimatic and microclimatic conditions for the maintenance of viable populations. This is a key-point for the future preservation of extant populations, also considering the increasing risk of loss that recurrent droughts and heatwaves are posing to sensitive species such as *T. baccata* (Thomas & Garcia-Marti 2015), and the fact that 23.8% of the dead yews found in our study perished during the last 6 years. Even if more fine-scale models are required to better identify microclimate niches for the preservation of boreal-temperate species and communities in Mediterranean contexts (Bazzato *et al.* 2021), this study represents the first attempt to identify those climatic variables better explaining and strongly conditioning the presence of a relic Tertiary species as *T. baccata* and the priority habitat it represents. This tree can be therefore considered the reference species to protect a pool of taxa having the same ecological requirements whose survival in the Mediterranean area is threatened by climate change.

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6. **Appendices**

Table S1 – Estimates of average contribution and permutation importance of the environmental variables used in MaxEnt modeling of Taxus baccata.

Variable code	Variable name	Percent contribution	Permutation importance
bio1 (°C)	Annual mean temperature	23.6	0.1
bio5 (°C)	Mean temperature of warmest month	22.6	2.8
bio3 (%)	Isothermality (bio2/bio7) (×100)	20.2	2.3
bio10 (°C)	Mean temperature warmest quarter	4.9	0.4
bio2 (°C)	Mean diurnal range - Mean of monthly (max temp - min temp)	4.8	43.3
bio14 (mm)	Precipitation driest month	4.1	7.7
bio9 (°C)	Mean temperature driest quarter	3.5	1
bio7 (°C)	Temperature annual range (bio5-bio6)	3.3	1
bio6 (°C)	Minimum temperature coldest month	2.8	0.4
bio11 (°C)	Mean temperature coldest month	2.1	9.8
bio4 (°C)	Temperature seasonality (SD ×100)	1.9	0.6
bio8 (°C)	Mean temperature wettest quarter	1.8	0.1
bio16 (mm)	Precipitation wettest quarter	1.7	0.5
bio18 (mm)	Precipitation warmest quarter	0.8	25.4
bio13 (mm)	Precipitation wettest month	0.7	0.2
bio15 (%)	Precipitation seasonality (Coeff. of Variation)	0.5	1.3
bio12 (°C)	Annual precipitation	0.4	0.2
bio17 (°C)	Precipitation driest quarter	0.4	2.6
bio19 (°C)	Precipitation coldest quarter	0.1	0.2

Chapter 4

Ecological and anthropic factors affecting dead wood and regeneration of Sardinian yew (*Taxus baccata* L.) stands: implications for conservation

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Abstract – The effect of key ecological and anthropic factors on the structure and function of the European priority habitat 9580* (Mediterranean *Taxus baccata* woods) in Sardinia has been analysed. After a bibliographic and cartographic research, followed by field surveys, we found 234 sites where *T. baccata* grows or was known in a recent past. Then, we selected 40 sites, distributed in 14 different mountain chains, characterised by different Diameter at Breast Height (DBH), ranging from 13 to 130 cm. We investigated the effect of ecological, structural and anthropic factors on amount of dead wood and stand recruitment. Dead wood was positively correlated with number of adult trees and distance from buildings, while it was negatively correlated with recruitment and current human impact. No correlation was found with average DBH, suggesting that naturalness affects yew stands more than age. Stand regeneration was negatively correlated with dead wood and grazing (both from livestock and wild animals) but was positively correlated with female biased sex ratio. These data confirm that the lack of recruitment is linked to overgrazing due to browsing animals, which was evident in many stands. Additionally, the positive correlation between recruitment and females confirms the risks due to habitat fragmentation and sex isolation on dioecious species. Finally, guidelines for conservation and restoration of *T. baccata* have been outlined.

Keywords: *Dead wood, EU Habitat, Human Impact, Old growth, Overgrazing, Recruitment.*

1. **Introduction**

The Mediterranean basin is considered one of the most altered biodiversity hotspots on Earth (Myers *et al.* 2000). For a long time, many Mediterranean habitats suffered from human exploitation and transformations (Malone 2003; Falcucci *et al.* 2007; Blondel *et al.* 2010; Puddu *et al.* 2012). Consequently, only a small percentage of its primary vegetation, equal to 4.7%, is today preserved (Hoekstra *et al.* 2005). In forested habitats, human disturbance caused simplification of their structure, changes in plant community composition, species abundance and distribution (Blasi *et al.* 2010). It is estimated that native forests without clearly visible human activities and where ecological processes are not significantly disturbed, cover in Europe approximately 1.4 million ha, representing 0.25% of land (Sabatini *et al.* 2018). These forest stands, unaffected by recent human disturbance, show recovered compositional, structural and functional features that can be also defined as old-growth forests or long untouched forests (*sensu* Buchwald 2005; Chirici & Nocentini 2013).

In the island of Sardinia (western Mediterranean Basin), forest extension was considerably reduced starting from Punic and Roman times, as a result of massive deforestation for timber and subsequent extensive agricultural and pastoral activities, combined with fire to maintain pastures (Barreca 1974; Meloni 1975; Pungetti 1985; Caterini 2013). Among residual woods known in literature, some yew (*Taxus baccata*) stands were cited (Desole 1948, 1966; Camarda & Valsecchi 2008; Farris *et al.* 2012; Camarda 2020; Fantini *et al.* 2020). Nevertheless, there is not much knowledge about the distribution, composition, structure and function of residual fragmented old growth stands with yew in Sardinia.

Taxus baccata has been recognised as one of the most ancient forest species in Europe, with origin in the early Miocene (Kunzmann & Mai 2005; Ellenberg 2009). Yew can form pure woods, mostly in the centre of its range across Central Europe to the British Isles, with smaller areas known elsewhere (Thomas & Polwart 2003; Farris *et al.* 2012; Vessella *et al.* 2015). In the Mediterranean Basin, *T. baccata* becomes mostly a montane tree, preferentially growing in the understorey of taller trees and on north-facing slopes (Thomas & Polwart 2003).

Yew is a dioecious, slow growing tree, and is considered one of the longest-lived trees of all Europe, readily reaching a maximum age of over 1,000 years and possibly even 5,000 years old (Mitchell 1990; Pridnya 2002; Thomas & Polwart 2003). However, it is difficult to determine the age of yews accurately since the old specimens are generally hollow, making tree ring-based age estimation impractical (Mitchell 1972; Thomas & Polwart 2003).

Previous studies showed how reproductive ecology of dioecious species is important in the understanding of different dynamics related to the diffusion of such species (Iszkuło *et al.* 2009; Vessella *et al.* 2015). The importance of sex ratio in the analysis of population evolution is related to the fact that in many species male prevalence was highlighted, especially under stressful conditions (Obeso 2002). On the other hand, females are subject to higher stresses, due to the major effort put on the reproductive phases, resulting in a diminished structural increase, as well as a higher mortality when under stress (Leigh *et al.* 2006; Massei *et al.* 2006). Consequently, plant populations characterised by wind pollination and a biotic dispersal were found to have more often male biased sex ratios (Sinclair *et al.* 2012).

Concerning *Taxus baccata*, recent studies showed how the growth rate of females was lower than that of males, together with a higher water request for females (Iszkuło *et al.* 2009, 2011). Thus, Mediterranean climate regime would favour male prevalence more than other European regions (Vessella *et al.* 2015). It was also evidenced how sex ratio changed with the height and diameter of the trees, being male biased in larger ones (Iszkuło *et al.* 2009, 2011). Consequently, it was supposed that older populations were male sex biased (Iszkuło *et al.* 2009; Vessella *et al.* 2015).

In the Mediterranean area, yew has become rarer probably as a result of regression after the last Ice Age (Bennett *et al.* 1991; García *et al.* 2000). During the last millennia, yew locally disappeared or remained isolated in small populations (Tittensor 1980; Svenning & Magård 1999; Thomas & Polwart 2003; Dhar *et al.* 2006a; Ruprecht *et al.* 2010; Iszkuło *et al.* 2016). This reduction was mostly attributed to anthropic factors (Thomas & Polwart 2003; Piovesan *et al.* 2009). More precisely, the main factors of reduction were recognised as human pressure, overgrazing, poor competitive ability compared to other species, changes in water table depth, droughts, fungal infections, and dioecy related problems (Lewandowski *et al.* 1995; Iszkuło 2001; Thomas & Polwart 2003; Iszkuło 2011; Iszkuło *et al.* 2012; Iszkuło *et al.* 2014; Devaney *et al.* 2015; Garbarino *et al.* 2015). Land-use contributed to the contraction of yew habitats, through logging of old stands, in combination with grazing and burning, which transformed forest landscapes, affecting vegetation dynamics, especially of shade-tolerant and late-successional species such as yew (Busing *et al.* 1995; Piovesan *et al.* 2009). In particular, habitat fragmentation is a typical result of human activities that negatively impact yew pollination, since the formation of viable seeds requires co-existence of both sexes (Piovesan *et al.* 2009). In Europe, where yew is among the trees more affected by human interventions, cuttings constitute an important factor of decrease (Svenning & Magård 1999; García *et al.* 2000). Yew reduction has also been attributed to overgrazing of seeds and small plants from animals, as well as the scarcity of suitable sites for recruitment (Hulme 1996; García *et al.* 2000; García & Obeso 2003).

In the southern range of its area, yew decline was also attributed to climate changes, due to high temperatures, long term droughts and water stresses due to changed annual rainfall distribution (Thomas & García-Martí 2015). Yew community habitats (9580* - Mediterranean *Taxus baccata* woods and 9210* - Apennine beech forests with *Taxus* and *Ilex*) are consequently listed as priority habitats in the European Habitat Directive 92/43/EEC (Biondi et al. 2010). Protected areas and priority habitat status (European Commission 1992) have been established to conserve the natural distribution of this species (Svenning & Magärd 1999; Thomas & Polwart 2003; Mysterud & Østbye 2004; Iszkuło *et al.* 2016).

In Italy, several studies have been carried out to define yew distribution, ecology and regeneration (e.g., Gianguzzi & La Mantia 2004; Mazzola & Domina 2006; Farris & Filigheddu 2008; Piovesan *et al.* 2009; Salis 2011; Farris *et al.* 2012; Vessella *et al.* 2015). Some of these studies highlighted that yew regeneration was directly related to the basal area of the yew trees (Piovesan *et al.* 2009). Specifically, regeneration was higher in less developed vegetational stages, while where yew density increased regeneration decreased (Vessella *et al.* 2015). This fact suggests that yew conservation cannot be limited to presently occurring populations, despite the longevity and potential for vegetative reproduction of the species. Long-term existence of yew depends on maintaining and expanding shrubs near the yew patches (Farris & Filigheddu 2008). To maintain such a rare and endangered species, specific conservation measures should be taken, included *in situ* silvicultural treatments and conservation activities (Dovciak 2002; Ruprecht *et al.* 2010) based on species ecological status.

The main aims of this study were to: i) identify and describe old growth stands with yew from an ecological point of view; ii) evaluate relevant factors affecting structural and functional parameters (amount of dead wood and regeneration) of yew stands; iii) assess conservation measures useful for the future protection of this habitat.

2. **Material and method**

2.1 Study area

Our study area is the island of Sardinia, which is the second Mediterranean island by extension with a surface of about 24,090 km^2, including smaller islands and islets. Sardinian geology is characterised by a rich diversity. Granitic substrates predominate mostly the eastern half of the island, while effusive rocks are frequent on the western one. Moreover, metamorphic and sedimentary carbonate reliefs are widespread in many parts of Sardinia (Carmignani *et al.* 2001). Sardinian climate is typically Mediterranean, characterised by mild-wet winters and dry-hot summers (Bacchetta *et al.* 2009; Canu *et al.* 2015).

Biogeographically, Sardinia is located in the central-western part of the Mediterranean Basin and in the Italo-Tyrrhenian Super-province (Ladero-Alvarez 1987; Bacchetta *et al.* 2013). Together with Corsica and Tuscan Archipelago, it represents the Sardinian-Corsican province (Bacchetta *et al.* 2012, 2013). The island has been recently divided in six biogeographic sectors and 22 subsectors (Fenu *et al.* 2014).

Having several mountain areas that remain relatively isolated and scarcely populated, the island preserves wilderness of many natural environments; some of these areas have difficult access and are therefore relatively well preserved (Fois *et al.* 2019). For the high concentration of endemic taxa (especially plants and invertebrates), it has been identified as a biodiversity hotspot of global and regional importance (Fois *et al.* 2018). Sardinian woods have been estimated to cover a surface of 1,241 km^2 (Gasparini & Marchetti 2019). They consist mostly of holm oak (*Quercus ilex*) and cork oak (*Q. suber*) evergreen woods and deciduous oak woods (*Q.* gr. *pubescens* aggr.). Moreover, particular edaphoclimatic conditions enable the establishment of several other wood types, which make the island landscapes quite diverse, such as mixed to pure woods with junipers (*Juniperus* spp.), pines (*Pinus* spp.), strawberry trees (*Arbutus unedo* L.), wild olive tree (*Olea europaea* var. *sylvestris*), manna ash (*Fraxinus ornus*), holly (*Ilex aquifolium*), privet mock (*Phillyrea latifolia*), hop hornbeam (*Ostrya carpinifolia*), quaking aspen (*Populus tremula*) and bay laurel (*Laurus nobilis*) (Camarda & Valsecchi 2008; Bacchetta *et al.* 2009; Calvia & Ruggero 2020). Riparian gallery forests are mainly composed of black alders (*Alnus glutinosa*), willows and poplars (*Salix* spp. and *Populus* spp.), tamarisks (*Tamarix* spp.) and oleanders (*Nerium oleander*). Plain woods of silver poplars (*Populus alba*) and narrow-leafed ash *(Fraxinus oxycarpa)* are also present (Bacchetta *et al.* 2009). Relic yew stands, which can be found mainly on gorges and mountain slopes, are a very interesting example of wood related to specific edaphoclimatic conditions (Farris *et al.* 2012).

2.2 Data collection

We recorded all localities reported in literature (e.g., Angius 1851; Desole 1948, 1966; Bacchetta & Farris 2007; Farris et al. 2012). In addition, we found further information through interviews to local people (forestry workers, shepherds, environmental guides) and by consulting maps issued by the Italian Military Geographic Institute (IGM, scale 1:25.000 maps, toponyms recalling the yew, i.e., Tassu/Tassos; Eni/Enis; Longufresu/Longuvresu). Then we created a dataset containing all yew localities found from different sources. Finally, we carried out field surveys (from 2015 to 2020) to collect ecological and structural data and to evaluate current status of known yew populations. All confirmed localities were geo-referenced and recorded into a GIS, by using the Open-Source Geographic Information System Quantum GIS (QGIS 3.18). Then, we generated a distribution map with all yew sites found, finally updating the current Sardinian *T. baccata* distribution.

Within the 234 sites with yew found in Sardinia, we selected 40 stands from the entire distributional range of the species in the island (Table S1). The sites were selected on the basis of geographical, ecological and structural features, as follows. From a geographical point of view, we selected a proportional number of sites from each mountain area, thus representing all sectors and lithoid substrates. Then, required ecological features were related to morphology, i.e. drier (slopes) and moist sites (streams, gorges). Then, we collected other information related to ecology (area, declivity, summer humidity, canopy closure, layers of the woods) and human related disturbance (grazing, evidence of human activities).

From each site we also gathered structural and reproductive information, such as number of adult trees, sex ratio, presence/absence of recruitment, presence/absence of dead yews, both snags and logs. We selected also sites with average DBH ranging from 13 to 130 cm, in order to infer possible differences between young formations and older stands.

2.3 Statistical analysis

Variables that were used in the analysis are presented in Table S2. The two state variables of interest were dead wood, measured as the sum of the number of standing dead trees and fallen trees (DW = Snag + Log) and recruitment, measured as the sum of the number of saplings and seedlings (Renew = Sap + Seed). The two state variables were hypothesized *a priori* to be related to meaningful (Burnham & Anderson 2002) ecological and anthropic variables, as follows. The total amount of DW should increase with tree population dimension (measured as the number of adult trees, nAT), stand age (measured as average DBH, Daver) and eventually layer complexity (Layer = 1, 2 or 3, where 3 refer to the maximum level of complexity, see Fantini *et al.* 2020). Tree growth and mortality, and thus DW, could also be affected by lack of summer humidity (Shum = yes or no), steep slopes (Pend = average declivity °), morphology (Morph = slopes or watercourse); current human impact (CHI = yes or no) and distance from: a) charcoal kilns (Coal), b) traces of past wildfires (WF), c) cultivated or reforested areas (Agric), d) roads or paths (Roads), e) building or human settlings (Builds). Presence of grazing animals, wild or livestock (GrazT), and Renew could also be related to DW. Renew could be affected by the same factors that were related to DW, with the addition of canopy closure (Clos = % ground cover of canopy projections) and sex ratio [SR = Females/(Females + Males)], which has been shown to be very important for recruitment in yew stands. CHI has been established through the collection in the field of any evidence related to current impacts attributable to humans: livestock and/or their signs (e.g. excrements, tracks, fur/wool on the bark and on branches) found in site; recent clearcuttings; signs of trampling (hikers, off road motorbikes/cars); spreading of alien tree species due to reforestations; buildings (farms, fountains, houses, picnic areas, windfarms) and roads within the sites.

The state variables of interest are counts. Preliminary analysis with Generalized Linear Models (GLMs) and Poisson regression showed high overdispersion, thus suggesting the use of the negative binomial distribution to model variance. The analysis was performed with software R version 3.6.3 (R Core Team, 2020), using the *glm.nb* function implemented in the package MASS (Venables & Ripley 2002).

Considering small sample size (n = 40), a univariate GLM analysis was first performed, where each effect was evaluated at a time, according to the following model (see R Script):

M1 = glm.nb (formula = DW ~ nAT + Effect 1).

The effect model was contrasted with the null model M0 = glm.nb (formula = DW ~ 1), with 1 intercept and no effect hypothesized. However, given that the amount of DW was positively correlated with population dimension, which is widely ranging among investigated yew stands, the effect of nAT was assumed in every univariate model, and for the remaining effects the null model was considered DW ~ nAT. recruitment was modelled similarly, without the need of assuming nAT effects.

Univariate models were compared with M0 by means of AICc (Burnham & Anderson 2002) and Likelihood Ratio Test (LRT). Models that had ΔAICc higher than 2 or that differed significantly from M0 according to the LRT were considered for multivariate analysis.

Effects supported by the univariate model selection were then combined and evaluated with backward multivariate model selection. Simplification started from the full model, with all supported univariate effects, by removing effects that were non-significant in the multivariate analysis, starting from higher p values (see R script for details).

Model selection tables based on AICc were developed using the R package AICcmodavg (Mazerolle 2019), while LRTs were performed using the R package lmtest (Zeileis & Hothorn 2002).

3. **Results**

The data collected in the field allowed us to report the current presence of *Taxus baccata* in 229 Sardinian sites, while in other 5 the species is locally extinct. The selected 40 stands with *T. baccata* are located in 14 different mountain chains of the Island (Figure 1). Geologically, they grow in several substrata: limestones (15), granitoids (12), metamorphic rocks (7), effusive rocks (4) and granodiorites (2) (Table S1).

The average elevation of selected stands is 620-1250 m a.s.l. The majority of stands are located in northern aspects, excepted five growing in southern aspect. Almost all selected stands grow in the Mediterranean Pluviseasonal Oceanic bioclimate, while four stands grow on the Oceanic temperate one (Figure 2).

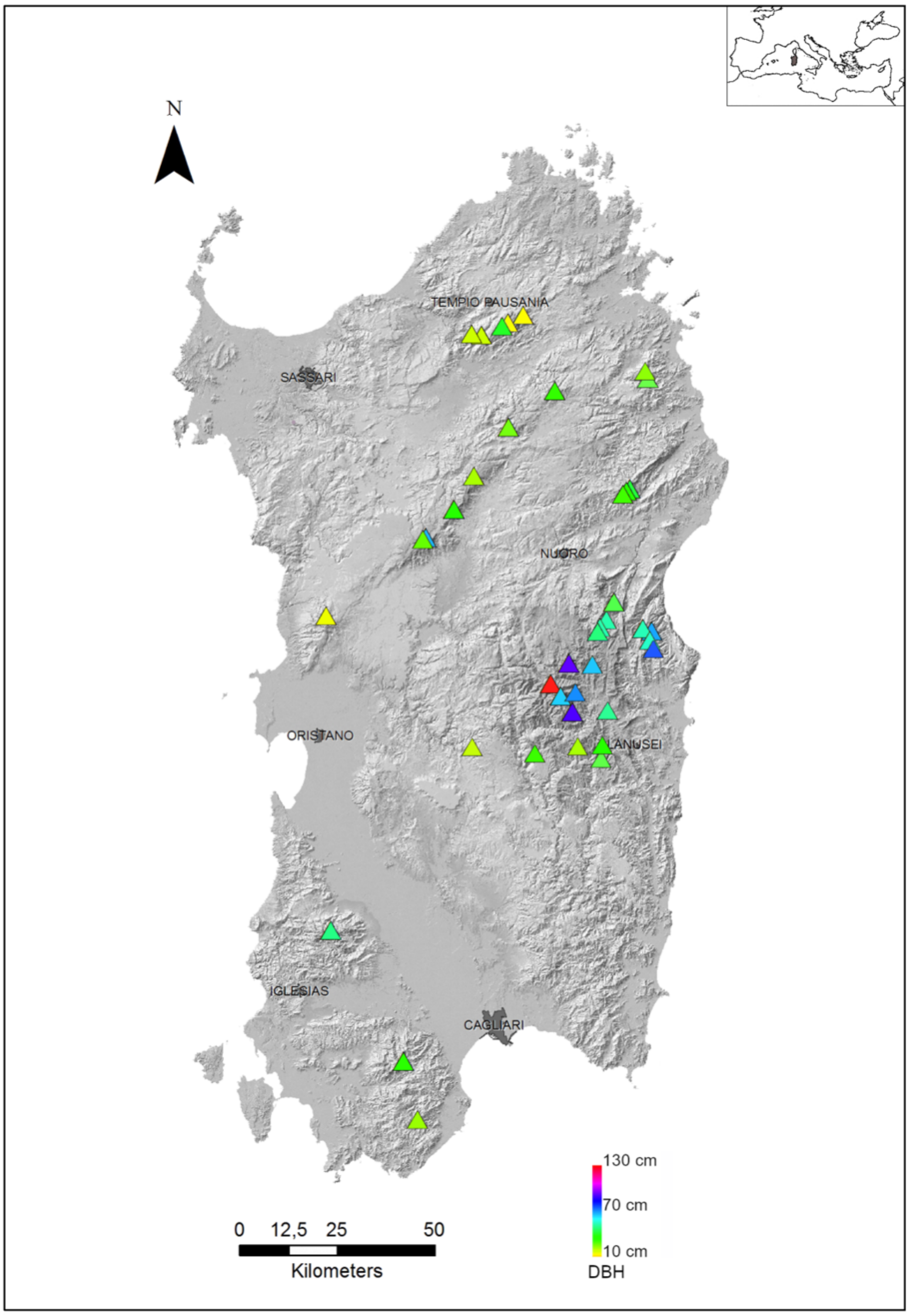

Figure 1 – Distribution map of old growth stands with yews of Sardinia and their DBH average ranges.

The number of living adult yews per site (nAT) is rather low, being in 23 cases lower than 50 individuals. In 7 cases they are comprised between 51 and 100, while in 10 sites there are more than 100, one of which with more than 500 (site 20, nAT = 836).

Overall, we measured DBH of about 3,500 yews from 40 localities. The central mountains show the highest average DBHs and the richest percentage of senescent trees (sites 1-13; see Table S2), while the northernmost and some of the southern stands were among the youngest formations found (Figure 1).

The maximum DBH recorded was in site 20 (221.3 cm). We found trees having a maximum DBH larger than 100 cm in 19 sites. The smallest DBH average was in site 40, with 13.8 cm, while the larger one was from site

1, where the sampled trees reached an average of 130.4 cm. Other two sites have average DBH equal or slightly higher than 90 cm (site 2, 90.5 cm; site 3, 90 cm). The sex ratio recorded is male dominated. In 11 sites a slight female prevalence has been recorded (see Table S2).

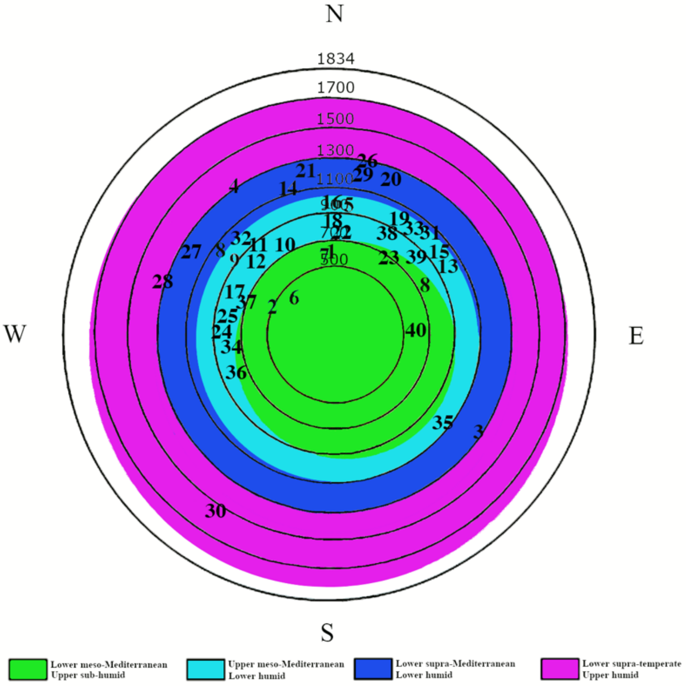

Figure 2 – Elevation, aspect and bioclimatic features of the studied stands with yews of Sardinia.

Our first question was related to the existence of a correlation between ecological factors, human disturbance and old-growthness of yew stands, the latest approximated by the amount of dead wood (DW). Raw data shows that nine sites were devoid of dead yew samples; we found seven sites with snags only and three with logs only. Overall, we found 241 snags in 28 sites and 84 logs in 24 sites.

Variables affecting DW evaluated with univariate model selection are shown in Table 1. We found support for the correlation between DW and Build, Renew, Pend, CHI and nAT. However, the multivariate backward model selection provided support for model DW ~ nAT + CHI + Renew + Builds (AICc = 217.54), excluding the effect of Pend. Parameters estimates taken from the best multivariate model are thus the following: nAT = 0.0073 ($p < 0.001$), CHI Yes = -0.7768 ($p = 0.022$), Renew = -0.1745 ($p = 0.003$), Builds = 0.2793 ($p = 0.019$). Residual Deviance of the best model is 44.59 on 35 degrees of freedom, showing a good fit of the negative binomial model to the data.

Parameter estimates show that dead wood (DW) is proportional to the number of adult trees (nAT) and inversely correlated with stand regeneration (Renew = Saplings + Seedlings). Current human disturbance (CHI yes) reduces DW and sites that are more distant from buildings (e.g. farms, shepherd huts, villages, charcoal kilns, quarries) have higher amounts of DW. Therefore, higher amounts of DW can be found in areas less affected by human disturbance.

Table 1 – Variables affecting dead wood (DW). Abbreviations: K = number of model parameters; AICc = corrected Akaike Information Criterion; ΔAICc = difference between the AICc of the model and that of the best model selected (1st); wt = Akaike weight; LL = model log likelihood; cum.wt = cumulative Akaike weight.

Rank	Code	Model structure	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt
1	M14	DW ~ nAT + Builds	4	221.98	0.00	0.56	-106.42	0.56
2	M3	DW ~ nAT + Renew	4	223.95	1.97	0.21	-107.40	0.76
3	M5	DW ~ nAT + Pend	4	226.38	4.40	0.06	-108.62	0.83
4	M8	DW ~ nAT + CHI	4	226.48	4.51	0.06	-108.67	0.88
5	M1	DW ~ nAT	3	228.35	6.37	0.02	-110.84	0.91
6	M10	DW ~ nAT + Coal	4	229.02	7.05	0.02	-109.94	0.92
7	M4	DW ~ nAT + Layers	4	229.38	7.40	0.01	-110.12	0.94
8	M2	DW ~ nAT + Daver	4	229.62	7.65	0.01	-110.24	0.95
9	M13	DW ~ nAT + Roads	4	229.97	7.99	0.01	-110.41	0.96
10	M12	DW ~ nAT + Agric	4	230.10	8.12	0.01	-110.48	0.97
11	M6	DW ~ nAT + Shum	4	230.19	8.22	0.01	-110.53	0.98
12	M7	DW ~ nAT + GrazT	4	230.62	8.64	0.01	-110.74	0.99
13	M9	DW ~ nAT + Morph	4	230.70	8.72	0.01	-110.78	0.99
14	M11	DW ~ nAT + WF	4	230.72	8.74	0.01	-110.79	1.00
15	M0	DW ~ 1	2	243.02	21.04	0.00	-119.35	1.00

The second question was related to variables affecting stand regeneration (Renew). Variables affecting Renew, evaluated with univariate model selection, are shown in Table 2. We found support for the correlation between Renew and SR, GrazT, Daver, Layers, DW and Morph (LRT M0 vs M3, p = 0.09). However, the multivariate backward model selection provided support for model Renew ~ DW + GrazT + SR (AICc = 161,33), excluding the effect of Daver, Layers and Morph. Parameters estimates taken from the best multivariate model are the following: DW = -0.0442 (p = 0,031), GrazT yes = -0.878 (p = 0.009), SR = 5.0292 (p = 0.006). Residual Deviance of the best model is 46.39 on 36 degrees of freedom, showing a good fit of the negative binomial model to the data.

Parameter estimates confirm that Renew and dead wood are inversely correlated. Renew is also negatively correlated with grazing (GrazT = Graz wild + Graz Livestock) and positively correlated with sex ratio (SR = F/(F+M)). Indeed, recruitment found during our research was often very low or absent, especially in areas where grazing is still a considerable factor of current impact. We did not find recruitment in 15 sites out of 40, equalling to 37.5% of the studied stands. Saplings were more present than seedlings and we found them in a higher number of sites (25 with saplings and 15 with seedlings). Overall, we found more recruitment in sites where grazing has long disappeared.

Moreover, of the 10 sites characterised by the smaller DBH average, nine had among the richest presence of recruitment (Renew = Seedlings + Saplings). Among them, there was often a positive female rate, being those woods female-dominated in 6 cases, while in other two the number of females was high anyway.

Table 2 – Variables affecting recruitment (Renew). Abbreviations are as in Table 1.

Rank	Code	Model structure	K	AICc	∆AICc	AICcWt	LL	Cum.Wt
1	M11	Renew ~ SR	3	167.02	0.00	0.76	-80.18	0,76
2	M7	Renew ~ GrazT	3	170.83	3.81	0.11	-82.08	0,87
3	M2	Renew ~ Daver	3	171.99	4.97	0.06	-82.66	0,93
4	M4	Renew ~ Layers	3	173.19	6.17	0.03	-83.26	0,97
5	M9	Renew ~ DW	3	175.08	8.06	0.01	-84.21	0,98
6	M3	Renew ~ Morph	3	177.22	10.20	0.00	-85.27	0,99
7	M0	Renew ~ 1	2	177.65	10.63	0.00	-86.67	0,99
8	M6	Renew ~ Shum	3	178.02	11.00	0.00	-85.68	0,99
9	M8	Renew ~ CHI	3	179.14	12.12	0.00	-86.24	1,00
10	M1	Renew ~ nAT	3	179.17	12.15	0.00	-86.25	1,00
11	M10	Renew ~ Clos	3	179.97	12.95	0.00	-86.65	1,00
12	M5	Renew ~ Pend	3	180.00	12.98	0.00	-86.66	1,00

4. **Discussion**

Human disturbance has been and currently is a driving factor to environmental transformations that negatively affect many habitats and threatened species such as *Taxus baccata* (Piovesan *et al.* 2009).

Starting from a database that was rich in old growth samples and stands, it could be easy to hypothesize that yew stands of Sardinia were mostly constituted by old-growth remnants. Our results show how this could be not totally correct, at least from a naturalness point of view. While human impact has certainly reduced in some areas of the island, allowing on the one hand a substantial recover of yew stands, on the other hand it is remarkable the strong pressure that human related activities such as overgrazing, due to abundant livestock, have on a high number of *T. baccata* stands (Farris & Filigheddu 2008).

A typical example of how a wood constituted by old-growth yews only does not correspond to a natural old-growth wood, according to our results, is visible in site 20, where in an about 7 ha wide pure *T. baccata* wood a rural road cuts the wood, there is a fountain with a picnic area, and logs are continuously removed. Moreover, seven alien species planted in the past grow in the site, one of which (*Acer pseudoplatanus*) is spreading in the glades, and cattle browse the undergrowth.

Our results showed that recruitment appears to be inversely correlated with the presence of dead wood. We can interpret this negative relation as the possibility that woods with higher mortality have also lower regeneration, possibly suggesting contraction and bad conservation status of these stands. On the other hand, positive correlation was found between recruitment and female presence in the sites. Overall, 42% of censused trees were females, but with a disproportion among sites. In particular, more females were often found in younger stands. Besides, older formations were generally poor in recruitment. This data is in line with previous studies suggesting a positive correlation between basal area and regeneration as well as less evolved vegetation stages (Piovesan *et al.* 2009; Vessella *et al.* 2015).

For what concerns recruitment, our results confirm what was observed in the field, namely that overgrazing affects yew regeneration. Among the sites where a lack of recruitment was recorded, only two were totally devoid of livestock, although wildlife grazing was present, especially by mouflon. The presence of grazing animals, both livestock and wildlife (cattle, goats, horses, sheep, deer and mouflon), was recorded in 29 sites, four of which are currently characterised by sporadic presence of recruitment. On the other hand, 11 sites with no evidence of grazing preserved recruitment, sometimes abundant, confirming that a lower pressure of herbivorous mammals favours a more abundant and successful yew recruitment (Iszkuło 2011). *Taxus baccata* is known to be browsed by vertebrate herbivores, although being poisonous in almost all the parts of the plant (García *et al.* 2000; García & Obeso 2003; Thomas & Polwart 2003; Mysterud & Østbye 2004; Farris & Filigheddu 2008). According to Farris & Filigheddu (2008), farmers believed that yew were poisonous only to those animals browsing it for the first time, during adulthood without having ingested it before, being otherwise harmless to those livestock that regularly browsed yew foliage since their youth, thus developing tolerance to it. However, other studies highlighted that some animals (e.g. horses) are more susceptible than others (i.e. ruminants) to yew alkaloids (Piovesan *et al.* 2009).

In the studied sites, *T. baccata* recruitment was often limited to a few seedlings or saplings, but in sites characterised by younger formations not affected by grazing, we observed more than 100 individuals each. Moreover, in the sites still affected by animals, the growth of seedlings and saplings was favoured by bramble and heather (e.g. site 9), which partially prevented the grazing of livestock. This confirms previous reports suggesting that *T. baccata* recruitment depends on the facilitative effects of shrubs (Hulme 1996; García *et al.* 2000; García & Obeso 2003; Farris & Filigheddu 2008), especially in systems wherein the browsing pressure is high (García *et al.* 2000; Farris & Filigheddu 2008). In browsed localities, where some rare young trees were present, these were assuming the typical hourglass shape, characteristic of open woods affected by intense browsing (Marzolff *et al.* 2020). In this case, shrubs protected the saplings during their first growing phase, allowing a slow but constant development.

4.1 Implications for conservation

For what concerns the conservation of the stands with yew studied here, it is worthy of interest that only 10 sites (25% of them) are recorded in official maps as priority habitat 9580*, though the total sites included in Special Areas of Conservation (SACs) are 28. On the other hand, 12 sites among 40 are not included in protected areas according to the Habitats Directive (1992). However, three sites are both included in Special Areas of Conservation and are also recognised as “Regional Monuments” according to the Sardinian Regional Law 31/89. Moreover, five sites are included in the Gennargentu National Park also, while other two are part of the “Gutturu Mannu” Regional Nature Park. One of these latter is also included in the “Monte Arcosu” WWF oasis.

Many of the yew stands studied here are close to areas that suffered from deforestation or other human activities during the last centuries. Important evidence of cuttings is found especially where coppices and charcoal kilns exist not far from the yew stands, locally bordering them. The literature (Desole 1948, 1960) as well as the observation of past aerial photographs, show a rather stable condition of the stands during the last 70 years, highlighting how human impact have been drastically reduced.

In 16 cases, the preservation of these stands was favoured by isolation from human disturbance of the places where yews grow (i.e., sites). The favourable conditions for the preservation of durable stands were recently highlighted by Fantini *et al.* (2020), although too steep sites can be negatively impacted by natural events such as landslides.

In order to preserve such a delicate environment, conservation measures should be taken. Firstly, all the stands were yew form the habitat 9580* should be identified and consequently recorded as such. Secondarily, for the reintroduction or management of seedlings and saplings in the suitable sites (e.g. open sites around scattered females), seedbeds should be protected by shrubs, such as heather (Farris & Filigheddu 2008). Moreover, for controlling the browsing pressure, herbivory should be excluded from the patches by establishing fences and shelters (Dhar *et al.* 2006b).

5. **Conclusions**

DBH average did not appear as correlated to a higher presence of dead wood. This means that we cannot identify yew stands with high DBH averages as old growth stands. The anthropic removal of dead wood, as well as the presence of current human impact and presence of buildings, prevent the recognition of a typical old growth stand. Thus, in the Sardinian case, we can affirm that the naturalness of the older stands is often low, and mostly compromised by human activities. Among the impacting factors, grazing reduces considerably the recruitment. Together with grazing, other human disturbance can condition naturalness of yew stands. If charcoal kilns and traces of past wildfires testify a strong past disturbance that has been locally overcome by the vegetation recovery, the presence of buildings and current human impact (CHI) seems to be still influencing the processes of natural reconstitution of an undergrowth typical of old growth stands (i.e. with a significant presence of dead wood). Moreover, the low recruitment of the older stands, which could be considered as a possible index of old growthness, is influenced by external factors such as overgrazing.

The old growth yews of Sardinia are declining. The factors influencing this reduction have been also investigated. Both environmental and anthropogenic factors are correlated with the current decline of these stands. If senescence seems to be a critical problem, together with the reduced areas of these stands and their declining number in several sites, the low presence of recruitment represents a future challenge for the conservation and management of this threatened habitat. In view of future habitat modifications connected with climate change, the active protection of these relict stands could prove to be fundamental for the conservation of this declining species at the extremes of its range.

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7. **Appendices**

Table S1 – List of the studied sites, their location, coordinates and lithology (Bas = basalts; Gra = granitoids; Grd = granodiorites; Lim = Limestones; Met = metamorphic rocks.

code	Zone	Locality	Municipality	Coordinate X	Coordinate Y	Lithology
1	**Gennargentu**	Rio Aratu (CuileS'Arena)	Desulo	4429965.68	524514.86	Met
2	**Gennargentu**	Funt. S'Enis (RiuCorreboi)	Fonni/Villagrande S.	4434953.89	529090.74	Grd
3	**Gennargentu**	Cuile Mattarano	Arzana	4423401.94	530028.84	Grd
4	**Supr. Ba. Ur.**	Su Clovu	Baunei	4440926.51	549738.75	Lim
5	**Gennargentu**	Bacu Searthu (Rio Is Enis)	Villagrande Strisaili	4428453.29	528739.61	Met
6	**Supr. Ba. Ur.**	Bacu Addas	Baunei	4443448.22	550511.05	Lim
7	**Marghine**	Mularza Noa	Bolotana	4467473.85	492382.21	Bas
8	**Gennargentu**	Bacu Sa Mandara	Villagrande Strisaili	4434900.87	534512.49	Met
9	**Gennargentu**	Fun. Ortu is Arangios	Desulo - Arzana	4426807.76	527057.69	Gra
10	**Supr. Ba. Ur.**	S'Eni Pidargiu	Baunei	4441941.45	549299.43	Lim
11	**Supr. Ba. Ur.**	Gorroppeddu	Baunei/Urzulei	4444073.28	548113.99	Lim
12	**Supr. Ol. Or. Ur**	M. Novo S. Giovanni	Orgosolo	4441061.81	535337.22	Lim
13	**Supr. Ol. Or. Ur**	Riu S'Eni	Orgosolo	4441083.20	537149.01	Lim
14	**Ogliastra**	Baccu Is Enis	Villagrande Strisaili	4425022.46	540808.37	Met
15	**Catena del Linas**	Canali 'e Nesta	Gonnosfanadiga	4366499.67	467928.70	Gra
16	**Supr. Ol. Or. Ur**	Monte Fumai	Orgosolo	4439778.13	534058.66	Lim
17	**Montalbo Lula**	Sa Marmurata	Lula	4480001.45	544856.07	Lim
18	**Limbara**	P. Berritta (Valle Suprappare)	Berchidda	4521812.33	514725.33	Gra
19	**Supr. Ol. Or. Ur**	Su Suercone	Orgosolo	4450898.69	540725.44	Bas
20	**Goceano**	Sos Nibberos	Bono	4474704.18	499667.91	Met
21	**Montalbo Lula**	S'Ortu 'e Trullìo	Lula	4479573.54	544357.29	Lim
22	**Ogliastra**	Su Candelassargiu	Gairo	4413262.05	539209.76	Lim
23	**Monti del Sulcis**	Canale Longufresu	Uta	4333134.82	486580.45	Gra
24	**M. di Alà**	Ferulas (Tassu Mannu)	Alà dei Sardi	4505089.50	524355.92	Gra
25	**Barbagia Seulo**	Rio Longufresu (Stampu Turrunu)	Seulo/Sadali	4411121.58	522656.55	Lim
26	**Ogliastra**	Rio Taquisara	Gairo/Ussassai	4410059.66	538644.05	Lim
27	**Montalbo Lula**	Su Renagliu	Lula	4479336.81	544107.03	Lim
28	**M. Nieddu Gal.**	S'Inferru	San Teodoro	4509821.26	548552.41	Gra
29	**Marghine**	Rio Biralotta	Bolotana	4467122.61	492323.45	Bas
30	**Lerno**	Rodè	Pattada	4495729.55	513584.56	Gra
31	**M. Nieddu Gal.**	Rio Badde Niedda	Padru	4512162.56	548449.86	Gra
32	**Monti del Sulcis**	Canale Longuvresu	Pula	4320046.36	490859.66	Gra
33	**Ogliastra**	Rio Ermolinus	Seui	4413476.21	533629.79	Lim
34	**Goceano**	Funtana Tassu (Nuraghe Su Tassu)	Bultei	4484445.08	505586.34	Met
35	**Limbara**	Riu di Li Tassi	Tempio	4519283.38	504768.00	Gra
36	**Sarcidano**	Funtana Mela (Rio Bau Onu)	Laconi	4413936.19	508007.54	Lim
37	**Limbara**	Rio Rizzolu 'e Curadore	Oschiri/Tempio	4520055.63	507713.74	Met
38	**Montiferru**	Rio S'Abba Lughida	Cuglieri/S. Lussurgiu	4445650.43	467208.66	Bas
39	**Limbara**	P. Bandera NW (Funtana Bandera)	Tempio/Calangianus	4522636.70	515748.78	Gra
40	**Limbara**	Ghjroni (M. Niiddoni. NE)	Calangianus	4524101.23	517679.64	Gra

Table S2: – Variables used in this study and their values.

code	nAT	Dmax	Daver	Fem	Male	Sap	Seed	Snag	Log	Pend	Area	Shum	Clos	Layers
1	58	1840	1304	11	16	0	0	2	1	30	2.5	Yes	60	2
2	32	1750	905	15	16	3	2	3	0	21	1	Yes	50	2
3	30	2000	900	12	18	0	0	1	0	12.5	1.2	Yes	75	2
4	16	1000	745	6	10	1	0	3	2	22.5	0.6	No	50	1
5	23	1750	700	5	8	0	0	0	1	15	0.5	Yes	60	2
6	23	1050	682	8	15	0	0	0	1	24	0.5	No	50	1
7	181	1650	658	47	55	0	0	54	17	20	3.2	Yes	80	2
8	21	1500	650	6	13	0	0	4	2	15	1	Yes	75	1
9	182	1080	636	69	63	0	0	17	10	20	7.5	Yes	55	1
10	15	1500	557	5	10	2	2	0	0	7.5	0.8	No	50	2
11	21	1210	534	9	12	3	2	0	0	5	0.6	No	80	1
12	78	800	523	17	12	2	3	1	1	30	1.2	No	65	1
13	24	1300	520	9	15	2	0	2	1	20	3	No	70	2
14	36	1200	500	8	15	2	0	2	0	20	0.5	Yes	80	3
15	17	1200	490	3	14	0	0	0	0	30	0.4	Yes	80	1
16	31	790	488	13	11	2	0	0	2	42.5	1	No	60	1
17	42	820	425	21	19	0	0	7	1	35	0.5	No	70	1
18	52	1220	404	26	21	3	2	1	3	42.5	3.5	No	60	2
19	158	1224	384	45	69	0	0	5	21	45	4.3	No	60	1
20	836	1690	352	263	573	0	0	77	2	11	6.6	Yes	90	1
21	48	840	350	18	29	1	0	1	1	35	1.5	No	90	1
22	58	570	345	19	30	0	0	0	0	10	1.2	No	75	1
23	23	780	321	9	14	1	0	1	3	40	0.8	Yes	90	1
24	25	790	317	12	13	2	0	1	1	25	0.5	Yes	85	2
25	93	1110	314	30	43	3	0	6	0	12.5	3	Yes	80	2
26	19	640	302	8	8	2	2	0	0	3.5	1	Yes	70	2
27	57	650	300	23	27	2	0	8	1	30	4	No	90	1
28	77	1005	289	27	32	4	2	6	2	40	3	Yes	70	3
29	45	1120	281	19	21	0	0	3	0	2.5	7.8	No	85	2
30	17	570	267	7	10	0	0	0	0	30	0.4	Yes	90	2
31	54	500	236	12	11	5	3	3	0	30	2.5	Yes	85	3
32	11	460	224	1	3	0	0	10	5	45	0,5	No	70	1
33	198	650	215	58	71	4	3	5	1	23.5	10	Yes	80	2
34	103	400	210	42	43	3	3	2	0	5	4.5	Yes	75	1
35	35	900	183	18	11	3	3	0	0	22.5	1.5	Yes	85	2
36	115	560	182	34	29	4	2	0	0	20	5	Yes	80	3
37	135	950	180	62	35	4	2	1	1	27.5	7.8	Yes	80	3
38	26	380	151	7	6	3	0	0	0	20	2	Yes	85	2
39	368	930	145	143	166	5	4	2	1	34	3	Yes	55	2
40	293	660	138	126	114	5	4	13	3	22.5	4.5	Yes	85	2

Table S2 – Variables used in this study and their values (prosecution).

code	GrazL	GrazW	GrazT	CHI	Coal	WF	Agric	Roads	Builds	Morph
1	Yes	Yes	Yes	Yes	5	1	1	1	1	S
2	Yes	Yes	Yes	Yes	5	5	1	4	5	W
3	Yes	Yes	Yes	Yes	5	2	1	1	1	W
4	Yes	Yes	Yes	Yes	5	1	1	1	5	S
5	Yes	Yes	Yes	Yes	5	4	1	1	4	W
6	Yes	Yes	Yes	Yes	5	2	5	5	5	S
7	No	No	No	No	4	2	1	2	4	W
8	Yes	Yes	Yes	Yes	5	1	3	1	3	W
9	Yes	Yes	Yes	Yes	5	5	1	1	4	S
10	Yes	Yes	Yes	Yes	5	1	1	1	5	S
11	Yes	Yes	Yes	Yes	1	2	4	1	5	W
12	Yes	Yes	Yes	Yes	3	2	2	2	2	S
13	Yes	Yes	Yes	No	5	3	3	3	5	W
14	No	No	No	No	2	4	3	1	4	W
15	No	Yes	Yes	No	1	5	5	5	5	S
16	Yes	Yes	Yes	Yes	3	1	1	2	5	S
17	Yes	Yes	Yes	No	1	3	3	3	4	S
18	No	No	No	No	5	2	3	3	3	S
19	No	Yes	Yes	No	5	4	5	4	5	S
20	Yes	No	Yes	Yes	1	5	1	1	1	S
21	Yes	Yes	Yes	No	1	3	3	3	4	S
22	Yes	Yes	Yes	Yes	2	3	3	1	5	S
23	No	Yes	Yes	No	3	2	5	3	5	W
24	Yes	Yes	Yes	Yes	5	1	5	2	2	S
25	Yes	No	Yes	No	1	2	2	1	3	W
26	No	No	No	No	1	3	1	1	1	W
27	Yes	Yes	Yes	No	1	2	3	3	3	S
28	No	No	No	No	1	2	3	3	5	W
29	Yes	No	Yes	Yes	3	3	1	1	3	S
30	No	Yes	Yes	No	1	2	2	2	4	W
31	No	No	No	No	1	2	3	3	4	W
32	No	Yes	Yes	No	1	5	5	1	5	S
33	No	Yes	Yes	No	1	3	2	1	2	W
34	Yes	Yes	Yes	Yes	1	3	1	1	1	S
35	No	No	No	No	1	2	2	1	2	W
36	No	No	No	No	1	3	2	1	1	W
37	No	No	No	No	1	5	1	1	1	W
38	No	Yes	Yes	Yes	1	4	1	1	1	W
39	No	No	No	Yes	4	3	1	1	1	S
40	No	No	No	No	1	2	4	1	5	W

Summary

1.1 **General conclusions**

This PhD thesis was conceived to improve the knowledge on conifer stands in Sardinia, an important part of the wood contingent that needed a review. The main findings of this thesis are:

In chapter 1 we described the different kinds of pine woods naturally growing in Sardinia from a phytosociological point of view. In total, 66 plots of at least 200 m^2 were sampled, distributed in three different sectors of the island Sardinia, for what concerns the three pine species. A total of five associations were reported, of which four are here described for the first time.

In chapter 2, we improved the knowledge about the distribution and recent historical vicissitudes of pine stands in Sardinia. The finding of geographical data was possible using of literature, LEK, toponyms, as well as the photo interpretation and analysis of aerial photographs. This turned out to be a useful baseline for a first indication about the diachronic changes in distribution areas of the conifer's extent, as well as for the individuation of forest changes trends through time.

In chapter 3 we improved the knowledge of the distribution, ecology and threats of *Taxus baccata* populations in Sardinia. In addition, we analysed climatic factors in order to describe yew's ecological niche and define the species potential distribution in the island. In this study, we found 234 different localities were *T. baccata* grows or was known in recent times, then confirming how the potential distribution is similar to the real one. On the other hand, we highlighted that in many localities the presence of the species is today related to isolated to scattered old individuals.

In chapter 4, among the 234 sites with *Taxus baccata*, we selected 40 sites, a part of which are characterised by the presence of *T. baccata* old-growth woods. We compared these woods with others where human impact and mean dimensions of the samples identify them as younger formations. This comparison was useful to understand which of the structural features are significantly differentiating old-growth stands with yew from younger ones, and can therefore have a methodological value.

1.2 **Final considerations**

A complete analysis of the distribution, ecology and floristic composition of the natural pine woods of Sardinia, belonging to *Pinus halepensis*, *P. pinaster* subsp. *pinaster* and *P. pinea*, was for the first time produced in Sardinia by means of aerial photographs, literature, LEK and phytosociological surveys carried out within the areas where the three pine species are considered native. The phytosociological work allowed the description of two new associations for *P. halepensis* woods, as well as the confirmation of a previously described one; a new association related to *P. pinaster* subsp. *pinaster* woods with two new sub-associations; finally, a new association for *P. pinea* woods. The diachronic study of pine woods' decrease and subsequent recovery represents an important step in the analysis of how human impact and land use change can influence the vegetation dynamics of pioneer species with restricted distribution ranges in insular contexts. In this respect, the help of local people and toponymy was crucial for trying a reconstruction of the loss happened in recent times. The method here applied can be an example for further research on rare and declining species.

The knowledge of Sardinian *Taxus baccata* stands has been enhanced as well. Many factors are driving this species to become more and more rare in the Mediterranean environments. Often, only old-growth trees surviving in different contexts and edaphic conditions are visible, allowing to sustain the hypothesis that this species is vulnerable to factors such as human activities and climate change. The places where the species still thrives today are subject to a long pressure by overgrazing and are often the remnants of wider populations reduced by practices such as wildfires, cuttings, and subsequent reforestations. This work increases the knowledge in relation to the distribution of the species in Sardinia. Moreover, it represents a crucial point for its conservation since it shows how in a changing climatic condition, this relic from the glaciations could be affected by extreme droughts and rising temperatures. In this respect, future conservation measures seem to be necessary to preserve the most endangered populations. In managed forests, silvicultural systems should be able to maintain, restore or develop structural attributes useful to a reprise of yews free of competition of alien naturalised taxa. Moreover, the application of protection protocols can represent an effective tool for the characterization of the old growth stands with yews, in order to plan better management and conservation measures.