Shrub cover and soil moisture affect Taxus baccata L. regeneration at its southern range

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Abstract

The effect of key ecological and anthropic factors on recruitment of the common yew (*Taxus baccata*) in Sardinia (Italy) has been analysed. After a bibliographic and cartographic research, followed by field surveys, we found 232 sites where *T. baccata* grows in Sardinia (opposed to 69 previously reported in literature). Among them, we selected 40 sites, distributed in 14 different mountain chains, characterised by a number of individuals ranging from 11 to 836 adult yews with average Diameter at Breast Height (DBH) from 13 to 130 cm. By means of generalised linear modelling, we investigated and weighted the effect of ecological, structural, and anthropic factors on amount of *T. baccata* recruitment. Stand recruitment was positively correlated to shrub cover and soil moisture, and was negatively correlated to browsing (both from livestock and wild animals). Our data confirm that the presence of a protective layer of bushy and/or spiny shrubs is a crucial factor for seedling and sapling survival, mostly in relation to protection from summer drought and browsing of large herbivores. Finally, guidelines for conservation and restoration of *T. baccata* communities, referred to the EU priority habitat 9580* (Mediterranean *Taxus baccata* woods), have been outlined.

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 forest 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 fraction of its primary forest vegetation, equal to 4.7%, is today preserved (Hoekstra et al. 2005). In wooded habitats, human disturbance caused simplification of 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).

The common yew (hereafter yew), *Taxus baccata*, has been recognised as one of the most ancient forest species in Europe, with origin in the early Miocene (Kunzmann and Mai 2005; Ellenberg 2009). Yew can form pure stands, mostly in the centre of its range across Central Europe to the British Isles, with smaller areas known elsewhere (Thomas and Polwart 2003; Farris et al. 2012; Vessella et al. 2015). Interestingly, in southern Italy, large Mediterranean islands and in the Hyrcanian forests (northern Iran) yew dominates or co-dominates relic stands with high biogeographical meaning (Vessella et al. 2009; Karami-Kordalivand et al. 2021). In the Mediterranean Basin, yew becomes mostly a montane tree, preferentially growing in the understorey of taller trees and on north-facing slopes (Thomas and Polwart 2003).

Yew has become rarer in many parts of its range, probably as a result of regression after the last Ice Age (Bennett et al. 1991; García et al. 2000), locally disappearing or remaining isolated in small populations during the last millennia (Tittensor 1980; Svenning and Magård 1999; Dhar et al. 2006; Ruprecht et al. 2010; Iszkuło et al. 2016). The main factors of reduction were recognised as human pressure,

overbrowsing, 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; Iszkuło 2011; Iszkuło et al. 2012; Iszkuło et al. 2014; Devaney et al. 2015; Garbarino et al. 2015; Thomas and García-Martí 2015). Land-use contributed to the contraction of yew habitats, through logging (Svenning and Magård 1999; García et al. 2000), in combination with browsing and burning, which transformed forest landscapes by particularly affecting shade-tolerant and late-successional species such as yew (Busing et al. 1995; Piovesan et al. 2009). Consequent wooded habitat fragmentation, caused by human activities, negatively impacted yew pollination by reducing its populations' size, since the formation of viable seeds requires co-existence of both sexes (Piovesan et al. 2009). Yew reduction has also been attributed to overbrowsing of seedlings and saplings by herbivores, likewise the scarcity of suitable sites for recruitment (Hulme 1996; García et al. 2000; García and Obeso 2003; Farris and Filigheddu 2008).

For the reasons illustrated above, in the EU context there are six forest habitats with yew (9120, 9180, 91J0, 9210, 9380, 9580) included in the Habitats Directive 92/43/EEC, of which two are prevalent in Italy and listed with priority status (9580* - Mediterranean *Taxus baccata* woods, and 9210* - Apennine beech forests with *Taxus* and *Ilex*) (European Commission 1992; Biondi et al. 2010). To conserve the natural distribution of this species, protected areas have been established and included in the Natura 2000 network as Special Areas of Conservation (SACs), which must be managed to maintain habitats in favourable conservation status (Epstein et al. 2016). To achieve this goal, the specific structure and functions necessary for long-term persistence of habitats must be maintained and the conservation status of typical species must be favourable (European Commission 1992; Epstein et al. 2016). Therefore, to achieve the aim of maintaining a favourable conservation status of EU habitats, it is crucial to understand key factors affecting the "structure and function" of these habitats, so that informed management decisions can be taken.

Here, we try to identify the main ecological and anthropic factors affecting yew habitat maintenance in the island of Sardinia, in the southern Mediterranean range of the species' distribution. Specifically, we focus on yew regeneration as a key process for population persistence.

The main aims of this study were to: i) update the present distribution of yew in Sardinia and define the main structural parameters (density, DBH and sex ratio) of the extant populations; ii) evaluate the most relevant factors affecting yew regeneration; iii) assess conservation measures useful for the future protection of this tree and the habitat it identifies.

2. Materials And Methods

2.1 Study system

The object of this study are yew stands growing in 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. Sardinia is located at the centre of the west-Mediterranean Basin, being its latitude N 38°51'52"

(Capo Teulada) and N 41°15’42” (Punta Falcone) at its southern and northern extremes. Sardinian landscape is mostly hilly, locally characterised by plateaus and plains, while the main mountains are low (average heights ca. 1,000 m a.s.l.) and often isolated, rarely grouped in chains or massifs, the highest of which is the Gennargentu (1,834 m a.s.l.). Sardinian substrates are heterogeneous, with the main outcrops represented by Cambrian metamorphites, Carboniferous granitic batholiths and Palaeozoic limestones; in addition, local sedimentary complexes related to a Mesozoic marine transgression, Tertiary marine and volcanic depositions related to the opening of the Tyrrhenian Basin, and Quaternary alluvial deposits are present (Carmignani et al. 2016).

From a bioclimatic point of view, though Sardinia mostly falls within the Mediterranean Pluviseasonal Oceanic climate, some differences can be found from north to south. In particular, two macrobioclimates (Mediterranean and Temperate submediterranean), four classes of continentality (from weak semi-hyperoceanic to weak subcontinental), eight thermotypic horizons (from lower thermomediterranean to upper supratemperate) and seven ombrothermic horizons (from lower dry to lower hyperhumid) define the entire region (Bacchetta et al. 2009; Canu et al. 2015).

Sardinian forest extension was considerably reduced starting from Punic and Roman times, as a result of massive deforestation for timber and extensive agricultural and pastoral activities, combined with fire to maintain pastures (Barreca 1974; Meloni 1975; Pungetti 1985; Caterini 2013). In several mountain areas that still remain relatively isolated and scarcely populated, the island preserves wilderness of natural environments with difficult access, which are therefore relatively well preserved (Fois et al. 2019). Relic yew stands can be found in some of these low disturbed areas, on gorges, sinkholes, mountain slopes and tops, and are very interesting examples of woodlands related to specific edaphoclimatic conditions (Desole 1948, 1966; Bacchetta and Farris 2007; Farris et al. 2012; Camarda 2020; Fantini et al. 2020). From a floristic-vegetational point of view, Sardinian woodland communities dominated or co-dominated by *Taxus baccata* are referred to two main associations (*Cyclamino repandi-Taxetum baccatae, Polysticho setiferi-Taxetum baccatae*) belonging to the Cyrno-Sardinian endemic alliance *Lathyro veneti-Taxion baccatae* (Mucina et al. 2016). Moreover, two subassociations of oak woodlands (*Glechomo sardoae-Quercetum congestae taxetosum baccatae* and *Saniculo europaeae-Quercetum ilicis taxetosum baccatae*) are known (Farris et al. 2012).

2.2 Data collection

We recorded all localities with presence of *Taxus baccata* individuals reported in literature (e.g., Angius 1851; Desole 1948,1966; Bacchetta and Farris 2007; Farris et al. 2012). In addition, we found further information about yew distribution in Sardinia through interviews to local people (forestry workers, shepherds, environmental guides), by consulting maps issued by the Italian Military Geographic Institute (IGMI, scale 1:25.000), and locating toponyms recalling the yew, i.e. Tassu/Tassos/Tassi; Eni/Enis; Longufresu/Longuvresu; Niberu/Nibberu – this latter meaning mostly juniper, but locally it is used for yews. Then we created a dataset containing all yew localities found from different sources. Finally, we carried out field surveys (from 2015 to 2021) 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, updating the current Sardinian distribution.

Later, we selected 40 sites from the entire distributional range of the species in the island (Fig. 1; Table S1). The sites were selected based on geographical, ecological, and structural features. From a geographical point of view, we selected a proportional number of sites from each mountain area, thus representing all mountain sectors. The average elevation of selected stands was 620–1250 m a.s.l. Among the studied stands, 14 can be classified within the phytosociological association *Cyclamino repandi-Taxetum baccatae*; four within the *Polysticho setiferi-Taxetum baccatae*; eight within the subassociation *Saniculo europaeae-Quercetum ilicis taxetosum*; and one within the *Glechomo sardoae-Quercetum congestae taxetosum*. Other 13 stands were not assigned to any phytosociological unit. Almost all selected stands grew in the Mediterranean Pluviseasonal Oceanic bioclimate, while four stands grew in the Oceanic temperate one. These stands were characterised by being part of woodlands where yew had a relevant presence, with at least 15 adult trees per site (only site 32 - which is the southernmost - excepted, with 11 living samples).

Yew regeneration (abundance of seedlings + abundance of saplings) was estimated in two to five 20 × 20 m plots at each site (see Table S1) unless the site area was smaller as to allow a complete sampling. Plots were sampled both within the stands and in clearings/edges of woodlands, to infer potential diversity between places with different light availability. Abundance of juveniles was subdivided in six classes: absent (0); very rare (1 = < 1/ha); rare (2 = 1–10/ha); scarce (3 = 11–50/ha); frequent (4 = 51–100/ha); abundant (5 = > 100/ha).

At each site we measured the following ecological and structural variables (Table S2), to which yew regeneration was hypothesized to be related:

1. Wood age; according to previous studies, yews start reproducing at ages comprised between 35 and 70 years (Thomas and Polwart 2003); consequently the youngest formations are not capable of an efficient system of sexual reproduction. On the contrary, older trees can produce abundant quantities of pollen and seeds, allowing an easier dispersal through frugivorous animals. Wood age was approximated by average diameter at breast height (aDBH), measured on as much as possible (often all) individuals counted per site. We selected sites with average DBH ranging from 13 to 130 cm, to infer possible differences between young formations and older stands.
2. Sex ratio [SR = Females/(Females + Males)]; reproductive ecology of dioecious species is important in the understanding of different dynamics related to the spread 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 dioecious species male prevalence was highlighted, especially under stressful conditions (Obeso 2002). Females are subject to higher stresses, due to the major effort put on the reproductive phases, resulting in a diminished structural increase, and a higher mortality when under stress (Leigh et al. 2006; Massei et al. 2006). Plant populations characterised by wind pollination and abiotic dispersal were found to have more often male biased sex ratios (Sinclair et al. 2012).

Recent studies showed how the growth rate of *T. baccata* females was lower than that of males, together with a higher water request for females (Iszkuło et al. 2009, 2011). Mediterranean climate regime would favour male prevalence more than other European regions (Vessella et al. 2015). Moreover, it was supposed that older populations were male sex biased (Iszkuło et al. 2009; Perrin and Mitchell 2012; Vessella et al. 2015). Consequently, we supposed that sex biased populations were less capable of reproduction. Sex ratio was detected by analysing all possible individuals in the field, through the observation of pollen strobiles on male trees and arils on females. Although pollen and arils occur in different periods of the year, the contemporary observation of sexual elements on the same populations was possible by searching their remnants both on the branches and on the ground, under the trees' canopies. In the case of larger populations, more checks were carried out.

3. Wood closure (Clos); shading could affect seed germination and seedling establishment (Vessella et al. 2015; Devaney et al. 2015). The structure of older yew stands could affect yew regeneration by impeding or reducing the growth of seedlings, mostly where canopies of conspecific trees do not allow a viable light quantity (Tittensor 1980; Dovciak 2002; Devaney et al. 2015; Vessella et al. 2015). Closure was estimated as % ground cover of canopy projections.
4. Browsing (Bro = yes or no); the action of herbivores is well known to negatively affect survival and establishment of seedlings, thus regeneration of yews (Mysterud and Østbye 2004; Farris and Filigheddu 2008). Browsing was assessed by recording any evidence related to current impacts attributable to livestock and wild animals and/or their signs (e.g., physical presence observed in the field, excrements, tracks, fur/wool on the bark and on branches, branches decorticated by deer's antlers etc.).
5. Shrub cover (Shrub + Spi); shrubs could protect seedlings from drought and browsing, thus promoting regeneration of trees (García and Obeso 2003; Farris and Filigheddu 2008). Here, total shrub cover was measured as the sum of abundance indexes of spiny shrubs (Spi, ranging from 0 to 5) and other shrubs (Shr, 0–5), meaning 0 = absent; 1 = very rare; 2 = rare; 3 = sporadic; 4 = frequent; 5 = abundant.
6. Soil summer moisture (Ssmo = Yes or No); Mediterranean habitats are characterised by more or less long dry periods that could negatively affect yew recruitment (Thomas and Polwart 2003). Water availability has been considered a limiting factor for yew regeneration at the southern range of the species (Linares 2013). Ssmo was assessed by observing in the field the soil moisture of the sites at the peak of the dry season.
7. Site morphology (Morph = Slope or Watercourses); rockiness and exposure to climatic factors (sun irradiation, winds, precipitations, frost) could affect microhabitat features, particularly in relation to microclimate (dryness and moisture). In particular, watercourses have higher moisture and it is supposed that they allow a better regeneration than slopes (Thomas and Polwart, 2003). Half of the selected sites (20) were chosen at dry conditions (slopes) and other 20 sites at moist localities (streams, gorges, springs).
8. Site slope (Pend); declivity was supposed to be important for persistency of more natural conditions of the wooded formations (Fantini et al. 2020) and for a longer lasting moisture (Sanz et al. 2009).

Site slope was quantified as average declivity and was calculated as the average of different slopes detected using an inclinometer.

2.3 Statistical analysis

The state variable of interest, Recruitment (Recr), was expressed as a count (range = 0–9). The analysis was thus performed using Generalised Linear Models (GLMs) with Poisson error structure, with software R version 4.1.1 (R Core Team 2020). Considering the limited sample size (n = 40), a univariate analysis was first performed to screen for supported effects. That is, each effect was evaluated at a time, according to the following model (see R Script, Online Resource 1, for details):

MEffect1 = glm(formula = Recr ~ Effect1, family = Poisson)

Univariate effect models were compared with the null model, M0 = glm(formula = Recr ~ 1, family = Poisson), by means of AICc (Burnham and Anderson 2002) and Likelihood Ratio Test (LRT) (Kent 1982).

Models that, compared to the null, 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 in a general multivariate model and evaluated with backward model selection. General model simplification proceeded by removing effects that were non-significant in the multivariate analysis, starting from higher p values. Multivariate model selection was also performed using the automated model selection routine of R package glmulti (Calcagno and de Mazancourt 2010) (see R script, Online Resource 1, 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 and Hothorn 2002). By mean of multivariate model selection, simultaneous effects of variables selected with the univariate screening could be evaluated, considering also possible interactions.

The explanatory power of models was estimated as Deviance explained:

DE = (deviance(M0)-deviance(MEffect))/deviance(M0)).

3. Results

The data collected allowed us to report the current presence of *Taxus baccata* in 232 Sardinian sites, while in other 5 the species is locally extinct. Among these sites, 168 are here recorded for the first time, while other 69 were previously reported in literature. The species is present in 15 different mountain areas, where it normally does not form extended communities, being mostly represented by single or sparse individuals. In 188 sites yew populations were constituted by less than 40 trees (110 of them with a spatial distribution of isolated individuals); other 25 sites had between 41 and 100 trees; we found more than 100 adult yews in 19 sites, 12 of which can be defined as pure or almost pure yew woodlands. In the other cases, yews formed small mixed woodlands with other tree taxa (*Alnus glutinosa*; *Fraxinus ornus*;

Ilex aquifolium; *Ostrya carpinifolia*; *Quercus ilex*; *Q.* gr. *pubescens* etc.). Among these populations, 86 had extension smaller or equal to 0.5 ha. Other 85 sites had extension ranging from 0.5 ha to 3 ha, whereas 52 sites were larger than 3 ha. Yew density was often low, being higher than 20 yews per hectare in 41 cases and otherwise lower. Mean DBH of Sardinian adult yews ranged from 107.8 to 734.6 mm (mean 421.2 mm), calculated on more than 80% of the observed trees. Sex ratio of more than 8300 yews showed a prevalence of males, corresponding to 55.6% of the total adult trees studied.

Among abiotic factors characterising Sardinian yew sites, declivity averaged from 7.3 to 32.7° (mean 20°). Geologically, 77 sites were located on limestones, 76 on granites, 61 on metamorphic rocks. In the remaining 34 sites, yews grew on different substrates (andesites, basalts, granodiorites, rhyolites, trachyte). 119 yew sites were related to wet habitats (gorges, springs, streams), whereas 118 yew sites were related to drier habitats (cliffs, rocks, slopes, mountain tops). Regeneration was absent in 134 yew sites, while we found abundant recruitment in 9 sites.

The 40 sites selected for the GLM analysis showed a mean site area ranging from 0.4 and 5.1 ha (mean 2.6 ha), an average 92 living adult yews per site (nAT in Table S2), average density of 10 to 64 yews per hectare (mean 37) and average DBH ranging from 184 to 681 mm (mean 443 mm). Sex ratio was often unbalanced in favour of males (57% of the total observed samples), which were prevalent in 55.7% of sites (28 sites), while we found a slight female prevalence in 11 sites and equity of sexes in one site. Recruitment was absent in 15 sites; very rare in three sites; rare in seven sites; scarce in eight sites; frequent in four cases; and abundant in three cases.

Univariate model selection supported the effect of Shrubs, Sex Ratio, DBH, Morphology, Browsing and Summer moisture (first 6 models in Table 1) on yew regeneration, which has AICc much lower than the null model M0. The effect of Shrubs (1st model) is by far the strongest, with an improvement of AICc of more than 91 compared to M0 (7th), an estimate of overdispersion based on deviance (c_hat) = 1.27 and Deviance explained = 0.66.

Table 1

Variables affecting common yew regeneration supported by the univariate analysis. Recr = recruitment; Shrub = shrubs; SR = sex ratio; DBH = Diameter at Breast Height; Morph = morphology; Bro = browsing; Ssmo = soil summer moisture; Clos = closure of canopies; Pend = declivity.

Rank	Model structure	K	AICc	ΔAICc	LL	Dev. Expl.
1	Recr ~ Shrub	2	130.2244	0.0000	-62.9501	0.6606
2	Recr ~ SR	2	183.2421	53.0176	-89.4589	0.2877
3	Recr ~ DBH	2	187.7552	57.5308	-91.7154	0.2560
4	Recr ~ Morph	2	209.8880	79.6635	-102.7818	0.1003
5	Recr ~ Bro	2	211.1093	80.8849	-103.3925	0.0917
6	Recr ~ Ssmo	2	213.5470	83.3225	-104.6113	0.0746
7	M0: Recr ~ 1	1	221.9372	91.7127	-109.9159	0.0000
8	Recr ~ Clos	2	223.8796	93.6551	-109.7776	0.0000
9	Recr ~ Pend	2	224.1561	93.9317	-109.9159	0.0000

Considering supported effects, multivariate backward model selection started from the full model below:

MFull<-glm(formula = Recr ~ Shrub + SR + DBH + Morph + Bro + Ssmo, family = Poisson).

The full model has an estimate of overdispersion based on deviance (c_hat) = 1.19, residual deviance (39.247 with 33 df) and sum of Pearson (36.70), which are lower than the five-percent critical value for a chi-squared distribution (47.40), thus providing an adequate description of the data.

Backward model selection provided support for model Recr ~ Shrub + Morph + Bro (1st in Table 2), which is significantly different from the second ranked (p LRT = 0.06134) and shows the significant effects of shrubs, morphology (watercourse, W) and browsing on yew regeneration. Other effects previously supported by the univariate model selection have no support with the multivariate analysis. Parameters estimates taken from the best model are Shrubs = 0.4446 (p = 0.0003), Morph (W) = 0.7009 (p = 0.0050), Bro (yes) = 0.4833 (p = 0.0608). The effects observed with the univariate models for Shrub (0.4028) and Morph (0.7487) are consistent with the multivariate analysis, whereas the sign of Bro is opposite in univariate (-0.7612), possibly suggesting interactions between the variables Shrubs and Bro. Additionally, the effects of SR and DBH, which seemed rather strong in the univariate analysis, are lost in the multivariate, possibly due to correlations with Shrubs (cor of Shrub vs DBH = -0.470556; cor of Shrub vs. SR = 0.6325661).

Table 2

Variables affecting common yew regeneration supported by the multivariate analysis. Shrub = shrubs; Morph = morphology; Bro = browsing; DBH = Diameter at Breast Height; Ssmo = soil summer moisture; SR = sex ratio.

Rank	Effects on yew regeneration	K	AICc	ΔAICc	wi	LL	Dev.Expl.
1	Shrub + Morph + Bro	4	127.1372	0.0000	0.4248	-58.9972	0.7162
2	Shrub + Morph	3	128.1617	1.0245	0.2545	-60.7475	0.6916
3	Shrub + DBH + Morph + Bro	5	129.3459	2.2087	0.1408	-58.7906	0.7191
4	Shrub	2	130.2244	3.0872	0.0907	-62.9501	0.6606
5	Shrub + DBH + Morph + Bro + Ssmo	6	131.4385	4.3013	0.0494	-58.4465	0.7240
6	Shrub + Bro	3	132.5451	5.4079	0.0284	-62.9392	0.6608
7	Shrub + SR + DBH + Morph + Bro + Ssmo	7	134.3926	7.2554	0.0113	-58.4463	0.7240
8	Morph + Bro	3	208.3445	81.2073	0.0000	-100.8389	0.1277
9	Morph	2	209.8880	82.7508	0.0000	-102.7818	0.1003
10	Bro	2	211.1093	83.9721	0.0000	-103.3925	0.0917
11	None	1	221.9372	94.8000	0.0000	-109.9159	0.0000

Automated model selection performed with glmulti (Calcagno and de Mazancourt 2010), with interactions allowed (see R script, Online Resource 1, for details), selected the same best model, Recr ~ Shrub + Morph + Bro, and provided model-averaged estimates of parameters that confirm the positive effects of Shrubs and Morph (W) and a negative effect of browsing on Recr (Shrubs = 0.3688, Unconditional variance = 0.0148; Morph (W) = 0.5945, UV = 0.1850, Bro (yes) = -0.0893, UV = 0.5003). Additionally, values of deviance explained showed in Table 2 evidence that Shrub has a strong effect, explaining 66% of deviance, while Morph provides an additional 3% and Browsing 2% of explanation (see models ranked 4th, 2nd and 1st).

4. Discussion

Although the effects of biotic (browsing) and abiotic (soil aridity and/or moisture) factors on yew (and other trees) recruitment in Mediterranean environments are well-known (Debussche and Isenmann 1994; García et al. 2000; García and Obeso 2003; Gómez-Aparicio et al. 2008; Sanz et al. 2009; Linares 2013; Casals et al. 2015), a comprehensive analysis able to measure the relative weight of each single factor, and the interactions among factors, was still missing. Our results suggest that, albeit several ecological variables can simultaneously affect yew regeneration, shrub cover results by far the main factor

positively affecting yew regeneration, especially when associated to the presence of moist sites (watercourses), while browsing negatively affects the establishment and survival of seedlings and saplings. The multivariate analysis carried out on multiple factors and their interactions, proved to be more conservative than the univariate, selecting fewer effects. Below, we will discuss the effects supported by the multivariate analysis.

Shrub cover is by far the strongest effect. Shrubs can protect tree seedlings from browsing, by providing shelter and associational resistance (Casula and Murgia 2017), and from drought by shading plants and facilitating mycorrhization (Richard et al. 2009; Fitzsimons et al. 2008; Lopez-García et al. 2013).

Furthermore, shrub canopies create favourable conditions for yew dispersion and germination, by exerting a perch effect that attracts frugivores releasing seed rain under the canopy of fleshy-fruited shrubs, and for seedling survival, by maintaining a moister environment under their canopies and avoiding or reducing browsing by large herbivores (García et al. 2000; Perrin and Mitchell 2012; Linares 2013). Yew seedlings and saplings appear to be more light shade tolerant than adults (Perrin and Mitchell 2012), thus, their growth can be favoured under shrubs, allowing an interaction “shrub and yew” which facilitates yew juveniles’ survival. Moist and nutrient-rich sites are more suitable microhabitats for seedling survival, and can be identified as favourably microsites, especially in relation to summer drought in Mediterranean environments (Mendoza et al. 2009), but contemporary protecting yew juveniles from large herbivores, when dense (and maybe spiny) shrubs are present. The protection of yew seedlings and saplings by shrubs appears to be the most relevant factor determining the associative pattern observed in this study. Among the other positive connections, shrubs provide shelter against ungulates both for their relative unpalatability and thickness (e.g. *Arbutus unedo*, *Erica arborea*, *E. scoparia*) (Casula and Murgia 2017) or due to their spinescence (e.g. *Crataegus monogyna*, *Prunus spinosa*, *Rubus* gr. *ulmifolius*) (Farris and Filigheddu 2008). As a result, in areas where a higher livestock presence was evident, juvenile yews were often absent in unprotected sites and, where some young trees were present, these were assuming the typical hourglass shape, characteristic of open woodlands affected by intense browsing (Marzolff et al. 2020). In these cases, shrubs protected seedlings during their first growing phases, then allowing a slow but constant development and establishment of saplings. Thus, spiny and unpalatable shrubs act as natural fences to prevent the herbivores from browse seedlings, saplings and young trees.

Soil moisture, particularly during the dry season, is another factor that our study highlighted as important for yew recruitment. It is well known that at the southern extreme of its distribution, i.e. the Mediterranean and Irano-Turanian biogeographic regions, moister and fresher sites act as niche refugia for boreal plants such as yew (Thomas and Polwart 2003; Thomas and García-Martí 2015; Karami-Kordalivand et al. 2021). The presence of springs and/or watercourses nearby yew populations positively affects regeneration, very likely by providing more humid conditions to seedling establishment and survival. Along stream courses yews find better environmental conditions, even extending their suitable climatic and moisture requirements under the limits otherwise reached by the species in normal conditions (Sanz et al. 2009; Farris et al. 2012). On the other hand, water shortage has been considered as a limiting factor for yew recruitment (Linares 2013). In relation to predicted consistent precipitation decrease due to

climate change, water stress will be one of the challenges that yews have to face in the future, particularly in the Mediterranean Basin (Mendoza et al. 2009; Linares 2013; Thomas and Garcia-Martì 2015).

Browsing negatively affects yew regeneration acting mainly against seedlings and saplings growth rather than seedlings emergence (García et al. 2000; Farris and Filigheddu 2008; Casals et al. 2015). Yew is browsed by vertebrate herbivores, though being toxic in almost all the parts of the plant (García et al. 2000; García and Obeso 2003; Thomas and Polwart 2003; Mysterud and Østbye 2004; Farris and Filigheddu 2008). In our study, among the 15 sites where a lack of recruitment was recorded, only two were totally devoid of livestock, although wildlife herbivores were locally present, meaning that apart from local climatic conditions, browsing animals appear to be a relevant factor limiting yew recruitment. The presence of browsing animals, both livestock and wildlife (cattle, goats, sheep, deer, and mouflon), was recorded in 29 sites, four of which are currently characterised by a rare to sporadic presence of yew recruitment. On the other hand, the remaining 11 sites with no evidence of browsing preserved recruitment, sometimes abundant, confirming that a lower pressure of herbivorous mammals favours a richer and successful yew recruitment (Iszkuło 2011).

4.1 Implications for conservation

Our study on the regeneration of *Taxus baccata* populations at the species' southern range has confirmed that yew recruitment is positively correlated with woody and spiny shrubs, which protect juveniles from drought and herbivores/browsers (García and Obeso 2003, Gómez-Aparicio et al. 2008), create through their shade a shield against negative climatic drivers (Gómez-Aparicio et al. 2008), and maintain better soil conditions that facilitate the development of recruits' root apparatus (Farris and Filigheddu 2008; Sanz et al. 2009). Therefore, actions such as maintaining or actively increasing shrub cover appear as important management activities to foster yew recruitment.

Moreover, since yew regeneration of Mediterranean populations is higher in places having moister soil conditions and fresher microclimates, actions such as *in situ* seed dispersion and/or seedling plantations should be provided after prior checks of sites, in order to select suitable microsites for regeneration (Thomas and Garcia-Martì 2015).

Site management alone could not be sufficient to guarantee yew regeneration, since it was already shown that minimum requirements for a population to be self-perpetuating are populations extended over an area of at least 0.5-3 hectares (Piovesan et al. 2009), with no less than 40 adult individuals and approximately equal portions of males and females (Iszkuło et al. 2009). Nonetheless, our study confirms that site management can be a crucial factor and should be aimed mainly at maintaining or increasing shrub cover close to sparse yew females, possibly by identifying those places where soil moisture is higher during summer droughts. These sites could be identified in places nearby springs or streams, as previously detected by Sanz et al. (2009). According to Casals et al. (2015) for young yews non dense woodlands are most likely to represent optimal sites for regeneration and, where possible, should be

managed for this purpose. Accordingly, we remark the relationship between density of shrub cover and yew regeneration, which consequently puts on evidence their potential facilitative interaction.

Previous studies on yew stands were mostly concentrated on the negative impacts of browsing on yew regeneration (e.g. Garcia et al. 2000; Mysterud and Ostbye 2004; Perrin et al. 2006; Farris and Filigheddu 2008; Casals et al. 2015). Some of these works showed that the creation of specific protected areas for the species were not sufficient, in the absence of herbivores control (Thomas and Polwart 2003; Mysterud and Østbye 2004; Dhar et al. 2006). Sardinian yew populations are mostly affected by browsing of livestock (Farris and Filigheddu 2008), to which wild animals have to be added. Our findings are based on sites where herbivory is long disappeared and yew populations are increasing (Calvia and Ruggero 2020), opposed to areas with a limited to abundant herbivore load with no or low recruitment. The circle keeps turning since to a lesser presence of animals normally corresponds a higher and more uniform shrub cover and *vice versa* (Manier and Hobbs 2006; Riedel et al. 2012). For this reason, among the relevant actions to perform, the reduction and control of livestock load around yew populations should be enhanced, along with monitoring of wildlife effects on recruitment.

Based on previous data (Piovesan et al. 2009; Iszkuło et al. 2009), along with the scarce or null regeneration observed for several years during our study, some of the selected sites can be considered as non-self-perpetuating populations, posing serious questions about their active protection through *in situ* and *ex situ* actions. Specifically, it is important to remark that 38 out of 40 selected yew populations were extended over an area larger than 0.5 hectares, although only in 11 cases this was larger than 3 hectares. More alarming was the presence of 40 or more adults in only 18 out of 40 populations (Table S2). In those cases, planting of locally produced seedlings and/or saplings after the creation of shelters within selected microhabitats could be useful for the perpetuation of these otherwise threatened and prone to decline populations. These actions appear to be even more relevant in sites with strongly male unbalanced populations (e.g. site 15, where only 3 females compared to 14 males were recorded).

From a strictly protection point of view, only 10 (25% of the total) of the studied sites are recorded within official maps as EU priority habitat 9580* (*sensu* Habitats Directive, 92/43/CEE, European Commission 1992), despite the total yew sites included in Special Areas of Conservation (SACs) being 28. Moreover, three sites are both included in SACs and are also recognised as “Regional Monuments” according to the Sardinian Regional Law 31/89; five sites are also included in the Gennargentu National Park; additionally, other two are part of the “Gutturu Mannu” Regional Nature Park; finally, one of these latter is also included in the “Monte Arcosu” WWF oasis.

Given the paucity of viable yew populations, it seems important to include all Sardinian sites where yews form sufficiently large stands (≥0.5 ha) within the EU priority habitat 9580* and the Natura 2000 network.

Nevertheless, the low presence of recruitment represents a future challenge for the conservation and management of threatened yew habitats, both in protected and unprotected sites. Thus, active *ex situ* and *in situ* management could prove to be fundamental for the conservation of this species at the southern extremes of its range. *Ex situ* actions require, on the one hand, the collection of yew seeds from

threatened sites, and their conservation in seed banks, from which to draw in case of necessity. On the other hand, tree nurseries (both from seed and scion) acting as *quasi in situ* sites could be created to guarantee the conservation of living material safe from possible stresses (Thomas and Garcia-Martì 2015).

In situ actions can be provided by planting seedlings (possibly second years, to allow a better resistance from environmental conditions) that should be protected through the creation of artificial shelters on the surrounding areas of adult yews, specifically where there is no possibility to have a shrub cover (Thomas and Garcia-Martì 2015). Otherwise their plantation should be studied within sites where natural shrub shelters and soil moisture could enhance seedling survival, also in view of future possible habitat modifications connected with climate change.

Declarations

Statements and Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

This project was conceived and designed by Giacomo Calvia, Paolo Casula, Emmanuele Farris and Gianluigi Bacchetta with contributions from all other authors. Giacomo Calvia, helped by Sergio Fantini, conducted the field work and data collection. Paolo Casula performed the statistical analyses. Sergio Fantini and Giacomo Calvia created the map using GIS. Giacomo Calvia wrote the manuscript, with assistance from all the authors. All authors read and approved the manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

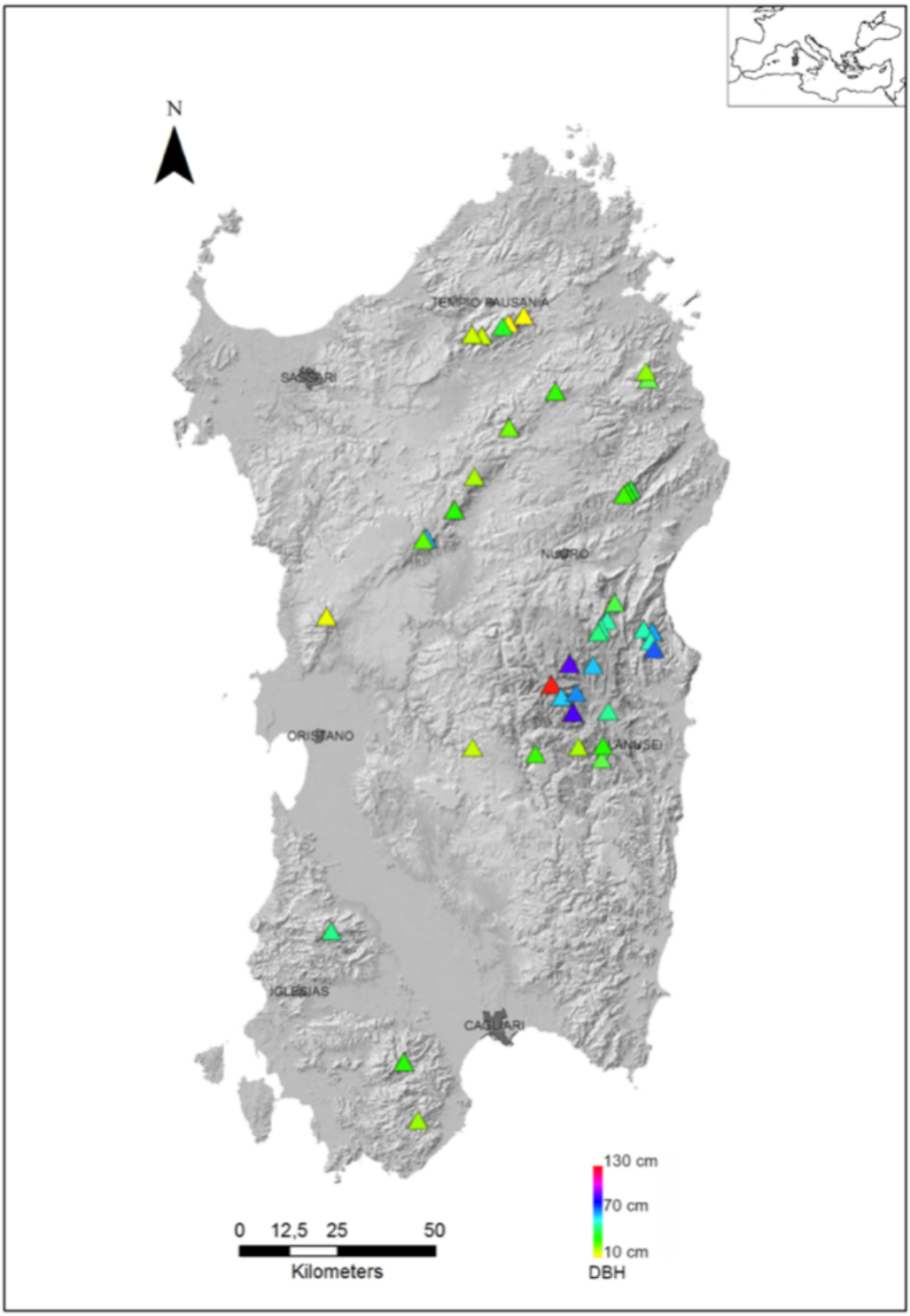

Figure 1

Distribution map of the Sardinian selected yew stands and their DBH average ranges.

Supplementary Files

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