
Highlights

► *Taxus baccata* shows a core-periphery trend towards diminishing population regeneration in marginal areas. ► Yew regeneration is limited by water shortage in its southern limits and by frost and canopy shade at core-to-northern ranges. ► Genetic diversity tends to decrease in small-size yew populations along the species range. ► Silvicultural activities should focus on moderate thinning in remnant yew populations from temperate areas.



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Review

Shifting limiting factors for population dynamics and conservation status of the endangered English yew (*Taxus baccata* L., Taxaceae)

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ABSTRACT

English yew (*Taxus baccata* L., Taxaceae) is a Tertiary relict locally endangered within parts of its large geographic range. In this paper, I seek to synthesise the literature and discuss the limiting factors for population dynamics and conservation status of this endangered tree. The literature was reviewed, focusing on yew fossil records, biogeography, molecular ecology, stand structure (size, age and sex ratios), and regeneration dynamics. The information reviewed illustrates diminishing population viability mainly in southern marginal areas of the geographical range of English yew. Water availability seems to be limiting yew regeneration to a greater extent than that of herbivory and shade at the southern margin, while at the northern margin such factors as light availability and frost and/or herbivory may be more important than water. Habitats with fleshy-fruited shrubs proved to be the best habitat for seed dispersion, seedling establishment and sapling survival and growth in the Mediterranean mountains. The results discussed here reveal a widespread lack of regeneration and evidence of increased genetic drift, elevated inbreeding, and depressed gene flow, mainly in southern European populations. The maintenance of healthy populations of yew in temperate forests seems to depend mainly on selective canopy opening to reduce light competition, while regeneration in Mediterranean mountains is strongly related to herbivory regulation and the conservation of well-developed forests, understories, and their community of avian dispersers. Gaps of knowledge for this species are the implications of life strategy for survival across long time periods, the different management of logging and herbivory across the yew distribution range and the predictions of recruitment under climate change.

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1. Introduction

English yew (*Taxus baccata* L., Taxaceae) is a relict tree species (sensu Hampe and Jump, 2011), prone to decline and included in

several conservation actions and laws in European countries. Forests harbouring yew have been designated as special protection areas by the European Community (Habitats Directive 92/43/EEC). Although in central Europe and the British Isles yew can form dense stands (Ruprecht et al., 2010; Thomas and Polwart, 2003; Svenning and Magård, 1999), in the Mediterranean basin, as with

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Fig. 1. Current yew populations at its southernmost distribution range are restricted to remote localities that have marginal value for human uses, such as steep slopes and rocky terrain. Individuals occur mostly as shrubs or as trees with polycormic stems. Author's photograph taken from a relict yew population at Valdepeñas de Jaén, southern Iberian Peninsula (37°35'N, 3°42'W, 980 m a.s.l.).

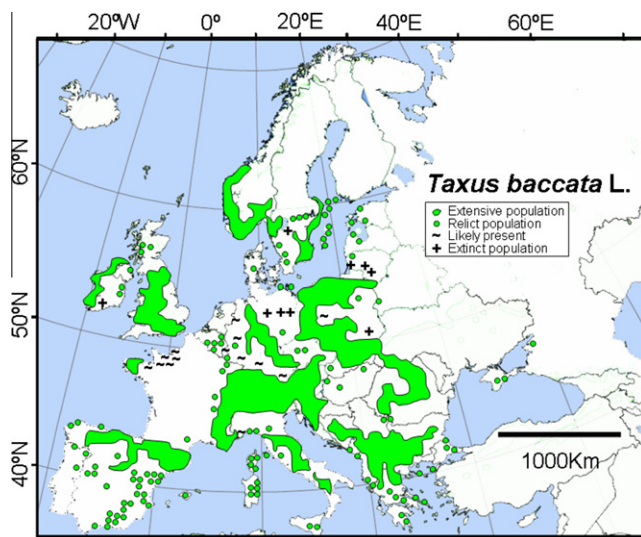


Fig. 2. Current distribution area of *Taxus baccata* L. in Europe. Review based on Jalas and Suominen (1973) and the references cited in the main text.

other plant species of boreo-alpine origin, yew appears as a reduced number of isolated patchy populations, located mainly in shady ravines on north-facing slopes (Fig. 1; Navarro-Cerrillo and Pulido-Pastor, 2003; García et al., 2000).

Yew is a drought- and frost-sensitive species, growing mainly under mild oceanic climates with relatively mild winters, abundant rainfall and high mist frequency (Thomas and Polwart, 2003). In Norway and Sweden *T. baccata* grows up to 61° northern latitude (Fig. 2). The eastern limit of the range in Europe extends to the Baltic Sea, Estonia and the Carpathians, while the western limit reaches the Azores islands (Schirone et al., 2010). The southern limit is found in the Baetic-Rifan Mountains, from south Spain and northern Morocco, as well as in the Atlas Range (Morocco and Algerian). At the northern limits of *T. baccata* distribution area, the annual precipitation is barely higher than 500 mm and

physiological drought, caused by frozen soil, has been related to high *T. baccata* seedling mortality (i.e. mean monthly temperatures of about -8 to -12 °C; see Iszkuło, 2010). On the other hand, at the southern limits of *T. baccata* distribution area, it grows under Mediterranean-mountain climate, where annual precipitation is typically above 900–1000 mm and mean annual temperature is about 10–11 °C; mean summer rainfall should reach at least 100 mm to allow some yew regeneration success (Sanz et al., 2009).

Yew conservation has been concerned primarily with regeneration processes, given the lack of viable seedlings observed in multiple regions (Sanz et al., 2009; García and Obeso, 2003; Hulme, 1996). Across its southern range (Fig. 2), yew populations are usually composed of about a dozen of individuals dominated by senescent trees, with a very low proportion of saplings and seedlings (Mendoza et al., 2009a; Navarro-Cerrillo and Pulido-Pastor, 2003; García et al., 2000). The poor regeneration may be caused by low seed production (by limited pollination, climate constraints, seed predation, etc.), difficulty in seedling establishment (by drought or frost, pathogens, etc.), and/or grazing pressure (Sanz et al., 2009; Farris and Filigheddu, 2008; García and Obeso, 2003; García et al., 2000; Hulme, 1996). In addition to inadequate regeneration, habitat fragmentation diminishes the size of yew populations and enhances their spatial isolation (Dubreuil et al., 2010). Such changes could be accompanied by declining genetic variation and increasing inter-population genetic divergence due to greater random genetic drift, increased inbreeding and reduced gene flow (González-Martínez et al., 2010; Young et al., 1996).

Furthermore, the interaction between stand structure and yew regeneration should require greater research effort to disentangle its complexity (Ruprecht et al., 2010; Piovesan et al., 2009; Dhar et al., 2007). For instance, regeneration failure has been related to human-induced habitat degradation by the clearing of forests (Lyubenova and Nedelchev, 2001). Nevertheless, an excessive canopy closure, following the abandonment of traditional forest uses, appears to explain yew decline in growth, survival, and reproduction in central and northern Europe (Ruprecht et al., 2010; Svenning and Magård, 1999). Hence, yew conservation should be

viewed in the framework of proactive management, where the limiting factors are likely shifting along the current distribution range of this species (Smith and Zollner, 2005).

1.1. Theoretical background and methods

The abundance of species declines commonly from the centre to the margin of the distribution range (Sagarin and Gaines, 2002). In addition to abundance, niche breadth is also thought to be greatest in the distribution centre and to decline towards range edges (Gaston and Lawton, 1990). Both, declines in abundance and narrowing niche toward the yew distribution limits are recognised patterns, which could be explained by different non-excluding processes, as unfavourable environment (Leuschner et al., 2009), competitive displacement (Iszkuło et al., 2012), or the influence of human uses (Lyubenova and Nedelchev, 2001).

Yew is a dioecious, low-growing, evergreen tree with a lifespan that can reach up to 1000 years. Thus the understanding of how life-cycle transitions affect long-term population dynamics should be a critical issue on conservation biogeography (Smith and Zollner, 2005). This review aims to test the following hypothesis: *T. baccata* shows a core-periphery trend towards diminishing population growth and regeneration from core (high number of reproductive individuals) to marginal (low number of reproductive individuals dominated by senescent trees) populations. It is also hypothesised that the main limiting factors for yew are shifting throughout the current distribution area. Specifically, it is hypothesised that yew regeneration is more limited by water shortage in its southern limits, and by frost and biotic factors (canopy shade and herbivory) at northern ranges, while genetic diversity should tend to decrease in both northern and southern marginal areas.

To fulfil this objective, data from the entire *T. baccata* distribution area are reviewed, but special attention has been paid to the most endangered southernmost populations, including yew fossil records, biogeography, molecular ecology, stand structure, and regeneration dynamics, compiling data in order to summarise current knowledge concerning the population dynamics and conservation status of this endangered tree. This review includes information from published sources, grey literature, and unpublished data, but papers included in the *Science Citation Index* have been used as far as possible in order to include a wide readership to examine the hypothesis of this work through the references used.

2. Late Tertiary and Quaternary persistence of yew at its current southernmost range

Recent estimates based on molecular clocks date existing *Taxus* species to the transition between the Cretaceous and the Tertiary (Hao et al., 2008), about 66 millions of years ago (My, hereafter). The oldest fossil record for *Taxus* in Europe dates to the Lower Miocene (about 23 My; Kunzmann and Mai, 2005). During the late Miocene and the Pliocene (5.3–1.8 My), European Mediterranean flora underwent extensive differentiation (Palamarev, 1989). The main selective pressure for plant communities in the late Tertiary seems to have been a long-term decline in summer precipitation (Suc, 1984). The drought associated with high temperatures during the growing season requires specific adaptations and can be assumed to have led to the yew segregation along elevational, latitudinal, and topographic gradients.

Presumably since the middle Miocene (about 15 My), and mainly during the Pliocene, advancing aridity forced the withdrawal in the range of the ancestral yew populations (Kovar-Eder et al., 2008). However, this regional drying trend may not have been spatially coetaneous throughout the Mediterranean basin.

Recent findings suggest that the long-term Mediterranean basin dryness could have followed a southeast (drier) to northwest (moister) spatial pattern (Jost et al., 2009; Bruch et al., 2006), the signature of which can still be read in present-day patterns of genetic structure of the remnant yew populations (Hewitt, 2000).

González-Martínez et al. (2010) have found a geographic gradient of decreasing genetic diversity and increasing population divergence from the north-west (central Europe and the northern Iberian Peninsula) to the south-east (Mediterranean Iberian Peninsula and North Africa). On the other hand, genetic diversity also tends to decrease at northern marginal limits compared to core populations (Myking et al., 2009). For instance, analyses of molecular variance (AMOVA) performed by Hilfiker et al. (2004) detected no significant differentiation among northern Swiss regions, suggesting a core-periphery trend towards diminishing population genetic diversity in both northern and southern marginal areas (see also Hampe and Petit, 2005). This pattern probably reflects the combined effects of Quaternary climatic changes and recent impact of human activities (Tröber and Ballian, 2011; Chybicki et al., 2011; Dubreuil et al., 2010; Lyubenova and Nedelchev, 2001). Climatic as well as anthropogenic factors appear to have led to a long history of population isolation, which may have significantly promoted population divergence through restricted gene flow and genetic drift (Couvet, 2002). A similar northwestern to southeastern gradient of diminishing genetic diversity has been found across the Mediterranean basin in the genus *Abies* (see Linares, 2011 for a review).

The persistence of yew populations in their current southern range is clearly favoured by Quaternary refugia located in southern Europe (Carrion et al., 2003; Tzedakis et al., 2002; Taberlet and Cheddadi, 2002). Southern Iberian pollen records suggest that yew survived at quite high elevations in southern European mountains during the last glacial stage (Carrion, 2002). Moreover, genetic data suggest that changes in the species' distribution range during the Quaternary climatic cycles in southern areas would have consisted mostly of altitudinal shifts, without large geographical displacements (Thompson, 2005; Hewitt, 2000, 1996).

The orographic complexity of Alpine Orogeny presumably fomented the genetic differentiation of southern yew populations, which has been interpreted as a consequence of recurrent bottlenecks, small effective population sizes, and prolonged isolation during glacial as well as interglacial periods (Schirone et al., 2010; Dubreuil et al., 2010; Petit et al., 2005; Thompson, 2005). This agrees with the hypothesis that tree survival would have been especially important in mountain ranges, such as those of the coastal Mediterranean basin, allowing rapid altitudinal displacements of tree populations in response to climatic pulses (Magri et al., 2006).

The palynological record shows that *Taxus* was much more widespread than today during most of the Middle-Late Pleistocene interglacials (781,000–11,500 calibrated radiocarbon years before present; cal year BP, hereafter) in France and Great Britain, especially during periods with mild oceanic influence (e.g. de Beaulieu et al., 2001). Pollen deposits from southern Iberia, dating from upper pleniglacial times (c. 20,000–17,000 cal year BP), frequently yielded *Taxus* pollen, but in percentages consistently below 2% (Carrion, 2002). Yew was better represented in late glacial times (c. 17,000–11,900 cal year BP) and especially in mid-Holocene times (c. 7400–5300 cal year BP). Pollen sequences showing late-glacial yew presence also comes from coprolites of spotted hyena (*Crocota crocuta* Erxleben), dated to c. 12,780 cal year BP (Carrion et al., 2007).

During the last 6000–4000 years, yew populations have decreased in number, connectivity, and size in many parts of Europe, as a consequence of several factors, including forestry practices, heavy grazing, and the competition with other tree species

(Ruprecht et al., 2010; Piovesan et al., 2009; Dhar et al., 2007; Thomas and Polwart, 2003; Tittensor, 1980). The habitat fragmentation into small and isolated populations would diminish genetic variation and increase inter-population genetic divergence due to greater genetic drift, intensified inbreeding, and restricted gene flow, as discussed in the next section.

3. Consequences of yew habitat fragmentation. From reduction of genetic variation to loss in adaptive capacity and increasing risk of extinction

Habitat fragmentation is a main driver for reduced fitness of plants species (Pautasso, 2009; Young et al., 1996). Tree species might be relatively resistant to habitat fragmentation because of their longevity and capacity for extensive gene flow (Petit and Hampe, 2006), however, recent empirical studies have reported negative genetic consequences, in particular after long-term habitat fragmentation, in European trees despite long-distance dispersal of seeds and pollen (Thompson, 2005; Couvet, 2002; Hewitt, 1996). Thus, it could be assumed that small and isolated yew populations suffer from reduced genetic variation and loss of adaptive capacity, which consequently magnifies their risk of decline (Chybicki et al., 2011; Schirone et al., 2010; González-Martínez et al., 2010; Dubreuil et al., 2010; Myking et al., 2009; Hilfiker et al., 2004).

Studies designed to characterise local genetic structure in natural remnant populations of yew have reported that, despite high dispersal potential (bird-mediated seed dispersal and wind-mediated pollen dispersal), yew populations show strong kinship structure, with a spatial extent of 50–100 m, and (bi-parental) inbreeding (Chybicki et al., 2011; Schirone et al., 2010). Yew populations from western Mediterranean islands (i.e. Azores, Corsica, Sardinia, and Majorca) and the eastern Iberian Peninsula show high genetic differentiation at short geographical distances (Schirone et al., 2010; González-Martínez et al., 2010; Dubreuil et al., 2010). However, yew populations from the core of the distribution area (Austria; Eastern Alpine mountains; about 47°N) show a higher level of genetic variation compared with other European regions (Klump and Dhar, 2011). Studies performed also at the core of the range, in a well-preserved *T. baccata* population (near to 3000 living yew trees) from Poland (about 53°N) showed low level of inbreeding and high genetic variation for parental trees (Lewandowski et al., 1995). However, the seedlings showed a low level of heterozygosity, which could be explained by mating between relatives (bi-parental inbreeding).

These results suggest that gene dispersal can be fairly limited in this species (Hilfiker et al., 2004) and contrast with those reported for other widespread temperate trees, usually characterised by high genetic diversity within populations and low differentiation of nuclear molecular markers, a genetic pattern that has been interpreted as a consequence of large population sizes and extensive gene flow (Petit et al., 2005). Based on the above discussed genetic results, yew should be expected to show only limited tracking of near-future climate changes (Pautasso, 2009), however, high genetic differentiation at short geographical distances could also be not so negative for climate-change tracking, mainly if at least some populations have appropriate genetic characteristics for survival under new climatic conditions.

4. The relation of yew distribution and regeneration to water supply

In the coming decades, global climate changes are expected to cause large shifts in vegetation distributions at unprecedented rates. These shifts are expected to be most rapid and extreme at

ecotones, the boundaries between ecosystems (Hampe and Petit, 2005). The recent and predicted trend towards higher temperatures and lower precipitation in the Mediterranean basin can be hypothesised to affect yew range dynamics by lowering population viability in the water-limited stands (Mendoza et al., 2009a; Sanz et al., 2009). However, uncertainties remain concerning the specific climate changes at the regional scale, tree species' inherent sensitivity, and their ability to cope with the impact (Hampe and Jump, 2011).

Intensified drought stress may augment the extinction risk of the southern yew populations in the coming decades (Mendoza et al., 2009b). Recent studies illustrate a consistent relationship between water supply and yew distribution and regeneration (Sanz et al., 2009 and references therein). Yew emergence and recruitment improve in places with higher rainfall. Furthermore, higher drought sensitivity and lower radial growth of female yew, as compared to male individuals, has been recently suggested as a driving factor of the sex ratio and extinction risk of *T. baccata* (Iszkuło et al., 2009).

Yew regeneration along a latitudinal European transect proved significantly lower above c. 55° northwards than those recorded for central and southern populations (Fig. 3). These also support, as it was pointed above for genetic diversity, a core-periphery pattern of diminishing population viability in both northern and southern marginal areas (Dubreuil et al., 2010; Hampe and Petit, 2005; Lawton, 1993), supporting the hypothesis that abundance of *T. baccata* decreases from the centre to the margin of their current range.

The trend towards water-driven boosts in regeneration northwards did not hold when including populations at the highest latitudes (Fig. 3b), even though it could be a water-shortage at these latitudes since rainfall is not so high at the northern yew distribution limit and water is mostly present in its solid state (Iszkuło, 2010). In Central Germany (the core of yew distribution range, see Fig. 2) *T. baccata* shows nearly the same relative frequency in all available soil moisture classes, while it is relatively abundant at very dry sites in Slovakia (the eastern distribution edge), which reveal, contrary to expectations, an apparently higher preference of dry sites at the eastern range margin than in the distribution centre (Leuschner et al., 2009).

At a regional scale, adult yew trees from the Mediterranean mountains grow mainly close to streams, where water stress is lower (Sanz et al., 2009). Moreover, this distribution pattern could also be related to anthropogenic disturbances, such as logging, which would cause lower impact in the less accessible mountains. Another factor to be considered is the lower risk of wildfire, usually associated with northern exposures, given that yew is particularly sensitive to fire damage (Thomas and Polwart, 2003). On the other hand, relict yew stands can be found not only close to streams and mountain springs, but also on north-facing slopes and in shady ravines (Mendoza et al., 2009a; Navarro-Cerrillo and Pulido-Pastor, 2003; García et al., 2000), where summer drought could be alleviated by lower solar irradiance (Mendoza et al., 2009b; Sanz et al., 2009).

Rising temperatures would extent the growing period of some populations or tree species. Nonetheless, higher temperatures are not expected to exert positive effects in Mediterranean population of yew because the resulting evapotranspiration could bring about soil-water deficits, thereby exacerbating yew vulnerability to climate change (Mendoza et al., 2009b; Sanz et al., 2009). Contrastingly, at northern latitudes high seedling mortality during the winter suggests that low temperatures are one of the primary determinants of *T. baccata* seedling survival (Iszkuło, 2010).

It has been hypothesised that *T. baccata* seedling mortality at northern latitudes could be the physiological drought caused by temperatures above 0 °C (Iszkuło, 2010). Given that the water transport is strongly reduced during soil frozen, low temperatures

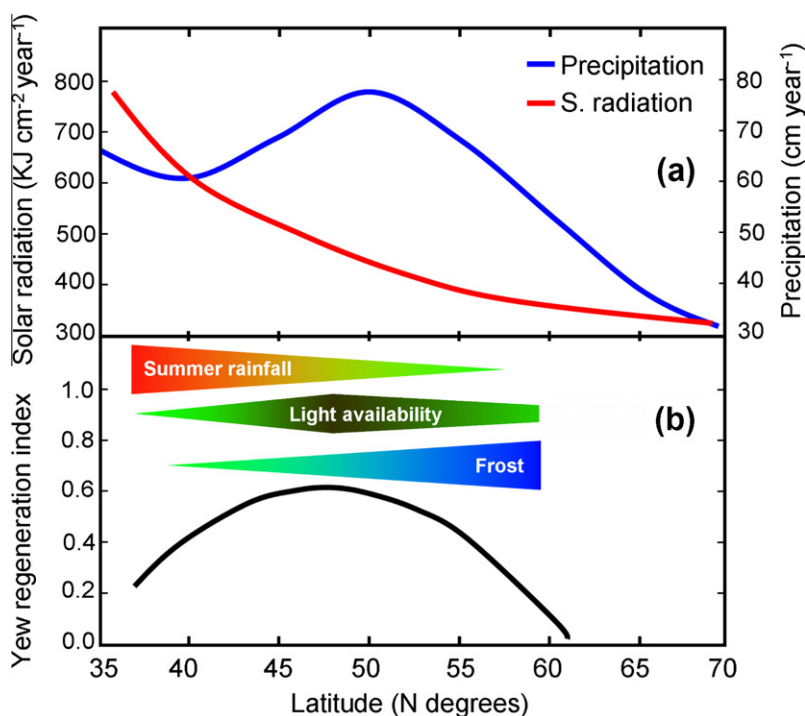


Fig. 3. (a) Northern hemisphere latitudinal distribution of annual solar radiation and precipitation, redraw from Chapin et al. (2002). (b) Relationship between latitude and yew regeneration index, calculated as the ratio of saplings plus juveniles to the total number of individuals including adults for 85 European populations of *Taxus baccata* L.; redrawn from Sanz et al. (2009). Theoretical size-effect for summer rainfall, light availability and frost are indicated.

377 can lead to yew seedlings desiccation in a similar way that summer
378 drought does at the southern yew range limits (Sanz et al., 2009).
379 These findings do not support the hypothesis about shifting limiting
380 factor, at least for seedling *T. baccata* survival, since drought
381 stress seems to constitute the main variable explaining yew-seedling
382 failure at both southern and northern edges.

383 **5. Stand-structure effects on yew population dynamics and**
384 **conservation status**

385 It is widely acknowledged that forest structure is a driving factor
386 behind tree-growth processes (Linares et al., 2010). Moreover,
387 structure is the attribute most often manipulated to achieve man-
388 agement objectives following the establishment of a forest stand.
389 Thus, a key factor to consider for yew regeneration would be stand
390 structure (Iszkuło et al., 2012; Ruprecht et al., 2010; Piovesan et al.,
391 2009; Dhar et al., 2007; Iszkuło and Boratynski, 2006).

392 Until around the 19th century, or even later, most European for-
393 ests were kept open by grazing, coppicing, etc., and succession to-
394 wards darker and more closed conditions has occurred when these
395 practices were abandoned (Peterken, 1996). Although yew is a
396 shade-tolerant tree (Thomas and Polwart, 2003), several studies
397 performed on yew populations from central and northern Europe
398 suggest that canopy closure by trees casting dense shade, such as
399 beech (*Fagus sylvatica* L.), is related to yew decline (Piovesan
400 et al., 2009). Meagre recruitment and the mortality of adults yews
401 have been suggested to be a result of dense canopy shading
402 (Iszkuło, 2010) and tree-to-tree competition (Ruprecht et al.,
403 2010; Dhar et al., 2007), while yew expansion has been reported
404 following canopy openings (see Svenning and Magård, 1999 and
405 references therein). Thus, although yew is shade-tolerant, it is
406 stimulated by an open canopy.

407 Open canopy stands have a higher relative proportion of healthy
408 yew trees, compared to denser stands where the competition with

crowding tree species is higher (Iszkuło et al., 2012; Ruprecht et al.,
2010; Dhar et al., 2007). The average height and diameter of yews
is lower under dimmer light conditions compared to those with
stronger irradiance. Likewise, a lack of recruitment has been attrib-
uted to heavy shade due to reduced seed production, and recruit-
ment in the sapling stage under a dense canopy (Ruprecht et al.,
2010; Dhar et al., 2007; Iszkuło and Boratynski, 2006).

Results from central-to-northern Europe indicate that succes-
sion leading to dominance of tall, shade-giving trees could be
responsible for the decline of many yew populations (Iszkuło
et al., 2005), while no evidence for excessive seed or seedling pre-
dation could be found, and seedlings showed no preference for
especially protected microsites (see for instance Svenning and
Magård, 1999 for a study in Denmark; 55°N). It is widely recog-
nised that seedlings and saplings may suffer severe damage from
browsing (Ruprecht et al., 2010; Piovesan et al., 2009; Dhar et al.,
2007), however, grazing intensity is not the only factor affecting
regeneration, stand density (mainly related to logging intensity)
are also likely to be of high significance, and this should be re-
flected in management plans (Perrin et al., 2006).

In addition to the negative effects on yew growth, survival, and
reproduction, a dense canopy could be responsible for the decline
of some yew populations from a genetic standpoint. Indeed, the
estimated kinship structure and inbreeding levels of yew popula-
tions, based both on amplified fragment-length polymorphism
and on microsatellite markers (see Chybicki et al. (2011) for de-
tails), were more pronounced in denser populations regardless of
the marker used. This result support the contention that, in spite
of high dispersal potential (bird-mediated seed dispersal and
wind-mediated pollen dispersal), yew individuals growing within
a dense canopy show strong kinship structure and bi-parental
inbreeding (Chybicki et al., 2011).

The results discussed above have substantial implications when
applied to the restoration and management of yew. Restoration of
native forests and management of forest dynamics in nature areas

are increasingly considered priorities in forestry and environmental policies (Ruprecht et al., 2010; Piovesan et al., 2009; Dhar et al., 2007; Jszkuło and Boratynski, 2006). However, land abandonment has also played a major role in promoting large continuous areas of dense and uniform early-successional vegetation (Peterken, 1996), which could result in low growth rates and some decay symptoms by stand stagnation (Linares et al., 2010). On the contrary, successful natural regeneration could be promoted by low-intensity logging and canopy opening. Selective thinning could generate small gaps and areas without a dense overhead cover and thereby encourage higher yew regeneration success (Ruprecht et al., 2010). However, the influence of selective logging on yew recruitment is less understood for the southern limit of the species, despite the higher evaporative demand in the sun, drought stress during the dry months could be more severe in the understory than in the open habitat (Valladares and Percy, 2002).

6. The protective role of woody shrubs in the regeneration ability of the yew

Facilitation among plants – that is, one species enhances the survival, growth, or fitness of another – results in the spatial association among them (Callaway, 1995). A benefactor plant (nurse) facilitates another by making the physical environment under its canopy more suitable for the beneficiary, by altering light intensity, temperature, soil moisture, or nutrient regimes (Gómez-Aparicio et al., 2004; García and Obeso, 2003; Verdú and García-Fayos, 2003). Besides these direct mechanisms, facilitation also emerges indirectly, when mediated by a third organism (Callaway, 1995). For example, some plants attract frugivores, seed dispersers of other species, resulting in an accumulation of seeds (dispersal focus) and promoting differential recruitment of the facilitated species under the nurse plant (Verdú and Garcia-Fayos, 1996; Herrera et al., 1994).

In other cases, nurse plants protect others from herbivory, by mechanical defences such as an crossed branching or prickly foliage (García and Obeso, 2003; García et al., 2000; Hulme, 1996). Yews are frequently damaged by vertebrate herbivores despite the foliage being strongly poisonous (Perrin et al., 2006; Mysterud and Ostbye, 2004; Thomas and Polwart, 2003). Under herbivore pressure, juvenile yews should benefit from the protective role of nurse plants which mechanically defend yews from browsers, suggesting that browsing by ungulates and understory composition can also shape local demographic structure and yew distribution patterns (Piovesan et al., 2009; Farris and Filigheddu, 2008; Mysterud and Ostbye, 2004).

Although most of the yew populations in the southern Iberian Peninsula are small, senescent and lack regeneration, a study in a montane pine stand in southern Spain (about 1800 m a.s.l.; 37°N) has provided valuable information on the effects of herbivory and the protective role of woody shrubs in the regeneration ability of the yew at its southern range limit (Mendoza et al., 2009a; García et al., 2000). This relict yew population is located in a *Pinus sylvestris* L. var. *nevadensis* Christ. open forest, with a dense shrub understory. The estimated density of the yew was about 300 individuals per hectare, where it is noticeable that more than 90% were seedlings and saplings, which were located mostly under fleshy-fruited shrubs (García et al., 2000).

Fleshy-fruited shrubs (FFSs) proved to be the best habitat for seedling establishment and sapling survival and growth (Fig. 4a). On the other hand, given that yew seeds are dispersed mainly by frugivorous birds (thrushes; *Turdus* sp.), suitable yew regeneration should also depend on the conservation of their community of avian dispersers (García et al., 2000; Verdú and Garcia-Fayos, 1996; Herrera et al., 1994). In this sense, yew seedling emergence

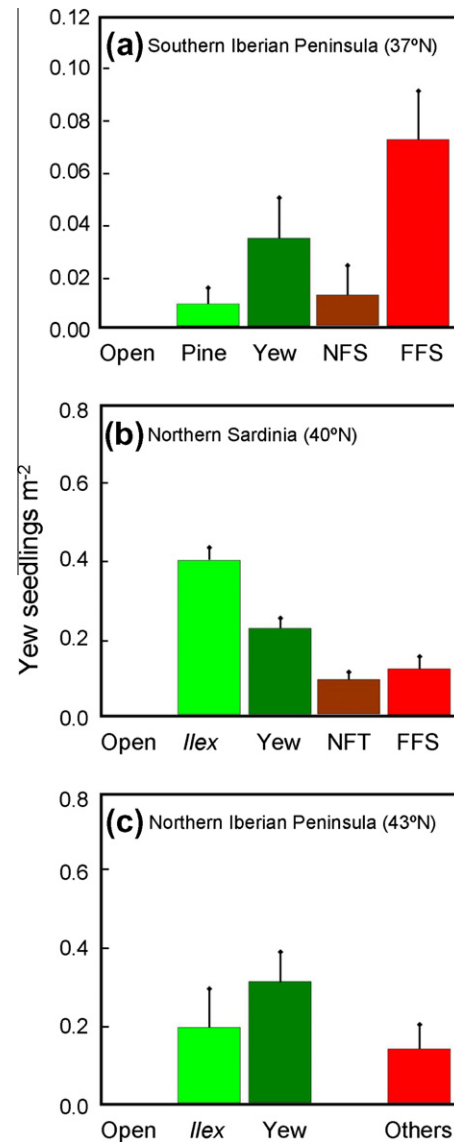


Fig. 4. Mean density of yew seedling (errors bars represent the standard deviation) for different microhabitats: *Open* indicates areas bare of tree or woody shrubs cover; *Yew* indicates areas under the canopy of adult *Taxus baccata* L., (in the (b) *Yew* indicates areas under the canopy of reproductive females); *Pine* indicates areas under the canopy of adult *Pinus sylvestris* L. var. *nevadensis* Christ.; *Ilex* indicates areas under the canopy of adult *Ilex aquifolium* L. ((b) indicates areas under the canopy of reproductive females); *NFT* indicates areas under the canopy of adult non-fleshy-fruited trees; *NFS*, areas below non-fleshy-fruited shrubs; and *FFS*, areas below fleshy-fruited shrubs. Redrawn from García et al. (2000) (a), Farris and Filigheddu (2008) (b), and García and Obeso (2003) (c).

was concentrated under fleshy-fruited shrubs, presumably because this vegetation attracts high numbers of avian frugivores during fall and winter, acting as sinks for the seeds of many species, including the yew (García et al., 2000). This hypothesis is reinforced by the reduced yew establishment under non-fleshy-fruited shrubs, places where the seed rain by avian frugivores rarely occurs. Similarly, studies on fragmented populations of *Juniperus thurifera* L. support the contention that dispersal and recruitment in this species are seriously reduced by the loss of thrushes (Santos et al., 1999).

Once the yew seeds have been differentially dispersed, fleshy-fruited shrubs can in addition operate as nurse plants, providing favourable micro-environmental conditions for germination and seedling survival (Gómez-Aparicio et al., 2004; García and Obeso,

2003; Tittensor, 1980). These improved conditions could be related mainly to improved soil moisture and the consequent protective role against summer drought, soil texture, and nutrient availability (Callaway, 1995). The nurse effect has been previously documented in other relict Mediterranean species as *Abies pinsapo* Boiss., *Juniperus communis* L., and *Rhododendron ponticum* L. (Mejías et al., 2002; García et al., 1999; Arista, 1995). Once established, the seedling-to-sapling transition can be fostered under shrubs, due to the characteristic shade tolerance of the juvenile yews for growth (Thomas and Polwart, 2003).

Shrubs protecting the yew against herbivores could constitute an additional factor determining the associative spatial pattern between juvenile yews and shrubs (Mysterud and Ostbye, 2004). In a study performed at northern Sardinia (about 1000 m.a.s.l.; 40°N), higher densities of seedlings were found under canopies of reproductive female *T. baccata* and *Ilex aquifolium* L. (Fig. 4b), while no seedlings were found in open habitats (Farris and Filigheddu, 2008). The sapling density was greater at ungrazed sites (about 0.11 saplings m⁻²) than at grazed sites (about 0.04 saplings m⁻²). Also, in southern Spain, García et al. (2000) reported that the habitats containing the highest sapling density were shrubby ones. No saplings were found in the open habitat at ungrazed sites and very few were observed at the grazed sites (Farris and Filigheddu, 2008), which could be related to a reduced seed rain by avian frugivores (García et al., 2000).

Another study, in northern Spain (between 700 and 1500 m.a.s.l.; 43°N), showed that the consequences of browsing on the recruitment of *T. baccata* are more evident in the late regeneration stages, such as saplings rather than first-year seedlings (García and Obeso, 2003). These data also confirm that shrubs provide vital mechanical protection against browsing, thereby facilitating the regeneration of *T. baccata* (Fig. 4c). Shrubs provide shelter against ungulates both for their relative unpalatability and crossed branching structure (e.g. shrub species such as *J. communis* and *Juniperus sabina* L.) or for their dense spinescence (e.g. *Berberis hispanica* Boiss. and Reut., *Rosa* spp., and *Prunus ramburii* Boiss.). As a result, ungulates attacked almost exclusively individuals unprotected by shrubs (Farris and Filigheddu, 2008; García and Obeso, 2003; García et al., 2000). Repeated browsing, when it does not kill the yew seedlings and saplings, forces the individual

to assume a shrub form, or to develop an irregular crown, stunting overall yew growth (Piovesan et al., 2009; Perrin et al., 2006; Mysterud and Ostbye, 2004; Thomas and Polwart, 2003).

Some previous studies reported that *T. baccata* regeneration was seed predator-limited and microsite-limited (Hulme, 1996) but the results discussed here also indicate that facilitation might be herbivore-mediated; indeed, yew saplings suffered serious herbivore damage when unprotected by shrubs (Farris and Filigheddu, 2008; García and Obeso, 2003; García et al., 2000). Grazing pressure from wild or domesticated animals have likely shaped yew populations for millennia, possibly even contributing to its disappearance from entire regions, such as Lithuanian forests (Navys, 2000). Understanding the current (and future) role of livestock and wild ungulates is therefore essential for yew conservation (Piovesan et al., 2009).

7. Concluding remarks for yew conservation

The results discussed here support the ongoing contention that traditional conservation strategies, mainly focused on the protection established individuals, may not be sufficient to maintain a population of slow-growing tree species in long-term decline. The current analysis of the environmental conditions, genetic variation, and community structure (including the maintenance of the functional interactive triad composed of yew, avian dispersers, herbivores and nurse woody plants; Fig. 5) should serve as an integrative assessment to adapt range-scale conservation of this widely threatened species (Smith and Zollner, 2005).

The genetic conservation of yew populations is essential for the maintenance of the species. Given that habitat fragmentation appears to be related to genetic impoverishment, such as increased inbreeding and decreased effective population size, remnant yew groups should become more and more connected by yew re-establishment in its potential habitat. In addition, as yew is a dioecious species, current habitat fragmentation lowers pollination and fitness because the formation of viable seeds requires the coexistence of healthy individuals of both sexes (Thomas and Polwart, 2003; Tittensor, 1980). Furthermore, although dioecy also secures cross pollination, it has been suggested that dioecious plant species have

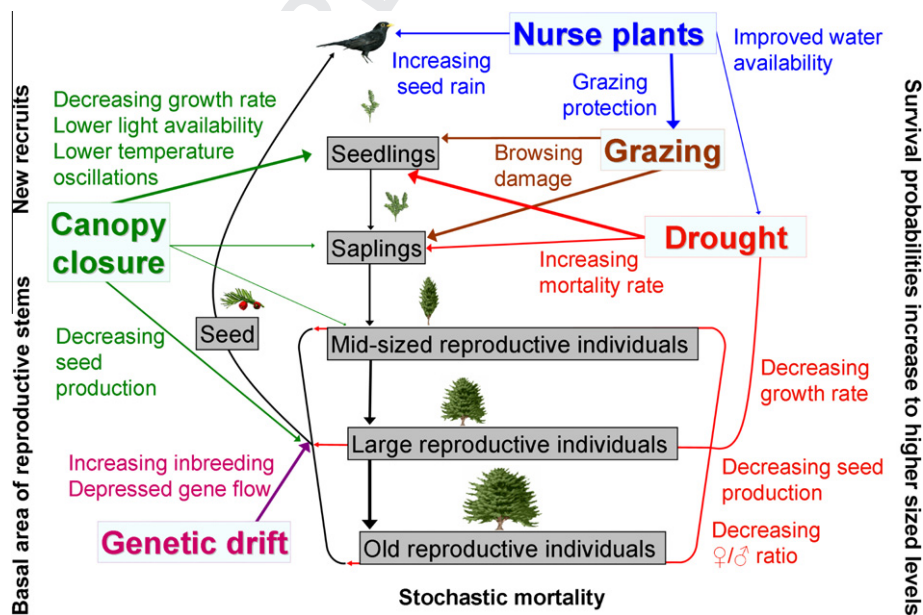


Fig. 5. Life-cycle of *Taxus baccata* including the main effects of the independent variables discussed in this paper: nurse plants, grazing (herbivores), drought, canopy closure, and genetic drift. Nodes represent stages (seed, seedling, sapling and reproductive adult stages) while arrows between nodes indicate transitions between stages; the thickness of the arrows represents transitions likelihood (between stages) and theoretical size-effect for the independent variables.

a higher probability of extinction than monoecious species (Heilbuth, 2000; Vamوسي and Vamوسي, 2005).

Regardless of yew population age, the percentage of females within populations has been positively correlated with precipitation, suggesting higher water demand than males. Mean tree-ring width in female yew individuals has been negatively correlated with high temperatures in August and September in the year prior to the formation of the tree ring, and correlated positively with precipitation in June and July in the current year (Cedro and Iszkuło, 2011). The hypothesised drought sensitivity and growth differentiation between males and females must be related to the greater reproductive effort of females (Obeso, 2002; Rozas et al., 2009), which may affect the range and viability of populations at the water-limited edges of the *T. baccata* range (Iszkuło et al., 2009).

Since high stand density can hamper regeneration (Iszkuło et al., 2012), conservation practices need to encourage expansion at the boundaries of dense yew nuclei, to promote edge regeneration, and avoid the risk of inhibited seed production because of senescence (Ruprecht et al., 2010; Svenning and Magård, 1999). In addition to successful regeneration, demographic studies showed that conservation efforts directed at long-lived, slow-growing trees should both protect established reproductive individuals and further enhance survival of individuals in other life-history stages, such as juveniles (see Kwit et al. (2004) for a study case on *Taxus floridana* Nutt.).

Recent studies have found that effective yew population size should have an area of about 0.5–3.0 ha, which might in turn represent the minimum patch size for yew preservation over the landscape (Piovesan et al., 2009), while the extension or reintroduction of yew populations requires a minimum number of 40 individuals with nearly a balanced gender proportion, signifying that at least 20 reproductive females would be needed as the seed source (Iszkuło et al., 2009). Silvicultural activities should focus on moderate selective thinning in order to reduce the inter-specific competition in yew populations from temperate areas (Ruprecht et al., 2010).

Preserving the community of fleshy-fruited shrubs and thrushes, as well as the regulation of browsing should be the main management measures to implement in order to preserve reproductive *T. baccata* stands in the Mediterranean area (García et al., 2000). Nevertheless, for the entire *T. baccata* range, browsing can be regarded as a negative factor in the yew seedling-to-sapling transition (Farris and Filigheddu, 2008; Mysterud and Ostbye, 2004). Considering that browsing is directly or indirectly driven by humans through domestic livestock, hunting regulation, or wild-ungulate management, the modulation of herbivore pressure should be a priority task in conservation programmes aimed to protect *T. baccata*.

This synthesis revealed, as one of the main gaps of the literature regarding yew conservation and ecology, a lack of demographic studies aimed to identify important life-history transitions on this slow-growing, long-lived species (Fig. 5). It should be taken into account that *T. baccata* has been able to cope with serious bottlenecks in the past, and it is, and has always been exposed to browsing, drought and shade. Nevertheless, it is widespread in the European biota, likely by a long-term persistence strategy. Nowadays, a deeper understanding of ecophysiological processes, subjacent to macroecological patterns, would require more investigation at the southern and northern distribution limits, where populations are likely more sensitive to ongoing climatic change.

8. Uncited references

Charlesworth and Charlesworth (1987) and Iszkuło et al. (2011).

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