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Synthesis of Knowledge to Develop Comprehensive Guidelines for the *in situ* and *ex situ* Conservation of European Yew (*Taxus baccata* L.)

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ABSTRACT

Taxus baccata L. (common yew) is a tertiary relict conifer and one of the longest-lived tree species in Europe, yet it has experienced one of the most severe population declines among European forest trees. This review synthesises current knowledge on the biology, ecology, distribution, genetic diversity, and conservation of *T. baccata*, with particular emphasis on the preservation of its genetic resources under ongoing environmental change. We summarise the species' taxonomy, morphology, reproductive biology, and ecological requirements, highlighting its pronounced shade tolerance, broad edaphic amplitude, and dependence on humid, mild climatic conditions. The present distribution of common yew is highly fragmented throughout its range, occurring predominantly in patchy, discontinuous populations that are often small and spatially isolated. Although the species is distributed across much of Europe, the Mediterranean region, North Africa, and western Asia, population size and continuity vary locally depending on habitat conditions, land-use history, and conservation status. Despite extensive historical decline driven by past timber exploitation, deliberate eradication due to livestock toxicity, and chronic browsing pressure, *T. baccata* retains relatively high levels of genetic diversity compared to other conifers. This resilience reflects its extreme longevity, outcrossing mating system, wind pollination, and effective seed dispersal. However, genetic structure varies strongly across the species' range, with low differentiation in core areas and pronounced structuring, reduced diversity, and increased inbreeding in peripheral and southern populations. Limited regeneration, skewed sex ratios, habitat fragmentation, and restricted gene flow pose significant risks to long-term population viability, particularly under climate change. Projected increases in temperature, drought frequency, and fire occurrence are expected to exacerbate pressures on southern and peripheral populations, while potential northward range shifts are constrained by slow growth, high juvenile mortality, and limited dispersal capacity. The review emphasises that effective conservation of *T. baccata* requires integrated strategies combining *in situ* genetic conservation, forest and herbivory management, promotion of natural regeneration, and maintenance of landscape connectivity. Where necessary, carefully designed population reinforcement, assisted gene flow, and *ex situ* measures can complement *in situ* efforts. Safeguarding the genetic integrity and adaptive potential of common yew is essential to ensure its persistence as a functional component of European forest ecosystems under future climatic and land-use change.

Keywords: *Taxus baccata*; forest genetic resources; population fragmentation; regeneration limitation; conservation genetics; climate change; European forests

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ECOLOGY AND DISTRIBUTION OF *TAXUS BACCATA*

Common yew (*Taxus baccata* L.) is a Tertiary relict species (González-Martínez et al. 2010) and is included in protection programmes in several European countries (Linares 2013). *T. baccata* belongs to one of the oldest extant conifer lineages, with the genus *Taxus* appearing in the fossil record during the Late Jurassic, approximately 145–160 million years ago (Farjon 2010).

T. baccata has a broad but discontinuous distribution in Europe, North Africa, and western Asia. Today, the species is highly fragmented throughout its range, typically occurring in patchy and often spatially isolated populations. Across its range, yew typically occurs in sheltered, mesic habitats, often in topographically complex microrefugia, reflecting its long-term sensitivity to climatic and anthropogenic pressures.

Common yew is one of the longest-lived tree species in Europe. However, accurate age determination is difficult. Recent dendrochronological analyses provide minimum ages of several centuries for large hollow yews (Hindson and Moir 2026). Historical exploitation of yew for its durable and elastic wood, particularly for longbow production, led to extensive harvesting across Europe. Between the 13th and 16th centuries, large quantities of yew timber from Central Europe were exported to England, which had a lasting negative impact on the regeneration of yew populations in the region (Kaiser et al. 2024). However, toxicity to livestock and associated grazing conflicts resulted in deliberate removal from many landscapes, contributing to one of the most pronounced population declines among European tree species (Habitats Directive 92/43/EEC, European Commission 2007, Benham et al. 2016). Genetic studies further support this widespread decline, with formal bottleneck tests revealing reduced effective population sizes and historical contractions in multiple populations (Mayol et al. 2020, Stefanowska et al. 2021, Chybicki et al. 2024).

In parts of central and northern Europe, common yew can locally form dense stands. However, at the landscape level, populations are generally scattered and spatially fragmented, a pattern also observed more widely across its range (Svenning and Magård 1999, Thomas and Polwart 2003, Ruprecht et al. 2010). In the Mediterranean region, common yew typically occurs as small, isolated stands or scattered individuals, reflecting the fragmented distribution characteristic of rear-edge populations persisting in montane refugia near the southern limit of the species' range (Kassioumis et al. 2004, Casals et al. 2015). Dense patches in both regions are usually restricted to specific microhabitats or influenced by historical management. Isolated trees are usually confined to shaded ravines or north-facing slopes (Król 1978, García et al. 2000, Navarro-Cerrillo and Pulido-Pastor 2003, Ballian 2014a, 2014b, Benham et al. 2016, Mayol et al. 2020). Within its core and northern range, common yew occurs in mixed forests with *Fagus sylvatica*, *Carpinus betulus*, *Fraxinus excelsior*, *Acer* spp., and *Ulmus* spp., often with *Abies alba* and *Picea abies*, and *Buxus sempervirens* in the shrub layer, reflecting oceanic and temperate forest communities (Svenning and Magård 1999, Thomas and Polwart 2003, Ruprecht et al. 2010). On Mediterranean islands such as Sardinia and Corsica, yew-dominated forests occur with *Ilex aquifolium*, *Buxus sempervirens*, *Sorbus aria*, and *Mercurialis perennis* (Schlegel and Heinze 2015).

Taxus baccata is currently assessed as Least Concern on the IUCN Red List of Threatened Species (Farjon 2013). While the species itself is not directly listed in the annexes of the EU Habitats Directive, many of the habitat types where it occurs are protected within Natura 2000 network, contributing to the conservation of key yew populations and stands.

Taxonomy

An overview of the taxonomic position of common yew follows recent systematic treatments by Farjon (2010). *T. baccata* is a coniferous seed plant (Spermatophyta), placed within the division Pinophyta, class Pinopsida, order: Pinales, family: Taxaceae, genus *Taxus*, species *Taxus baccata* L. According to several authors, more than 70 cultivars of common yew are recognised in Europe, including the well-known columnar Irish yew (*T. baccata* cv. Fastigiata Loudon) (Elwes and Henry 1906, Vidaković 1982, 1993, Vidaković and Franjić 2004).

Morphology

Common yew is an evergreen conifer that typically occurs as a small tree or shrub, although under favourable conditions it may reach heights of 20 m and more. The species is notable for its exceptional longevity, with individuals commonly exceeding several centuries and, in some cases, over 1,000 years, although precise age determination is often complicated by heartwood decay and trunk hollowing in older trees. Owing to its slow growth and ecological strategy, reproductive maturity is typically attained after several decades and may be substantially delayed under shaded conditions. These characteristics are well documented in range-wide syntheses and reviews of the species' ecology and biology (Thomas and Polwart 2003, Saulnier et al. 2026).

The species usually develops a single main stem, but early branching often results in multiple stems. The wood is hard, elastic, and dense (600–800 kg·m^{-3}), characterised by distinct heartwood coloration and the absence of resin canals (Schweingruber 1978, 1993, Richter 2015). The bark is thin and smooth in young individuals, later becoming fissured and exfoliating in thin, reddish-brown plates.

Unlike many conifers, common yew does not form whorled branches. Instead, branches are arranged irregularly or in loose spirals and frequently arise from epicormic shoots following damage or increased light availability, producing a dense crown. Although the species is shade-tolerant, optimal crown development generally occurs under higher light conditions. Needles persist for up to 8–10 years and are flat, dark green on the upper surface, with two pale green stomata-free bands on the lower surface. They are typically 20–30 mm long and approximately 2 mm wide, tapering towards a petiole-like base. Young twigs are green and polygonal, bearing numerous lateral shoots originating from dormant buds (Jovanović 1956, 1971, 2000, Negulescu and Săvulescu

1957, Rushforth 1987, Vidaković 1993, Thomas and Polwart 2003, Brus 2004, Vidaković and Franjić 2004, Benham et al. 2016).

The root system of common yew can penetrate compressed soils, allowing the species to survive in extreme conditions, such as rocky terrain and vertical cliff faces. This rooting strategy together with tolerance to temporary flooding and moderate drought, underlines the ecological adaptability of yew in a wide range of soil types and forest understorey environments (Benham et al. 2016).

Common yew is predominantly dioecious, with male and female reproductive structures borne on separate individuals, although monoecious individuals have occasionally been reported in natural populations and appear to be extremely rare (Iszkuło and Jasińska 2004). Male microstrobili appear in March and April in clusters of up to 20–30 and consist of small, globular, yellowish structures approximately 2–3 mm in diameter. These wind-pollinated strobili contain shield-shaped microsporophylls bearing 4–9 pollen sacs (Mundry and Mundry 2001). Female reproductive structures develop concurrently, are less frequent, and occur singly or in pairs in the axils of needles on young shoots. Each female structure bears a single ovule (approximately 1.5–2.0 mm long), which develops into a single seed (Jovanović 1956, 1971, 2000, Negulescu and Săvulescu 1957, Vidaković 1982, 1993, Rushforth 1987, Thomas and Polwart 2003, Brus 2004, Vidaković and Franjić 2004). Mature seeds are ovoid to slightly flattened, smooth, and brownish yellow, measuring approximately 6–7 × 5 mm, and are partially enclosed by a fleshy red aril about 9 × 7 mm in size. Seeds ripen within the flowering year, from August to late autumn, and are typically dispersed by birds attracted to the aril, enabling long-distance seed dispersal (Jovanović 1956, 1971, 2000, Negulescu and Săvulescu 1957, Vidaković 1982, 1993, Rushforth 1987, Thomas and Polwart 2003, Brus 2004, Vidaković and Franjić 2004).

Species Distribution

T. baccata has a broad but discontinuous natural distribution extending across the whole of Europe (northern limit in southern Scandinavia, ~63°N), North Africa, Caucasus and northern Iran (Figure 1). The species is unevenly distributed, typically occurring in small, fragmented populations of mesic and sheltered habitats, being largely absent from regions with strongly continental climates (Thomas and Polwart 2003, Farjon 2010, EUFORGEN 2016, Caudullo et al. 2017).

Common yew occurs predominantly at low to moderate elevations in the central and northern parts of its range, whereas in southern Europe, North Africa, and western Asia it is more frequently found in montane environments, reaching elevations ~2000–2500 m, although upper altitudinal limits vary geographically (Thomas and Polwart 2003, Farjon 2010, EUFORGEN 2016, Caudullo et al. 2017).

Ecology

Common yew generally occurs in humid, mild oceanic climates and shows its highest vitality in regions with relatively mild winters, high annual precipitation, high air humidity, and frequent fog (Meusel 1943, Tittensor 1980, Melzack and Watts 1982, Farjon 2010, Benham et al. 2016, Hayne et al. 2016). However, under very wet oceanic conditions, rising groundwater tables may negatively affect growth and can lead to the decline or local extinction of populations (Bebchuk et al. 2024).

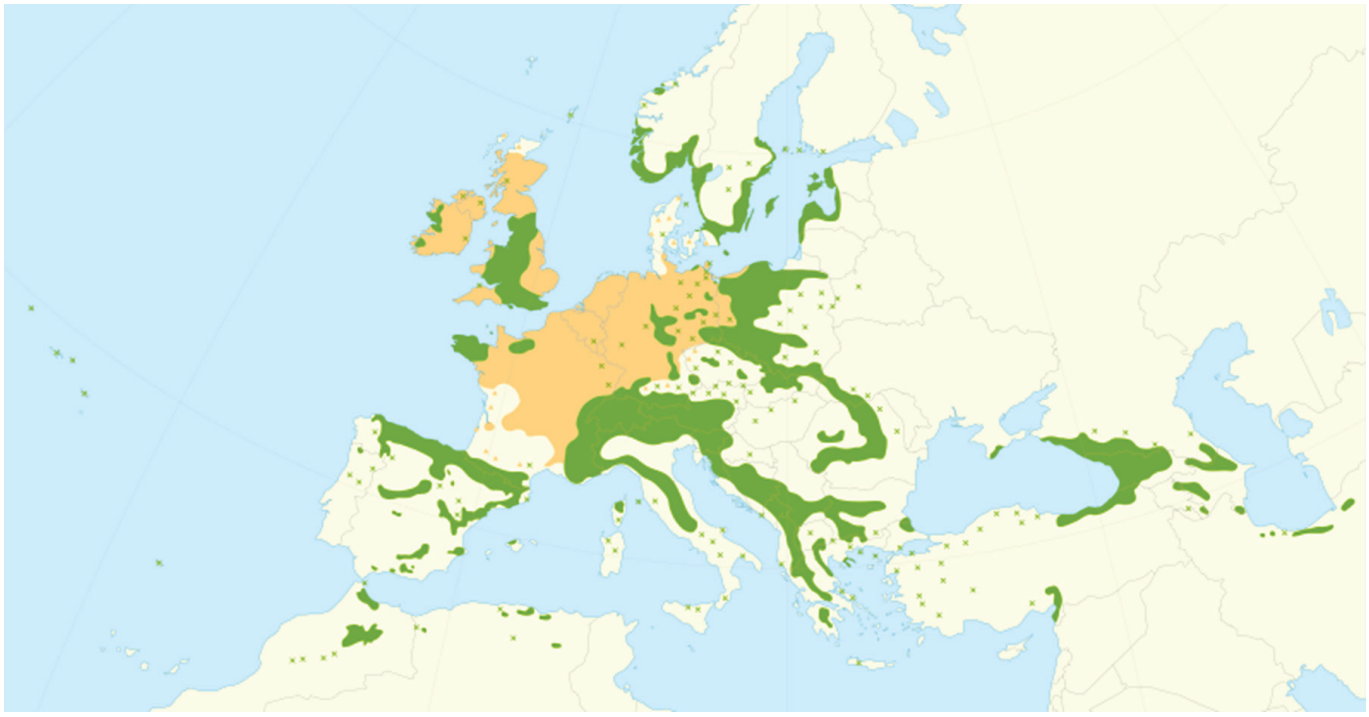


Figure 1. Natural distribution range (green) and introduced/naturalised (synanthropic) range (orange) of *T. baccata* (Caudullo et al. 2017).

At the northern limits of its distribution, annual sum of precipitation may be only slightly above 500 mm. In these areas, physiological drought can be an important factor limiting seedling survival, primarily because winter freezing and prolonged sub-zero temperatures reduce soil water availability during critical periods of seedling establishment. High mortality of yew seedlings after the first winter has been observed under natural conditions, especially where low temperatures interact with limited light availability, indicating that cold stress and frozen soils restrict water uptake and contribute to range-limit dynamics (Iszkuło 2010). At the southern margins of its range, common yew occurs primarily in Mediterranean mountain climates, where annual precipitation typically exceeds 900–1000 mm and mean annual temperatures are around 10–11°C. Successful regeneration in these areas requires summer rainfall of at least 100 mm (Sanz et al. 2009). Winter cold and cold spring winds further constrain the species at its southern limits (Voliotis 1986).

Besides long-term human impact, ecological constraints have also played a key role in shaping the fragmented distribution of *T. baccata* across its range. Low temperatures limit its expansion in northern regions, while continental climates in eastern parts of its distribution, prolonged summer droughts in south-eastern areas, and high temperatures combined with water scarcity in North Africa restrict its occurrence (Kamppa 1926, Król 1978, Środoń 1978). Near these climatic extremes, common yew is largely confined to moist microhabitats such as rock crevices, canyon systems, and shaded forest understories, where local conditions buffer against drought, frost, and excessive evapotranspiration (Sokolowski 1921, Hoffmann 1958, Faegri 1960, Król 1978, Tittensor 1980, Peñalba 1994, Saniga 2000, Pintarić 2002, Farjon 2010, Hayne et al. 2016). In the southern parts of its range, the species is particularly associated with shaded north- or north-west-facing slopes within deciduous or mixed forests that provide a comparatively mild microclimate (Schirone et al. 2003, 2010a, 2010b, 2010c, Thomas and Polwart 2003).

Common yew frequently occupies steep and inaccessible rocky habitats and canyon systems, where individuals may grow directly above watercourses or on vertical cliffs, thereby escaping grazing pressure and competition (Pigott 1969, Rodwell 1991). Although common yew is often associated with calcareous substrates, it can grow on a wide range of soil types, including silicate soils derived from igneous and sedimentary rocks (Elwes and Henry 1906, Watt 1926, Webb 1977, Król 1978, Kelly 1981, Vidaković 1991, Thomas and Garcia-Marti 2015). Regional differences in soil preference have been reported, with calcareous soils favoured in northern Europe and silicate substrates more common in southern populations (Voliotis 1986). Optimal growth generally occurs on deep, moist, well-drained sandy soils with some clay content, whereas extremely dry, shallow, or rocky soils support only small, isolated individuals (Webb 1977, Bugala 1978). Common yew shows low tolerance of prolonged waterlogging and performs poorly on wet acidic peats and heavy clay soils, although it may contribute to the woody structure of peat bogs in eastern England (Król 1978, Williamson 1978, Ellenberg 1988). Overall, the species is best characterised as a tree of the European temperate and mild climatic zone (Meusel 1943, Preston and Hill 1997).

Growth and Life-Cycle Constraints of *T. baccata* under Environmental Change

Requirements for Light

Common yew is a shade-tolerant species that develops successfully under partial shading, but it also tolerates full sunlight and generally exhibits faster growth in more open habitats (Watt 1926, Bugala 1978, Król 1978, Ellenberg 1988, Mitchell 1988, Vidaković 1991, Brzeziecki and Kienast 1994, Svenning and Magård 1999, Pintarić 2002, Thomas and Polwart 2003, Vidaković and Franjić 2004, Perrin and Mitchell 2013). Seedlings can survive under very low light conditions, particularly beneath parental canopies, with as little as 0.5% of full sunlight sufficient for development (Iszkuło and Boratyński 2006). However, such low light levels primarily support persistence rather than vigorous growth or full development, highlighting the species' strong shade tolerance during the earliest life stages. Reproductive processes, including seed production and aril development, may also occur in shaded environments (Bugala 1978). Light requirements vary seasonally, ranging from approximately 3.2 lux in winter to 175 lux during summer (Pavletić and Lieth 1958).

Water Requirements

Dendrochronological studies indicate that precipitation, particularly during late winter and early summer, has a strong positive influence on radial and height growth of common yew, especially on sandy and gravelly substrates (Moir 1999). Mild, wet winters combined with cooler summers provide optimal growth conditions, whereas hot and dry summers negatively affect growth (Galvin et al. 2014, Cedro and Cedro 2015). In Bulgaria, up to 93% of annual ring-width variability has been attributed to precipitation during January–June of the current year and October–December of the preceding year (Lyubenova et al. 2001). Optimal annual precipitation is close to 1000 mm, although southern populations persist under considerably lower rainfall, for example approximately 570 mm annually in Greece (Katsavou and Ganatsas 2012). While common yew tolerates short-term flooding associated with extreme weather events, it generally exhibits greater tolerance to prolonged dry periods and is regarded as among the more drought-tolerant European tree species (Brzeziecki and Kienast 1994).

Sex-specific growth responses to water availability have been reported, with a higher proportion of female individuals occurring in wetter environments, reflecting their greater reproductive water demand (Cedro and Iszkuło 2011, Iszkuło et al. 2011). Radial growth patterns in *T. baccata* can differ between males and females, reflecting differential resource allocation associated with reproductive investment; females often have lower radial growth than males, likely due to higher reproductive costs (Garbarino et al. 2015, Nowak-Dyjeta et al. 2017). Recent work has further refined this perspective by demonstrating that growth sensitivity to drought and precipitation may

also vary among different genetic groups, as shown in the first dendrogenetic study on common yew (Tonelli et al. 2025).

Regarding reproductive biology, a recent preprint by Bross et al. (2026) proposed a novel hypothesis on sex determinism in *T. baccata*, suggesting that sex expression may be more dynamic and environmentally influenced than previously assumed. As this hypothesis is currently based on a preprint and has not yet undergone peer review, it should be considered preliminary and requires further validation.

Temperature Requirements

T. baccata tissues exhibit relatively high heat tolerance compared with many other tree species, with foliage surviving brief exposure to temperatures near 51°C under experimental conditions (Lange 1961). However, specific data on seed viability following high-temperature exposure are limited, and seeds are likely less heat-tolerant than vegetative tissues. The optimal temperature range for photosynthesis and growth lies between 14 and 25°C, one of the highest ranges recorded among gymnosperms (Pišek et al. 1969). Adult trees tolerate summer maxima of 38–41°C, suggesting that increasing temperatures alone are unlikely to inhibit germination (Thomas and Garcia-Martí 2015). Nevertheless, the species is sensitive to prolonged and severe frosts, particularly late spring frosts, although winter survival has been recorded at temperatures as low as −33 to −35°C in southern Sweden (Brzeziecki and Kienast 1994).

Tree-ring width and wood density are closely correlated with late-winter and early-spring temperatures, reflecting the importance of mild winters for cambial activity (Groff 2013, Cedro and Cedro 2015). Elevated summer temperatures and associated drought stress can reduce primary and secondary growth in *T. baccata*, with radial increment negatively influenced by high summer temperatures and low precipitation in Mediterranean populations. Dendroecological analyses indicate that *T. baccata* growth exhibits sensitivity to climatic stress, especially during summer months, where warmer and drier conditions are correlated with reduced annual ring width (Tonelli et al. 2025).

Mineral Nutrient Requirements

Compared with many other conifers, common yew needles exhibit relatively high concentrations of nitrogen, phosphorus, potassium, manganese, zinc, boron, and molybdenum, but low aluminium, silicon, and iron contents (Fiedler et al. 1986, Allen 1989). Nutrient concentrations decline with increasing needle age. Soil chemistry strongly influences micronutrient accumulation, particularly manganese and aluminium in acidic silicate substrates (Nemec 1951, Fiedler et al. 1986).

Stress Tolerance and Pollution Resistance

Common yew demonstrates high tolerance to air pollution and is particularly resistant to sulphur dioxide, with no needle damage observed at concentrations exceeding 50 mg·m^{-3} (Mez 1963, Białobok 1978). Under elevated atmospheric CO_2 concentrations, growth responses are positive but largely restricted to heavily shaded environments, suggesting limited competitive advantage under high-light conditions (Hättenschwiler and Körner 2000, Hättenschwiler 2001).

Influence of Forest Stand Structure

Forest stand structure exerts a strong influence on common yew survival, growth, and regeneration. Although shade-tolerant, reproductive success and seedling survival improve under partially open canopies, with seed production requiring slightly more than 5% of daily sunlight and seedling survival approximately 2% (Dhar et al. 2007, Iszkuło 2010, Linares 2013). Dense stands dominated by competitive species such as beech increase adult mortality and suppress regeneration, whereas selective canopy opening promotes recruitment (Piovesan et al. 2009, Ruprecht et al. 2010).

Absence of Regeneration in Mature Stands

Germination is abundant below yew canopies (García and Obeso 2003, Thomas and Polwart 2003), which is consistent with both barochoric and avian seed dispersion (Iszkuło and Boratyński 2006), despite heavy seed predation by rodents (Smal and Fairley 1980b, Hulme 1996, 1997). However, seedlings rarely survive to the next life stage (Dhar et al. 2006, Piovesan et al. 2009, Linares 2013, Devaney et al. 2014, Devaney et al. 2018). This has been attributed to reduced light availability under the canopy (e.g., Iszkuło and Boratyński 2006, Linares 2013), whilst autotoxic effects have also been considered (Thomas and Polwart 2003, Piovesan et al. 2009, Devaney et al. 2014). On the other hand, regeneration can be found outside the yew canopy if saplings are not overgrazed by deer, confirming the dispersion potential (Mysterud and Østbye 1995, 2004). In Mediterranean yew stands, livestock grazing and browsing are repeatedly identified as key constraints on regeneration. In Sardinian yew woods, establishment and recruitment are particularly difficult due to intense browsing pressure from domestic livestock and wild herbivores, which reduce seedling and sapling survival in areas with limited shrub cover (Farris and Filigheddu 2008, Farris et al. 2012, Calvia et al. 2023). Areas with high herbivore load show low or no recruitment, while sites with extensive shrub cover, which helps protect juveniles from herbivory, exhibit higher regeneration success. Devaney et al. (2018) suggest that the lack of regeneration may also result from the phytotoxic substances in leaf leachates. More recently, disrupted gene flow and reduced connectivity among highly fragmented populations have been proposed as an additional factor potentially contributing to regeneration failure, by limiting effective reproduction (Chybicki et al. 2024).

Reproduction

Pollination

Common yew is predominantly wind pollinated. Pollen release typically occurs between March and April, although timing varies with latitude, altitude, and annual climatic conditions (Thomas and Polwart 2003). In *T. baccata*, male

individuals typically produce abundant pollen, as is common among anemophilous conifers (Thomas and Polwart 2003, Chybicki and Oleksa 2018). However, the spatial scale of effective pollen dispersal varies with population structure and landscape context: pollen movement is generally more extensive within continuous stands than among widely fragmented remnants. Genetic studies in yew have shown that long-range pollen dispersal occurs rather rarely, and that effective gene flow among isolated populations can be limited (Chybicki and Oleksa 2018). Pollination success and mating patterns are influenced by stand density, forest structure, and inter-tree distances, with reduced mating opportunities more likely in sparse, fragmented populations than in dense forests. Recent work further suggests that such limitations in gene flow and connectivity may have broader demographic consequences, potentially contributing to reduced reproductive success and regeneration failure in highly fragmented populations (Chybicki et al. 2024).

Generative Reproduction

Seed production in common yew begins relatively late, commonly after 30–70 years, depending on site conditions and light availability (Thomas and Polwart 2003). Reproductive output is typically irregular between years, a pattern reported for many long-lived tree species, although the specific climatic drivers of interannual variation in seed production in *T. baccata* remain insufficiently documented. In addition, reproductive success may be constrained in highly fragmented populations, where reduced connectivity and limited gene flow can affect effective pollination and seed set (Chybicki et al. 2024). Seeds ripen within the same year as flowering and are primarily dispersed by birds attracted to the fleshy red aril. Avian dispersal facilitates both local recruitment and long-distance gene flow, although post-dispersal seed survival is strongly affected by browsing, drought stress, light availability, and microsite conditions (García et al. 2000, Schirone et al. 2010b).

T. baccata seeds exhibit deep physiological dormancy and typically require a warm–cold stratification sequence to achieve reliable germination. This often involves a prolonged warm phase, sometimes with cyclic or diurnally fluctuating temperatures, followed by cold stratification, as demonstrated in practical propagation protocols (Suszka 1985). Germination usually occurs in spring after dormancy is broken, and successful seedling establishment is favoured in shaded, moist microsites with reduced competition.

Vegetative Reproduction

In addition to sexual reproduction, common yew is capable of vegetative regeneration through layering and basal sprouting, particularly following mechanical damage or canopy disturbance (Thomas and Polwart 2003). This regenerative capacity allows individuals to recover from browsing, cutting, or other forms of damage and contributes to the persistence of long-lived trees in established stands. Vegetative regeneration may locally compensate for limited seedling recruitment. However, it does not provide the genetic recombination associated with sexual reproduction (Thomas and Polwart 2003).

Genetic / Genomic Diversity and Population Structure

Common yew presents a complex pattern of genetic diversity across its natural distribution. Factors such as geographical location, climatic history, and postglacial recolonisation have influenced its genetic structure (Mayol et al. 2015). Phylogeographic evidence suggests that *T. baccata* colonized Europe from eastern refugia, leading to the formation of two major genetic lineages (eastern and western) with zones of secondary contact in Central Europe, Italy, and parts of the Mediterranean basin (Mayol et al. 2015).

Studies conducted across different European regions reveal variable levels of genetic differentiation among populations, depending on spatial scale, historical processes, and landscape features. For example, moderate differentiation has been reported in the Czech Republic (F_{ST} = 0.068, Komárková et al. 2022), while other studies in Great Britain and Switzerland indicate differing levels of structure (Hilfiker et al. 2004, Gargiulo et al. 2019). In general, genetic differentiation tends to increase with geographic distance and between regions, reflecting limited gene flow and historical isolation by distance, despite the species being outcrossing, wind-pollinated, and bird-dispersed (Hilfiker et al. 2004).

Distinct genetic clusters observed in parts of eastern and southern Europe are often associated with physical barriers and complex topography, such as mountain systems and fragmented habitats, which can restrict gene flow and promote spatial genetic structuring (Ohsawa et al. 2007, Ohsawa and Ide 2008, Hensen et al. 2012, Mayol et al. 2015, Vu et al. 2017, Koç et al. 2018, Litkowiec et al. 2018, Maroso et al. 2021).

Many studies have shown that gene flow and seed dispersal in *T. baccata* predominantly occur over short distances within populations (Mayol et al. 2015). The scattered distribution of common yew in the forest understory, where turbulence and wind velocity are low, further limits pollen and seed dispersal (Vranckx et al. 2014, Litkowiec et al. 2018, Gargiulo et al. 2019). Recent integrative analyses have further quantified these limitations, showing that both pollen and seed dispersal are often spatially restricted, resulting in reduced effective connectivity among fragmented populations (Chybicki et al. 2024). Restricted gene flow may increase the potential for inbreeding, as suggested by several studies (El-Kassaby and Yanchuk 1994, Senneville et al. 2001, Myking et al. 2009, Dubreuil et al. 2010, Miao et al. 2014, 2015). The understory habitat itself can exacerbate this effect by promoting mating between closely related individuals (Chybicki et al. 2012, Litkowiec et al. 2018).

It is important to note, however, that vegetative reproduction can locally buffer population persistence when sexual recruitment is limited (Thomas and Polwart 2003). While vegetative regeneration helps maintain individual numbers and stand structure, it does not restore genetic diversity or mitigate inbreeding, which still depends on sexual reproduction and effective gene flow.

Moreover, results have shown that the main distribution area of the species exhibits a notably higher genetic diversity, while peripheral areas show lower diversity, often due to inbreeding and genetic drift (Chybicki et

al. 2011). Chybicki et al. (2011) characterised the local genetic structure of two natural remnant *T. baccata* populations from the main distribution area in Poland, based on eight Simple Sequence Repeat (SSR) markers, and found higher levels of polymorphism (A = 20.6, H_e = 0.836), as did Lewandowski et al. (1995). Moderate levels of chemodiversity (taxane content), genetic (SSR) and epigenetic Methylation-Sensitive Amplification Polymorphism (MSAP) diversity were recently found in a study of Greek populations (Dalmaris et al. 2026). Gargiulo et al. (2019) investigated the genetic diversity of 13 British natural populations using eight SSR markers, also detecting high genetic diversity (H_e = 0.724). Furthermore, González-Martínez et al. (2010) studied genetic diversity and structure of 91 western Mediterranean *T. baccata* populations using seven nuclear SSR markers. Overall, they found moderate levels of genetic diversity (AR = 5.72; H_e = 0.660). However, they detected a reduction of genetic diversity and an increase of genetic differentiation moving from north-west (central Europe, northern Iberian Peninsula) to south-east (Mediterranean Iberian Peninsula, north Africa). Similar results have been found in populations of western Mediterranean islands and the Azores (Schirone et al. 2010a). New dendrogenetic evidence from the Italian Peninsula has confirmed strong genetic structuring in marginal and fragmented populations (Tonelli et al. 2025). Similarly high genetic differentiation was also recently found in Greek population at the south-eastern margin of the species natural range (Dalmaris et al. 2026), reinforcing the role of isolation and local environmental pressures in shaping genetic differentiation. These findings corroborate the fact that *T. baccata* abundance is reduced from core to marginal populations (Sanz et al. 2009). In fact, southern European yew populations usually consist of a few old trees (e.g., N = 12) with a low percentage of young trees and inadequate regeneration, factors that contribute to lower diversity levels (Mendoza et al. 2009). The lower genetic diversity at the margins has also been found in northern marginal populations, probably due to small census and effective population size (Myking et al. 2009). Overall, genetic differentiation appears to be lower in core distribution areas and higher in marginal populations (Myking et al. 2009, González-Martínez et al. 2010, Mayol et al. 2015, Litkowiec et al. 2018, Aravanopoulos et al. 2019, Gargiulo et al. 2019, Maroso et al. 2021, Komárková et al. 2022). Additionally, strong genetic structuring is especially pronounced in southern European areas (Lewandowski et al. 1995, Cao et al. 2004, Myking et al. 2009, Dubreuil et al. 2010, González-Martínez et al. 2010, Tröber and Ballian 2011, Chybicki et al. 2012, Mayol et al. 2015, Litkowiec et al. 2018, Maroso et al. 2021). These findings are consistent with the notion of strong fragmentation and inbreeding, which tends to decrease when moving towards the periphery of the species' distribution area.

The combination of low population size, geographic isolation, and low gene flow may indicate that the evolutionary potential of *T. baccata* at the local level may not be high (Pautasso 2009). Francisco et al. (2025), using a genomic offset analysis concluded that high-elevation *T. baccata* populations face higher vulnerability to climate change than low-elevation Atlantic and continental populations. These results are consistent with earlier findings highlighting adaptive genetic variation across environmental gradients, suggesting that climate-related selective pressures have contributed to shaping population differentiation and local adaptation in the species (Mayol et al. 2020). Moreover, *T. baccata* has a lower competitive ability compared to species of other genera, such as *Abies, Fagus,* and *Picea,* which commonly co-occur with *T. baccata*, especially at the regeneration stage (Iszkuło et al. 2009, Iszkuło 2010). Such findings, combined with the accelerating effects of climate change, highlight the importance of genetic conservation, especially in the remaining marginal populations of *T. baccata* (Iszkuło et al. 2009, Piovesan et al. 2009, Klumpp and Dhar 2011). Despite these advances, genomic resources for *T. baccata* have remained relatively limited until recently. A new targeted sequencing approach Single Primer Enrichment Technology (SPET) based on approximately 10,000 probes and generating over 50,000 SNP markers, provides a promising tool for high-resolution population genomic and adaptive studies in this species (Pinosio et al. 2026).

Species Threats

Common Yew Pests

Common yew is affected by a relatively limited range of insect pests, largely due to the presence of toxic taxanes that provide strong chemical defence (Daniewski et al. 1998). These compounds deter many herbivorous insects, including storage pests such as *Tribolium confusum*, *Trogoderma granarium*, and *Sitophilus granarius*. Nevertheless, several specialised or opportunistic species are regularly associated with yew. Scale insects, particularly *Parthenolecanium pomeranicum* and *Eulecanium pomeranicum*, damage needles and young shoots and may promote honeydew accumulation and sooty mould formation (Dennis 1964, Strouts and Winter 1994, Fischer 2016). Larvae of tortricid moths common on fruit trees, including *Ditula angustiorana* and *Hedya pruniana*, have also been recorded on yew (Ferguson 1995).

The gall midge *Taxomyia taxi* is widespread and induces characteristic shoot galls that suppress sapling growth and weaken trees (Redfern 1975, Siwecki 1978, Strouts and Winter 1994, Ballian and Kraigher 2021). The vine weevil *Otiorhynchus sulcatus* damages buds, needles, and young shoots, although feeding is partly inhibited by yew volatiles (Kapuściński 1947, Van Tol et al. 2000, Pehl and Wulf 2002). Mites represent the most diverse arthropod group associated with yew, with nearly 200 species recorded in England (Skorupski and Luxton 1998). Frequent species such as *Pentamerismus taxi*, *P. morishitai*, and *Epitrimerus gemmicola* damage buds and meristematic tissues, leading to crown deformation and reduced vitality (Pritchard and Baker 1951, Siwecki 1978, Thomas and Polwart 2003).

Common Yew Pathogens

Common yew hosts a diverse assemblage of fungi, bacteria, and other microorganisms, with approximately 250 fungal species reported in association with the species (Thomas and Polwart 2003). Most are saprotrophic or weakly pathogenic, although several taxa cause significant disease, particularly in seedlings and stressed individuals

(Pehl and Wulf 2002). Important pathogens include slime moulds (Myxomycota) and *Licea perexigua*, which is strongly associated with yew bark. Bacterial infections, notably *Agrobacterium tumefaciens*, may induce tumour-like swellings on roots (Smith 1942).

Pathogenic fungi affecting yew include *Phytophthora cinnamomi*, which causes wilting and mortality of seedlings (Hepting 1971), as well as representatives of Zygomycotina, Ascomycotina, Basidiomycotina, and Deuteromycotina (Peace 1962, Strouts and Winter 1994, Caruso et al. 2000). *Phytophthora* species represent the most serious threat in northern Europe and may directly cause tree mortality, whereas yew shows comparatively high resistance to *Armillaria* spp. (Strouts 1993, Strouts and Winter 1994).

Endophytic fungi are common in yew tissues and may contribute to host defence. Caruso et al. (2000) identified over 100 endophytic fungal strains, with *Alternaria*, *Fusarium*, and *Mucor* species occurring most frequently. Some endophytes, such as *Acremonium* spp., produce bioactive compounds (e.g. leucinostatin A) with antifungal properties that enhance resistance without causing visible symptoms (Strobel and Hess 1997). Root-lesion nematodes (*Pratylenchus penetrans*) may damage nursery stock, particularly on sandy soils, where infestations are difficult to detect and control (Bertrums 1998).

Herbivory

Despite containing toxic alkaloids and glycosides that deter many herbivores, common yew is subject to substantial browsing pressure from wild and domestic animals (Clarke et al. 1981, Thomas and Polwart 2003). Deer, particularly roe and fallow deer, browse shoots, buds, and bark, suppressing regeneration and altering population structure under high ungulate densities (Mysterud and Østbye 2004, Piovesan et al. 2009, Ballian and Kraigher 2021). Rabbits, hares, and grey squirrels also damage bark and shoots, while rodents may consume more than 60% of seeds during mast years (Hulme 1996, 1997, Hulme and Borelli 1999).

Domestic livestock, particularly goats and sheep, can exert strong impacts on *T. baccata* populations, even though ingestion of yew tissues may lead to lethal poisoning (Björkman 1958, Williamson 1978, Panter et al. 1993). Toxicity effects vary among animal species and are highest in fresh plant material (Panter et al. 1993), yet this does not necessarily prevent browsing. In fact, intense grazing has been observed to suppress yew regeneration in many regions. Although partial tolerance can develop following gradual exposure, the toxic nature of yew historically motivated deliberate tree removal to protect livestock, contributing to local and regional population declines (Navys 2000). Birds play a dual role as seed predators and dispersers, typically consuming the fleshy arils while avoiding the toxic seeds, facilitating gene flow despite high predation rates (Snow and Snow 1988, García et al. 2000).

Yew is also toxic to humans, with ingestion of needles, twigs, or seeds potentially causing fatal cardiac failure, and contact with wood occasionally inducing skin irritation (Clarke et al. 1981, Krenzelok et al. 1998).

Influence of Climate Change

Climate change is expected to intensify environmental stress on common yew, particularly in southern Europe, where rising temperatures, increasing drought frequency, and wildfire occurrence threaten population persistence. Severe fire events, such as those recorded in southern Bosnia and Herzegovina in 2014, have caused extensive local mortality. In contrast, northern and western European populations are projected to experience comparatively moderate impacts (Hanewinkel et al. 2013).

As a long-lived Atlantic forest species, yew exhibits limited capacity for rapid range shifts. Although northward and upslope migration is expected under future climates (Svenning and Skov 2004, Peñuelas et al. 2007), postglacial dispersal constraints and narrow ecological requirements restrict colonisation of newly suitable habitats. In western Europe, unfavourable carbonate soils further limit expansion, whereas eastern populations display broader edaphic tolerance (Elwes and Henry 1906, Voliotis 1986).

Generally, projected distributional changes are expected to be modest (Pautasso 2009). From an evolutionary perspective, recent studies suggest that adaptive genetic variation may influence resilience to climate change: high-elevation populations appear particularly vulnerable (Francisco et al. 2025), whereas population-specific adaptive patterns identified by Mayol et al. (2020) indicate potential for local adaptation, provided that genetic diversity is preserved. High genetic differentiation among southern populations may nevertheless facilitate local adaptation, provided that sufficient genetic diversity is maintained.

Decline of *Taxus baccata* in Europe: Patterns, Drivers, and Past Management Responses

Common yew has experienced one of the most dramatic contractions in range and population density among European tree species, reflecting the interplay of intrinsic biological traits and long-term human-induced landscape transformations (Habitats Directive 92/43/EEC, European Commission 2007, Benham et al. 2016). Among the most frequently cited factors contributing to its decline is its inherent toxicity, which has historically influenced patterns of herbivory and livestock management (Björkman 1958, Panter et al. 1993). Selective removal of yew to reduce livestock poisoning and protect grazing resources had long-term ecological implications. In many regions, remnant populations became increasingly restricted to inaccessible rocky outcrops, sacred sites, or burial grounds, where grazing pressure and anthropogenic clearance were lower. These refugia now represent important reservoirs of genetic diversity for the species (Navys 2000, Thomas and Polwart 2003). Another important driver has been the disruption of natural regeneration dynamics. Toxicity shapes browsing behaviour among wild ungulates: while some species, such as deer, can tolerate or selectively feed on yew, seedlings and juveniles remain vulnerable, and overall browsing often suppresses early regeneration (Chybicki et al. 2012, Litkowiec et al. 2018). Long-term studies in southwest Ireland have documented limited yew

regeneration under heavy deer grazing, with exclusion of deer markedly increasing seedling and sapling survival, indicating strong herbivore impacts on recruitment (Perrin et al. 2006). Herbivore pressure has also increased in parts of Europe following declines of large predators, allowing higher densities of deer and other browsers that can suppress early yew life stages (continental patterns of low recruitment and regeneration failures) (Saulnier et al. 2026). Domesticated grazing systems, which expanded during the medieval period, exerted additional pressure: intensive livestock grazing frequently eliminated seedlings and prevented the establishment of mature stands over large areas (historical land-use accounts show long-term forest clearance and grazing impacts on yew range) (Kaiser et al. 2024). In semi-natural woodlands, the combination of grazing pressure and deliberate tree removal for livestock safety sometimes led to local extirpations (historical decline of yew distributions following land-use change) (Benham et al. 2016). Further landscape transformations and long-term anthropogenic pressures compounded these effects. It should be noted that the emphasis on toxicity as a primary driver may reflect contexts dominated by livestock grazing, and other widely reported constraints also contributed to yew decline across Europe. These include light limitation under closed canopy and forest succession, habitat fragmentation, browsing pressure irrespective of toxicity, and forest management history (Svenning and Magård 1999, García et al. 2000, Thomas and Polwart 2003, Schirone et al. 2010b).

Despite the general species decline, some populations have persisted or expanded under favourable conditions or effective management. In Norway and Britain, yew shows signs of local expansion in recent decades (Seidling 1999, Svenning and Magård 1999, Preston et al. 2002, Dhar et al. 2006). The Danish case demonstrates a sizeable increase in a remnant population following stand thinning that improved light conditions and regeneration (Svenning and Mågard 1999). In southern Europe, increases in local yew populations have been observed following the abandonment of agricultural land and reductions in grazing pressure, especially where microclimatic conditions are favourable (Carvalho et al. 1999, Cortés et al. 2000, Kassioumis et al. 2004, Fernández-Manso et al. 2011, Serra and Garcia-Martí 2011, Ballian 2015, 2016).

Overall, contemporary conservation strategies must address both historical legacies and current ecological constraints to ensure that this emblematic species persists as a functional component of European forest ecosystems. This includes maintaining suitable microsites for regeneration, managing herbivore pressure, and safeguarding genetic diversity in remnant populations.

CONSERVATION OF *TAXUS BACCATA* GENETIC RESOURCES

Knowledge of the current population structure and environmental conditions, as well as associated forest communities, should serve as a basis for assessing the adaptation potential and conservation needs of common yew (Smith and Zollner 2005). Conservation genetic actions should be focused on the management of individual populations, with an emphasis on maintaining or restoring their long-term variability. Long-term conservation effectiveness is further enhanced when contemporary population assessments are integrated with palaeoecological, archaeological, and historical perspectives, which reveal that many present-day marginal populations represent remnants of formerly broader and more continuous distributions (Saulnier et al. 2026).

In situ Conservation

T. baccata is a long-lived, slow-growing conifer of high conservation value. Its protection within the EU is primarily achieved through the conservation of Annex I habitat types under the Habitats Directive 92/43/EEC, in which it occurs as a defining or characteristic species (e.g., yew-dominated woodlands). Historically widespread, the species now persists largely as fragmented, low-density populations, many of which show restricted natural regeneration despite consistently high seed production (Smal and Fairley 1980a, Thomas and Polwart 2003, Piovesan et al. 2009). Recent syntheses emphasize that this decline reflects a complex interaction between long-term climatic shifts, megafaunal loss, historical land use, and modern forest management, rather than a solely recent or climate-driven phenomenon (Saulnier et al. 2026). The conservation significance of the species has been further amplified by its socioeconomic importance, particularly the presence of taxanes—pharmaceutical precursors to anti-cancer drugs—found in its bark and foliage (Aravanopoulos et al. 2019, Dalmaris et al. 2019, 2020). *In situ* approaches are increasingly viewed as indispensable for allowing ongoing evolutionary processes to operate, especially in a species whose persistence historically depended on dynamic forest–disturbance mosaics and long temporal continuity (Saulnier et al. 2026). *In situ* conservation therefore constitutes a critical framework for safeguarding the species' genetic diversity, maintaining ecological functions, and enabling future restoration.

According to the European Information System on Forest Genetic Resources (EUFGIS 2025), *T. baccata* is represented in 74 *in situ* Gene Conservation Units (GCUs) distributed across Europe. These include Austria (30 units), Czech Republic (12 units), Germany (5 units), Spain (12 units), Italy (5 units), The Netherlands (1 unit), Norway (3 units), Slovakia (2 units), Slovenia (2 units), Turkey (2 units) (Figure 2). This number exceeds the EUFORGEN network average, highlighting both the conservation urgency and the coordinated European commitment to preserving the species' genetic resources. GCUs operate as long-term conservation stands where evolutionary processes are allowed to continue, while management focuses on demography, genetic integrity, and habitat stability (de Vries et al. 2015). From a genomic perspective, such population-level conservation units are particularly relevant because adaptive genetic variation in *T. baccata* is strongly structured at local and regional scales, even among geographically proximate stands (Francisco et al. 2025).

One of the primary aims of *in situ* conservation for *T. baccata* is the preservation of extant genetic diversity,

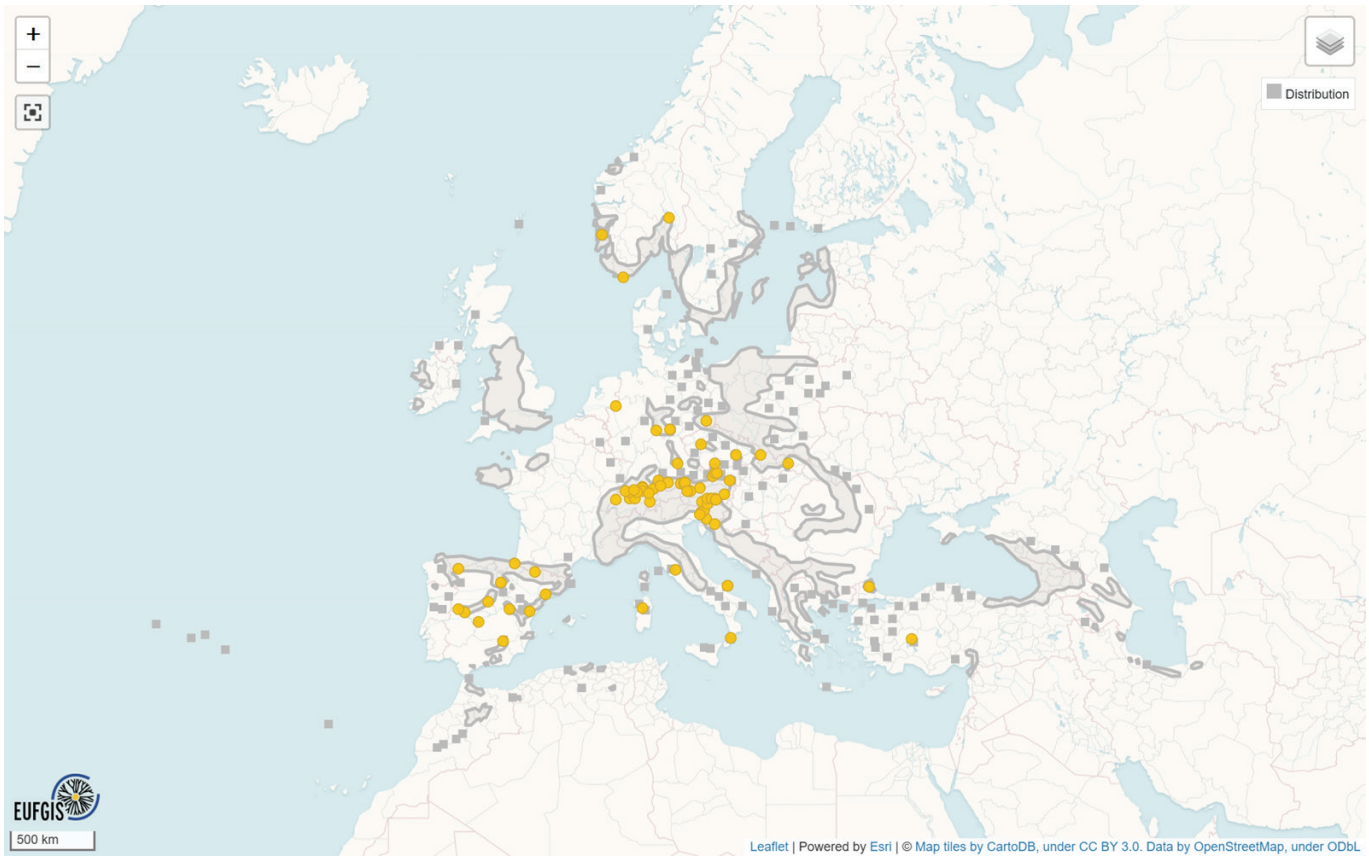


Figure 2. Conservation units of *Taxus baccata* in Europe (Source: EUFGIS 2025).

which is considered relatively high in many populations despite demographic decline. However, genetic structure varies considerably across Europe due to historical fragmentation, limited seed dispersal, and differential management pressures (Myking et al. 2009, Linares 2013). Genome-wide analyses reveal significant genotype–environment associations, with climate variables explaining a substantial proportion of genetic variance, indicating widespread but spatially heterogeneous local adaptation (Francisco et al. 2025). Three genetic priorities should characterize current conservation strategies:

(a) Maintaining within-population diversity. Given the species' long generation time and often fragmented distribution, both demographic and genetic factors must be considered. In this context, it is important to distinguish between census population size (Nc; number of mature individuals) and effective population size (Ne), which more directly determines the rate of genetic drift and loss of allelic variation. Small populations are particularly vulnerable to genetic erosion, reduced reproductive success, and increased extinction risk. While thresholds on the order of tens of individuals (e.g., <50 mature individuals) are sometimes cited in relation to short-term inbreeding risk, such values are not sufficient to ensure the long-term maintenance of adaptive potential. Long-term evolutionary processes—including the retention of adaptive variation and the capacity to respond to environmental change—require substantially larger effective population sizes. For a long-lived and frequently isolated species such as *T. baccata*, reduced connectivity among populations can further decrease Ne relative to Nc, exacerbating the effects of genetic drift and limiting gene flow. These processes may lead to deviations from historical gene–climate relationships, increasing genomic offset and vulnerability under future climate scenarios (Francisco et al. 2025). Consequently, conservation strategies should prioritise not only the maintenance of adequate population sizes, but also the preservation or restoration of connectivity to sustain effective population size and evolutionary resilience.

(b) Preventing inbreeding and genetic erosion. Empirical studies report high levels of inbreeding in some fragmented stands (e.g., Myking et al. 2009, Chybicki et al. 2011), prompting the need for active monitoring of mating systems, seed viability, and pollen flow. In small stands, the skewed sex ratio—frequent in dioecious species (Liu et al. 2021)—can exacerbate inbreeding risk. Genomic data further suggest that reduced effective migration rates among fragmented populations may limit the natural spread of potentially adaptive alleles (Francisco et al. 2025).

(c) Conserving locally adapted genotypes. Given the species' broad ecological amplitude—from Mediterranean to boreal climates—local provenance conservation is vital. GCUs play a pivotal role in capturing adaptive diversity shaped by site-specific selection regimes (climate, soil, browsing pressure).

Mediterranean and high-elevation populations, in particular, exhibit signatures of strong local adaptation but are simultaneously identified as among the most climate-

vulnerable, requiring targeted conservation attention (Francisco et al. 2025). There are several ecological constraints affecting *in situ* conservation. Primarily *T. baccata* faces limited regeneration despite high seed production. Although seed set in *T. baccata* is abundant, recruitment remains persistently low due to seed predation, browsing pressure, shade intolerance during early establishment, and competition with ground flora (Thomas and Polwart 2003, Piovesan et al. 2009). Historical evidence suggests that regeneration success was formerly enhanced under more heterogeneous forest structures, potentially maintained by large herbivores and natural disturbance regimes (Saulnier et al. 2026). Considerable herbivory and ungulate pressure by expanding populations of deer and other ungulates across Europe, exerts intense browsing pressure on seedlings and saplings. Selective feeding on yew shoot tips, despite its toxicity, results in truncated growth forms, demographic stagnation, and failure to transition to reproductive maturity. This chronic browsing pressure is increasingly recognised as one of the principal bottlenecks preventing population recovery across much of the species' range (Saulnier et al. 2026). To the above, there is an added burden of habitat fragmentation and microclimatic stress. Forest fragmentation reduces stand connectivity and dispersal opportunities for frugivorous birds responsible for seed dispersal. Furthermore, climate change—especially increased drought intensity in southern Europe—poses a growing threat to refugial populations. Genomic offset projections show that southern and montane populations are likely to experience the greatest mismatch between current genetic composition and future climatic conditions (Francisco et al. 2025).

The aims and priorities of *in situ* conservation should focus on:

(a) Preserving demographic stability through protection of existing mature individuals.
(b) Increasing population size where possible to strengthen resilience against stochastic events.
(c) Maintaining genetic integrity by preventing inbreeding and conserving local adaptive potential, including the avoidance of maladaptive translocations that could disrupt established gene-environment relationships.
(d) Securing material for future restoration, including seeds and vegetative propagules from genetically representative stands.
(e) Long-term genetic monitoring of evolutionary processes (e.g., shifts in genetic diversity, regeneration dynamics) to assess conservation effectiveness over time, which is essential to detect delayed responses in such a slow-growing species and to align management with evolutionary timescales.

Taken together, these measures form an integrated conservation model that aligns genetic, ecological, and environmental dimensions.

Ex situ Conservation

Application of *in vitro* Culture to *Taxus baccata* Conservation

In vitro culture includes a wide range of techniques that can assist plant conservation. Germplasm conservation (by *in vitro* maintenance in an active or slow growth state, or cryopreservation), embryo rescue, and plant production for habitat restoration can play a key role in plant conservation programmes.

Different cell and tissue culture procedures have been applied to *T. baccata,* and intensive investigation has been conducted to optimise *in vitro* production of paclitaxel (Malik et al. 2011). However, *in vitro* techniques commonly used for high production of secondary metabolites such as paclitaxel do not always allow the regeneration of whole plants and, consequently, they do not directly constitute a useful option for plant conservation. Nevertheless, diverse *in vitro* culture techniques with possible application in conservation programmes have been used in *Taxus* species, such as stem cutting (Chee 1995a), embryo culture (Flores and Sgrignoli 1991, Chee 1994, Zhiri et al. 1994, Chang and Yang 1996, Liao et al. 2006, Zarek 2007), propagation of plants *via* shoot organogenesis (Chee 1995b, Datta et al. 2006), and somatic embryogenesis (Datta and Jha 2008).

Under natural conditions, germination of *T. baccata* seeds is problematic due to several factors, including deep dormancy (Davarpanah et al. 2014). Different causes imposing dormancy have been reported in *T. baccata,* such as immaturity of embryos at the time of seed dispersal and the presence of endogenous inhibitors, including abscisic acid (Le Page-Degivry and Garello 1973, Thomas and Polwart 2003). However, an operational solution to overcome this dormancy has long been established through multi-phase warm–cold stratification protocols (Suszka 1985), which can result in high germination percentages after approximately 10–11 months of pretreatment. This approach has been widely applied in nursery practice supporting restoration efforts, although germination success may vary considerably among seed lots and individual trees (Lewandowski 1999, Peragón et al. 2015). In addition, environmental factors such as low temperature and limited light can influence seedling survival and growth, further contributing to variability in establishment success (Iszkuło 2010). *In vitro* culture techniques can help to overcome dormancy in *T. baccata*, particularly through embryo culture approaches in which excised embryos are grown under controlled conditions. These methods bypass seed-level dormancy mechanisms and enable the successful development of embryos that might otherwise fail to germinate under natural or nursery conditions. It is important to distinguish between high rates of embryo germination (i.e., initial emergence) and successful conversion into normal seedlings, as the latter often represents a critical bottleneck, with abnormalities such as weak growth or impaired shoot and root development frequently observed. Different *in vitro* culture strategies have been used to improve embryo conversion into plants. In most cases, the development of *in vitro* rescue protocols has been focused on the optimisation of the germination process, but *in vitro* culture techniques can also be applied to recover immature embryos (Sánchez-Romero et al. 2007, Márquez-Martín et al. 2009, 2017). Incubation of isolated immature embryos under culture conditions promoting embryo maturation may avoid low germination rates and the production of small, weak, and hyperhydric plantlets, observed when germinating immature embryos (Márquez-Martín et al. 2017).

In *T. baccata*, isolated embryos, after separating the aril and removing the external coat and the endosperm, have been cultured under different *in vitro* conditions. Various approaches have been applied to break seed dormancy imposed by inhibitors. Thus, Le Page-Degivry and Garello (1973) used a leaching medium containing sucrose or ions such as Ca^{2+} or K^{+} to remove inhibitors and enhance germination. Zhiri et al. (1994) leached seeds in running water for 7 days prior to culturing embryos on a modified Murashige and Skoog (MS) medium (Murashige and Skoog 1962) supplemented with casein hydrolysate, yeast extract, ascorbic acid, and activated charcoal. Tafreshi et al. (2011) found slightly higher germination percentages (100%) in embryos leached in running water for 7 days compared to those not leached (85%). However, leaching had a positive impact on late germination stages. While leached embryos germinated with extended roots, non-leached embryos were less than 5 mm and exhibited abnormal shapes. Absorbent substances have also been used to remove inhibitors. Zarek (2007) overcame dormancy by culturing isolated embryos for 28 days on basal MS medium with 5 $g \cdot l^{-1}$ activated charcoal. Tafreshi et al. (2011) supplemented MS medium with 0.8 $g \cdot l^{-1}$ polyvinylpyrrolidone (PVP) or 5 $g \cdot l^{-1}$ activated charcoal. Activated charcoal gave rise to better results than PVP. In addition, the application of a substance to absorb phenolic compounds yielded plants with larger shoots and roots and without any browning. Davarpanah et al. (2014) investigated the effect of activated charcoal concentration on embryo development into a seedling. The best results were obtained in MS medium with macronutrients at half strength (MS/2) supplemented with 2 $g \cdot l^{-1}$ activated charcoal, with seedlings more developed and showing fewer abnormalities, such as lack of shoot or root and twisting or thickening of the roots. Nevertheless, activated charcoal at high concentrations (6 $g \cdot l^{-1}$) caused abnormality of embryos.

Concerning the culture medium, investigations in several *Taxus* species, such as *T. mairei*, *T. baccata*, *T. canadensis*, and *T. cuspidata*, demonstrated that the composition of the culture medium is a critical factor in embryo culture (Davarpanah et al. 2014). In *T. baccata*, different mineral formulations have been tested. Chee (1994) cultured zygotic embryos excised from mature seeds on B5 medium (Gamborg et al. 1968), which had given rise to optimal results in previous experiments in *T. brevifolia*. Plants obtained were vigorous and suitable for acclimatization to *ex vitro* conditions. Tafreshi et al. (2011) investigated the effect of different strengths of MS macronutrients on embryo germination and seedling development, not observing significant differences in embryo germination. Later, Davarpanah et al. (2014) examined the influence of MS macronutrients at half and full strength, activated charcoal concentration (0, 2, 4, and 6 $g \cdot l^{-1}$), and gibberellic acid (GA_3) (1 $mg \cdot l^{-1}$) on embryo conversion into plants. In general, better embryo growth was obtained in culture media with MS macronutrients at half strength, with fewer abnormalities such as seedling twisting or browning.

In relation to plant growth regulators, Davarpanah et al. (2014) evaluated the effect of GA_3 on embryo culture. Despite the use of gibberellins to release different types of dormancy, including non-deep and intermediate physiological dormancy, photodormancy, and thermodormancy, *T. baccata* embryos cultured on MS/2 medium, supplemented with 1 $mg \cdot l^{-1}$ GA_3 did not show any considerable growth (Hartmann et al. 2014). All embryos remained white and showed no change after being transferred to light.

Environmental conditions during *in vitro* culture also had a considerable influence on seedlings production. Zarek (2007) found higher germination rates in darkness, but to obtain good quality seedlings, it was necessary to transfer cultures to light conditions (16-h photoperiod) after two weeks. Tafreshi et al. (2011) also reported that although to obtain seedlings with longer roots, embryos had to be incubated in MS/2 in darkness; for further development of the shoots, it was necessary to subculture seedlings in MS medium under light conditions.

Rooting of the obtained plantlets is also a crucial step when producing plants *in vitro*. Tafreshi et al. (2011) stated that to develop longer roots, embryo germination should be carried out in culture media supplemented with activated charcoal (5 $g \cdot l^{-1}$), and seedlings had to be maintained in MS/2 in darkness. However, Davarpanah et al. (2014) proposed that two different media should be used for precocious growth and rooting. According to these authors, the rooting medium can contain root formation stimulating compounds such as low concentrations of auxins (0.1 $mg \cdot l^{-1}$), L-tyrosine (up to 100 $mg \cdot l^{-1}$), and activated charcoal (1-4 $g \cdot l^{-1}$) to darken the medium and absorb the growth inhibitor exudates.

Micropropagation has also been applied to *T. baccata*. Majada et al. (2000) optimised a protocol for *in vitro* propagation of juvenile material combining seed handling and culture on the mineral formulation of Woody Plant Medium (WPM) (Lloyd and McCown 1980) and B5 vitamins supplemented with 5 $g \cdot l^{-1}$ activated charcoal and 22.19 mM 6-benzylaminopurine (BAP) for 30 days followed by 40 days on hormone-free medium. Decapitation of shoot apical ends significantly increased the propagation rates. Ewald (2007) micropropagated *T. baccata* using closed buds and shoot tips as explants. In this *in vitro* culture protocol, shoot multiplication was conducted by following a two-step procedure consisting of a first bud induction and propagation stage, followed by a bud elongation step to get rootable shoots. The first step was conducted in Wz medium, consisting of WPM medium supplemented with 1.5 $mg \cdot l^{-1}$ zeatin. Adding 200 $mg \cdot l^{-1}$ spermidine improved the results obtained. A callus phase, comparable to adventitious bud propagation in other conifers, was not observed. Elongation of shoot tips was achieved in Wdouble medium (consisting of double concentrated WPM macro and micronutrients) supplemented with 0.66 $mg \cdot l^{-1}$ zeatin, 0.64 $mg \cdot l^{-1}$ kinetin, 100 $mg \cdot l^{-1}$ PVP, and 100 $mg \cdot l^{-1}$ arginine. For stimulating elongation of lateral buds, a subculture in culture medium free of phytohormones was included, followed by a subculture with a low concentration of thidiazuron (TDZ) (0.01 $mg \cdot l^{-1}$). In general, the best shoot elongation was attained in Wdouble medium supplemented with 0.01 $mg \cdot l^{-1}$ TDZ and 200 $mg \cdot l^{-1}$ spermidine. Rooting was executed on L9 medium, consisting of a modified LS medium (Linsmaier and Skoog 1965) with 2 $mg \cdot l^{-1}$ indole-3-butyric acid (IBA) under a 16-h light-period. Abbasin et

al. (2010) cultured bud explants of *T. baccata* on several culture media supplemented with different combinations of cytokinins and auxins. MS medium supplemented with 2 mg·l^{-1} BAP gave rise to the highest number of shoots per explant and growth of shoot tips. Under these conditions, bud sprouting and shoot development were normal and stable within 3-4 weeks of culture, thus indicating a good hormonal balance (Abbasin et al. 2010).

In relation to organogenesis, Abbasin et al. (2010) reported shoot regeneration from calli developed at the base of *T. baccata* embryos. Half-strength MS and WPM culture media produced better quality calli than full strength media, reducing callus necrosis and increasing survival of explants. The combination of 2 mg·l^{-1} BAP and 0.3 mg·l^{-1} 1-naphthaleneacetic acid (NAA) resulted in an increase in callus development and shoot bud initiation, with up to 8 shoots per embryo cultured on half-strength MS medium. Good formation of roots was subsequently observed in MS/2 salts combined with forest soluble soil composition and 8 mg·l^{-1} IBA. The results obtained showed an important genotype effect.

Although somatic embryogenesis has been reported in other *Taxus* species, this *in vitro* culture technique has not been successfully applied to *T. baccata* (Ewald 2007).

Ex situ Plantations

For *T. baccata*, *ex situ* plantations—ranging from botanical garden collections to historically planted village trees and institutional arboreta—represent an important reservoir of genetic resources. Although traditionally viewed as static conservation repositories, these plantings have the potential to contribute significantly to restoration and species recovery, provided their genetic origins and conservation value are rigorously assessed. Botanical gardens, landscape parks, and ornamental plantings across Europe host a large number of *T. baccata* specimens, many dating back decades or even centuries. Such trees represent elementary static *ex situ* conservation, providing long-term living archives of the species but offering minimal direct conservation impact in their current form. Their main limitations are: (a) unknown or unverified provenance, as in much of Europe, the origin of planted yews is undocumented (Thomas and Polwart 2003, Hilfiker et al. 2004), (b) restricted evolutionary potential, as *ex situ* plantations typically lack the capacity for natural regeneration and, therefore, trigger evolutionary processes, and (c) limited applicability to large-scale restoration, as without clear genetic characteriszation, *ex situ* plantings cannot currently be incorporated into large-scale restoration programmes (Frankham et al. 2010, Weeks et al. 2011).

Despite these constraints, *ex situ* collections provide valuable opportunities when appropriately evaluated and integrated into broader conservation strategies, including the reconstruction of provenance and their potential use as already established assisted migration or conservation experiments (Oggioni et al. 2024). A notable example of the conservation relevance of *ex situ* populations comes from Bosnia and Herzegovina, where numerous old common yews planted in rural villages are preserved. Unlike many European plantings, the origin of some of these individuals is known through oral tradition, enhancing their value as potential genetic reservoirs for conservation and reintroduction programmes. This is significant for two reasons: (a) the preservation of historically important provenances, as local planting traditions in rural areas may have preserved unique genetic variants that have disappeared from surrounding natural populations due to logging, habitat conversion, or overgrazing, and (b) the potential for targeted conservation use, provided a molecular genetic characterisation is carried out before these individuals can be meaningfully incorporated into conservation or breeding programmes (Ballian and Memišević Hodžić 2024).

Overall, *ex situ* plantations can have a strategic role within an integrated conservation framework.

Conservation Interventions for *Taxus baccata*: Strategies for Long-Term Population Persistence in a Changing Climate

Conservation Challenges under Climate Change

Climate projections suggest that *T. baccata* may experience both northward expansion and southern range contraction, driven by temperature increases and altered precipitation patterns (Ahmadi et al. 2020, Sánchez-Martínez et al. 2021, Cruz Román et al. 2025). Northern populations may benefit from warmer winters and increased summer rainfall (Thomas and Garcia-Martí 2015), whereas southern populations, particularly in Mediterranean and sub-Mediterranean mountains, are already showing signs of decline due to recurrent drought, heat stress, and fire disturbance (Mendoza et al. 2009, Sanz et al. 2009, Camarero et al. 2015). Climate change is occurring at a pace that may exceed the ability of many species to track shifting suitable conditions, often described by climate velocity (Loarie et al. 2009). Correspondingly, species-specific models indicate that *T. baccata* may experience substantial changes in the distribution of suitable habitat under future climate scenarios (Zhang et al. 2026). Given the long lifespan of *T. baccata*, climate warming may pose particular challenges for maintaining populations at the southern edge of its range. However, dispersal and establishment constraints, particularly slow early growth and high juvenile mortality, limit the species' ability to track shifting climatic conditions, making effective range adjustments difficult for natural populations.

Southern and marginal populations frequently consist of only a few ageing individuals, with extremely limited potential for natural regeneration due to: (a) dioecy and skewed sex ratios, especially the disproportionate mortality of females under drought stress (Obeso 2002, Iszkuło et al. 2009), (b) reduced pollen production under warming climates, which may shorten the pollination window (Mercuri et al. 2013), and (c) genetic effects of fragmentation, including increased inbreeding and reduced mating distances (Lewandowski et al. 1995, Ballian 2005). Recent genomic and population genetic studies provide further insight into these vulnerabilities: high genetic differentiation in southern and fragmented populations (Chybicki et al. 2024, Tonelli et al. 2025, Dalmaris et al. 2026) and reduced adaptive genomic variation (Mayol et al. 2020, Francisco et al. 2025) suggest limited evolutionary

potential to respond to rapid climate change. Small populations may maintain moderate heterozygosity due to outcrossing during historical periods (Ledig 1986, Tröber and Ballian 2011), but ongoing fragmentation continues to lower effective population size and fertilization success (Allison 1990, Fahrig 2003).

The competitive balance between yew and co-occurring species is shifting as climate change favours fast-growing competitors, including beech (*Fagus sylvatica*), *Acer* spp., and chestnut (*Castanea sativa*) in parts of Europe (Packham et al. 2012, Ozolinčius et al. 2014). Herbivory by deer and domestic livestock remains a major limiting factor for seedling establishment (Svenning and Magård 1999, García et al. 2000), while reduced abundance of frugivorous birds undermines long-distance dispersal and gene flow (Jordano et al. 2007, Galetti et al. 2013). The development of genomic tools, such as the SPET array (>50k SNPs; Pinosio et al. 2026), provides opportunities to identify populations with higher adaptive potential, guide assisted gene flow, and design targeted conservation interventions under future climate scenarios.

Combined, these ecological, demographic, and genomic factors highlight that southern and marginal yew populations are particularly vulnerable, and **their** management requires integrating genomic knowledge with habitat protection, assisted regeneration, and adaptive conservation strategies to maintain population viability under climate change.

Principles and Aims of Conservation and Rescue Plans

Effective conservation of common yew must be multidimensional, aligning demographic stability with genetic integrity and climate resilience considering the disadvantage of the presence of small, highly threatened populations under strong anthropogenic influence.

The *T. baccata* conservation framework should emphasize: (a) stabilizing existing populations through habitat protection, herbivory control, and regeneration management, (b) safeguarding genetic diversity, particularly in marginal or relict populations vulnerable to demographic decline (Lewandowski et al. 1995, Hampe and Petit 2005, Myking et al. 2009, Sanz et al. 2009, Tonelli et al. 2025, Dalmaris et al. 2026), (c) enhancing adaptive capacity by supporting populations in climatically stable microrefugia (Dobrowski 2011), (d) facilitating climate-informed restoration, including assisted colonisation where appropriate (Aitken and Whitlock 2013). These aims are consistent with global principles of forest genetic resource management (Aravanopoulos et al. 2015, de Vries et al. 2015).

Conservation Interventions for *Taxus baccata*

Building on the conservation challenges outlined above, the following interventions are proposed to maintain and enhance *T. baccata* populations across its range. These actions are guided by ecological and genetic evidence, addressing limitations in natural regeneration, population fragmentation, and climate-driven pressures. By integrating habitat management, genetic conservation, and climate adaptation strategies, the measures aim to stabilise existing populations, facilitate recruitment, and preserve adaptive potential, particularly in marginal and relict populations vulnerable to ongoing decline.

(a) Facilitation of natural regeneration and habitat management. Ungulate browsing is among the strongest determinants of yew regeneration failure across Europe. Fencing and controlled grazing have repeatedly demonstrated measurable improvements in seedling survival, height growth, and stand structural complexity (Svenning and Magård 1999, Mysterud and Østbye 2004). Adaptive management, such as rotational herbivory exclusion, may prevent excessive shading by co-dominant species.

(b) Canopy and competition management. Yew seedlings require intermediate-light environments, while excessive shade inhibits growth and survival and high irradiance increases drought sensitivity and photodamage (Thomas and Polwart 2003). Selective thinning, gap creation, or maintenance of multilayered forest structure can improve microclimatic conditions. Competition control must be site-specific given regional variation in understory dynamics (Dhar et al. 2006, Ruprecht et al. 2010).

(c) Assisted migration and gene flow. Given the documented northward niche shift, carefully piloted assisted migration can be considered for regions projected to become suitable under future climate scenarios (Aitken and Whitlock 2013). Closely related, small-scale genetic rescue (assisted gene flow) interventions can be integrated here, ameliorating inbreeding depression in small populations while maintaining genomic compatibility to avoid outbreeding depression (Aitken and Whitlock 2013).

(d) Population reinforcement and assisted regeneration. For reinforcement or reintroduction, typical genetic standards for forest reproductive material must be considered. Local or ecologically matched provenances should be used to minimise the risk of maladaptation (Frankham et al. 2010, Weeks et al. 2011). Seed collection should be spatially and temporally representative to avoid genetic bottlenecks (Müller-Starck 1991, Konnert 1996). A minimum of approximately 40 genetically distinct seed donor trees is recommended for seed sourcing to capture local genetic variation; however, this does not represent the number of founders required for population establishment. For reinforcement or reintroduction, larger founder populations should be preferred, with balanced sex ratios in this dioecious species, and/or repeated introductions across cohorts to achieve a higher effective population size. This approach is consistent with conservation genetic recommendations that aim to reduce short-term inbreeding risk (Ne ~50–100) while maintaining long-term adaptive potential (Ne ≥500–1000).

(e) Drought and forest fire mitigation. In drought- and fire-prone regions, priority actions should include creation of firebreaks and fuel management around vulnerable stands, removal of lower branches to reduce vertical fire spread, and monitoring of drought stress indicators (Ballian and Kraigher 2021). Such measures have been shown to slow the decline of relict populations in Mediterranean ecosystems (Pausas 2004).

(f) Landscape-scale connectivity and habitat networks. Enhancing structural and functional connectivity is essential to sustain pollination, gene flow, and seed dispersal. Effective measures include conservation of bird communities that disperse yew seeds (García et

al. 2000), restoring hedgerows and riparian strips as dispersal corridors (Tewksbury et al. 2002, Krosby et al. 2010), maintaining stepping-stone populations to facilitate metapopulation stability (Saura et al. 2014). Recent results by Chybicki et al. (2024) highlight the spatial dynamics of pollen and seed dispersal in fragmented T. baccata populations, emphasizing the importance of connecting distant stands and designing corridors that support both effective gene flow and long-term population persistence.

(g) Ex situ support for *in situ* restoration. *Ex situ* germplasm (see also the *Ex situ* Conservation section above), such as seed orchards, clonal archives, and living collections, provides insurance against loss of unique genotypes. Yew seeds exhibit deep morphophysiological dormancy requiring extended stratification (Suszka 1985). Clonal propagation is useful for preserving elite phenotypes but must be balanced with the need to maintain population-level genetic diversity.

(h) Genetic and ecological monitoring. Successful interventions depend on continuous ecological and genetic monitoring, including: genomic markers to track hybridization, inbreeding, and gene flow (Dubreuil et al. 2008, Myking et al. 2009, Aravanopoulos 2011, 2016, Pearman et al. 2024, Shaw et al. 2025), population viability analyses to forecast extinction risk, dendroecological assessments to quantify climate sensitivity (Cedro and Iszkuło 2011, Camarero et al. 2015), permanent genetic monitoring within core GCUs and restored stands, and adaptive management allows practices to be refined as new data emerge.

The conservation of *T. baccata* requires an integrative, climate-informed approach that prioritises genetic diversity, population reinforcement, habitat management, and connectivity. Maintaining adaptive resilience in southern and marginal populations is particularly critical under accelerating anthropogenic and climatic pressures.

CONCLUSIONS

T. baccata is a relict, long-lived conifer whose present-day distribution, population structure, and conservation status reflect the combined effects of deep evolutionary history, postglacial dynamics, and sustained human pressure. This review synthesises evidence showing that, despite one of the most pronounced declines among European tree species, common yew has retained comparatively high levels of genetic diversity, largely due to its extreme longevity, predominantly outcrossing mating system, wind pollination, and effective seed dispersal by birds. However, this apparent genetic resilience conceals strong spatial heterogeneity, with southern, peripheral, and highly fragmented populations exhibiting reduced diversity, pronounced genetic structuring, and elevated vulnerability.

Across its range, limited regeneration emerges as the principal constraint on long-term population viability. Interacting factors including low light availability, intense browsing pressure, competition within closed forest stands, and episodic climatic stress frequently prevent successful recruitment, even where adult individuals persist for centuries. Climate change is expected to intensify these pressures, particularly in southern and montane regions, through increasing drought frequency, rising temperatures, and altered disturbance regimes. At the same time, potential northward or upslope range shifts are likely to be slow and incomplete, constrained by narrow ecological requirements, low juvenile survival, and limited dispersal capacity.

Effective conservation of *T. baccata* therefore requires an integrated, long-term strategy that explicitly incorporates genetic considerations. Priority actions include the protection of existing populations and their habitats, reduction of browsing pressure, promotion of forest structural heterogeneity to facilitate regeneration, and maintenance or restoration of landscape connectivity. From a genetics perspective, conserving large effective population sizes and regionally distinct genetic lineages is essential to preserve adaptive potential. Where natural processes are insufficient, carefully designed management interventions, including population reinforcement or assisted gene flow, may be warranted, provided they are guided by phylogeographic and ecological knowledge. Aligning conservation practice with the biological constraints and evolutionary legacy of common yew will be critical to ensuring its persistence as a functional and genetically viable component of European forest ecosystems under ongoing environmental change.

Author Contributions

FAA and MK conceived the research. DB, MMH and FAA designed the research. DB, MMH, CSR, FL, ED, ADFB, ZM, MK and FAA conducted the literature review. DB, MMH, ZM, MK and FAA supervised the preparation of the guidelines. DB, MMH and FAA drafted the manuscript. All authors reviewed the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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