Are mixed forests more resilient to a warmer and drier climate? A review on adaptive forest management of beech-oak forests in Europe

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Abstract

European forests are increasingly threatened by climatic extremes such as hot droughts, which impair their vitality and ecosystem services provision. Mixing tree species with contrasting functional traits and resource use, such as beech (*Fagus sylvatica* L.) and oaks (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L., and *Quercus pubescens* Willd.) may enhance forest resilience and decrease vulnerability to climate change. However, high uncertainties remain on how to effectively manage these mixtures, and their implications for ecosystem services. Through a comprehensive literature review, we assessed the geographical distribution, tree functional traits, and species interaction dynamics of mixed beech-oak forests across Europe. We further described how these mixtures are currently managed and which ecosystem services they provide. We revealed that despite distinct differences in tolerances to shade, drought, and heat between beech and oak, their mixtures do not consistently enhance climate resilience, as outcomes strongly depend on local conditions and management practices. Managed beech-oak mixtures can provide a wide range of ecosystem services, but often require intensive, costly interventions to maintain optimal beech-oak proportions and forest structure. A more integrated research effort is urgently needed to unravel how environmental conditions, species interactions, and silvicultural approaches jointly determine the resilience and ecosystem multifunctionality of mixed beech-oak forests across Europe.

Keywords: species interactions, climate change, *Quercus* spp., *Fagus sylvatica*, ecosystem services, functional traits, competition, silvicultural approaches

1. Introduction

European forests deliver a wide range of ecosystem services, including biodiversity provisioning, the production of roughly 500 million cubic meters of wood, protection against erosion and natural hazards, and recreational opportunities (Leal Filho *et al.*, 2021; 'State of Europe's Forests 2020'). They also play a crucial role in the global carbon cycle, taking up ~10% of European fossil fuel emissions (Ciais *et al.*, 2008; Migliavacca *et al.*, 2025). In Europe, forests cover about 35% of the total land surface (State of Europe's Forests, 2020). Most forests are mixed, composed of two or more tree species (67%), while 33% are monospecific stands, mostly composed by gymnosperm species (46%), angiosperm species (37%), or a mixture of these two groups (17%) (State of Europe's Forests, 2020).

European beech (*Fagus sylvatica* L.) is one of the most widely distributed tree species, covering around 14-15 million hectares across Europe (Brunet *et al.*, 2010), and plays a crucial role in the forestry sector (Vacek *et al.*, 2019; Antonucci *et al.*, 2021). Furthermore, beech forests host a wide diversity of native species, particularly fungi and beetles (Brunet *et al.*, 2010; Walentowski *et al.*, 2014; Schulze *et al.*, 2016). In the Middle Ages, pure and mixed beech forests were among the most widespread forest types in Central and Western Europe (Packham *et al.*, 2012; Paletto *et al.*, 2019). From the 18th century onward, however, these forests were increasingly replaced by fast-growing coniferous monocultures, particularly Norway spruce (*Picea abies* (L.) Karst.). This change was driven by changes in forest management practices and land-use, and increasing demand for commodity timber driven by industrialization (Pretzsch *et al.*, 2017; Vacek *et al.*, 2019). However, over the past decades, these monospecific conifer forests have shown to be highly vulnerable to increasingly frequent disturbances, such as summer droughts, windstorms, and pest outbreaks (e.g., bark beetles) (Anderegg *et al.*, 2015; Obladen *et al.*, 2021; Schiefer *et al.*, 2025), raising concerns about their long-term sustainability. These observations led to the development of new forest management strategies, which aim to promote mixed broadleaved forests, such as those composed of beech and *Quercus* species (e.g., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., and *Quercus pubescens* Willd.) to mitigate the impacts of changing climatic conditions (Mette *et al.*, 2013; Hanewinkel *et al.*, 2013; Vacek *et al.*, 2019).

Mixed-species forests, indeed, often deliver a broader range of ecosystem services than monospecific stands, including greater ecological stability under climatic extremes (van der Plas, 2019; Jourdan *et al.*, 2020; Schnabel *et al.*, 2021), increased productivity (Pretzsch *et al.*, 2013a; Forrester & Bauhus, 2016; Ammer, 2019; Depauw *et al.*, 2024), and higher biodiversity

(Scherber *et al.*, 2010; Tinya *et al.*, 2021). These positive effects are often attributed to functional differences in light requirements, water use strategies, and rooting depth between species, which can improve resource-use efficiency and microclimatic conditions in mixed forest stands (Loreau, 2000; Grossiord, 2019; Ammer, 2019). For example, in mixed stands managed for high-quality oaks, interactions between beech and oak trees are used to improve the quality of oak timber and facilitate natural regeneration processes (Von Lüpke, 1998; Bauhus *et al.*, 2017; Stimm *et al.*, 2022).

However, recent studies suggest that under extreme climatic stress, beneficial interspecific interactions may weaken or even become negative (e.g., Paquette *et al.*, 2018; Didion-Gency *et al.*, 2021; Haberstroh & Werner, 2022; Mas *et al.*, 2024; Serrano-León *et al.*, 2025), highlighting the need to identify species combinations that are more resilient to hotter and drier conditions. For instance, during the recent extremely hot and dry summers in central and southern Europe (e.g., 2018, 2022), beech has shown early leaf senescence, canopy dieback, and widespread tree mortality, raising concerns about its long-term persistence, including in mixed stands (Schuldt *et al.*, 2020; Obladen *et al.*, 2021; Knutzen *et al.*, 2025). In this context, developing proactive silvicultural strategies to facilitate the transition towards climate-resilient forests emerges as a key challenge. Yet, while the importance of mixtures in forest management approaches for climate change adaptation is widely recognized (Bolte *et al.*, 2009; Grace *et al.*, 2014; Brang *et al.*, 2014), their share increases only slowly in Europe. This may be related to a lack of knowledge and capacities for their establishment and management, and perceived increasing costs when compared to structurally and compositionally simpler forest stands (Willig *et al.*, 2025). Furthermore, the practical challenges and implications of applying such practices, especially in delivering key ecosystem services, remain poorly understood (Coll *et al.*, 2018; Cordonnier *et al.*, 2018; Antonucci *et al.*, 2021).

With this review, we aim to develop a perspective on how silvicultural strategies for beech-oak mixed forests may influence their resilience to climate change. In the following sections, we: i) provide an overview of the current distribution of mixed beech-oak forests across Europe; ii) summarize the existing knowledge on species-specific functional traits of common beech (*Fagus sylvatica* L.) and different oak species (*Quercus petraea* (Matt.) Liebl., *Q. robur* L., and *Q. pubescens* Willd.); iii) describe how these functional traits could modulate tree-tree interactions between beech and oak, including their competition dynamics under warmer and drier conditions; iv) assess the current management practices and ecosystem services of existing

mixed beech-oak forests; and v) discuss the challenges, implications, and future management of these mixtures under progressing climate change.

2. Beech-oak mixtures across Europe: distribution and ecology

European beech is widely distributed across the temperate region of Central and Western Europe, because it tolerates a wide range of soils (from acidic to alkaline; pH 3.5-8.5) and climatic conditions (Fig. S1) (Peters, 1992; Bolte *et al.*, 2007; Durrant *et al.*, 2016). Its distribution spans from Atlantic to subcontinental climates, with mean annual temperatures of 2–14°C and mean annual precipitation between 450 and 2000 mm (Durrant *et al.*, 2016; Bartsch *et al.*, 2020; Fuchs *et al.*, 2024). At its southern and eastern distribution range margins, it is commonly replaced at lower elevations by more heat- and drought-tolerant species such as sessile (*Quercus petraea* (Matt.) Liebl.), pedunculate (*Quercus robur* L.), and downy oak (*Quercus pubescens* Willd.). This confinement to higher elevations in these regions reflects its greater sensitivity to warm summer temperatures and reduced soil moisture (Fang & Lechowicz, 2006; Nocentini, 2009; Mette et al., 2013; Hohnwald et al., 2020).

Pedunculate and sessile oak also have broad distributions in Europe, ranging from Norway and Sweden in the north to much of the Mediterranean regions in the south, including parts of Turkey, with both species often co-occurring at many sites (Fig. S1) (Eaton *et al.*, 2016; Bartsch *et al.*, 2020; Černý *et al.*, 2024). The two species typically grow in regions with mean annual temperatures between 5 and 15°C and mean annual precipitation from 500 to 1500 mm, with pedunculate oak more abundant in continental climates, while sessile oak is more prevalent under Atlantic conditions (Eaton *et al.*, 2016; Gil-Pelegrín *et al.*, 2017). Both species grow on a wide range of soil types, but pedunculate oak predominates on moist, fertile soils and tolerates periodic flooding and moderate droughts, whereas sessile oak occurs more on well-drained, rocky slopes and hill tops, as well as more acidic soils (Eaton *et al.*, 2016; Konatowska *et al.*, 2024). Where they co-occur, pedunculate and sessile oak often hybridize, forming the *Quercus petraea – Quercus robur* complex and generating individuals that are morphologically and physiologically very similar (Gil-Pelegrín *et al.*, 2017; Kremer & Hipp, 2020).

Downy oak is a sub-Mediterranean species, occurring predominantly in southern Europe, where it occupies a wide elevational range and is most abundant at 200–800 m a.s.l., but reaches up to 1200–1300 m a.s.l. in warmer and drier regions (Fig. S1). Mean annual temperatures across its distribution range are between 5 and 17°C, and annual precipitation between 500 and 1100

mm (Wellstein & Spada, 2015; Pasta *et al.*, 2016). This species can tolerate moderate summer droughts and low winter temperatures, but performs poorly in continental climates, where such conditions are more frequent (López González, 2001). It is mostly found on well-drained soils that developed from limestone, yet can also grow in more acidic soil conditions in warmer regions (Contran *et al.*, 2013; Pasta *et al.*, 2016).

At a regional spatial scale, the natural distribution of beech and these three oak species largely overlaps, especially in Central and Western Europe for sessile and pedunculate oak, and in southern Europe for downy oak. At a local scale, beech tends to create monospecific stands, due to its high competitiveness (Ligot *et al.*, 2013; del Río *et al.*, 2014; Maleki *et al.*, 2020). This can create sharp ecotones between natural stands of beech and oaks where abrupt changes in site conditions occur, such as soil depth (Gärtner *et al.*, 2008; Deluigi *et al.* 2026). Mixtures tend to occur on less fertile and more acidic soils, under warm and dry conditions at the southern and eastern distribution edges of beech, where its competitive strength is reduced, or in managed forest stands, where competition between the species is controlled through management (Fig. 1) (Nocentini, 2009; Mette et al., 2013; Bauhus et al., 2017; Bravo-Oviedo et al., 2018; Bartsch et al., 2020). In northern Germany, for example, in managed mixed stands grown for high-quality oak timber, sessile oak typically accounts for 70-80% of basal area, while beech, which is used as a training species, contributes to 10-20% of basal area (Bartsch et al., 2020). In northern France, beech-oak mixtures are generally composed by ~55% of basal area of sessile or pedunculate oak, and ~22% of beech (Reboul & Allaer, 2019).

However, little information is available on the location, extent, and ecology of beech-oak mixtures across Europe. Research has examined mixed beech-oak stands across a wide array of countries, ranging from Atlantic (e.g., Germany, France, Belgium) to continental (e.g., Czech Republic, Poland, Romania, Hungary) and Mediterranean (e.g., Italy, Spain) regions (e.g., Pretzsch *et al.*, 2013a; Bravo-Oviedo *et al.*, 2018; Rubio-Cuadrado *et al.*, 2018; Hohnwald *et al.*, 2020; Jacobs *et al.*, 2022), suggesting that they span a wide ecological gradient. National forest inventory data can be used to map the occurrence of beech and oak species across Europe (Fig. 1). However, information on each species proportion and dominance, especially diameter distributions and basal areas, is needed to identify mixtures that may be more resilient to future climatic conditions. A better characterization of the distribution, structure, growth dynamics, and ecological functions of these mixed beech-oak forests across environmental gradients is thus crucial to better predict their vulnerability to and benefits under climate change.

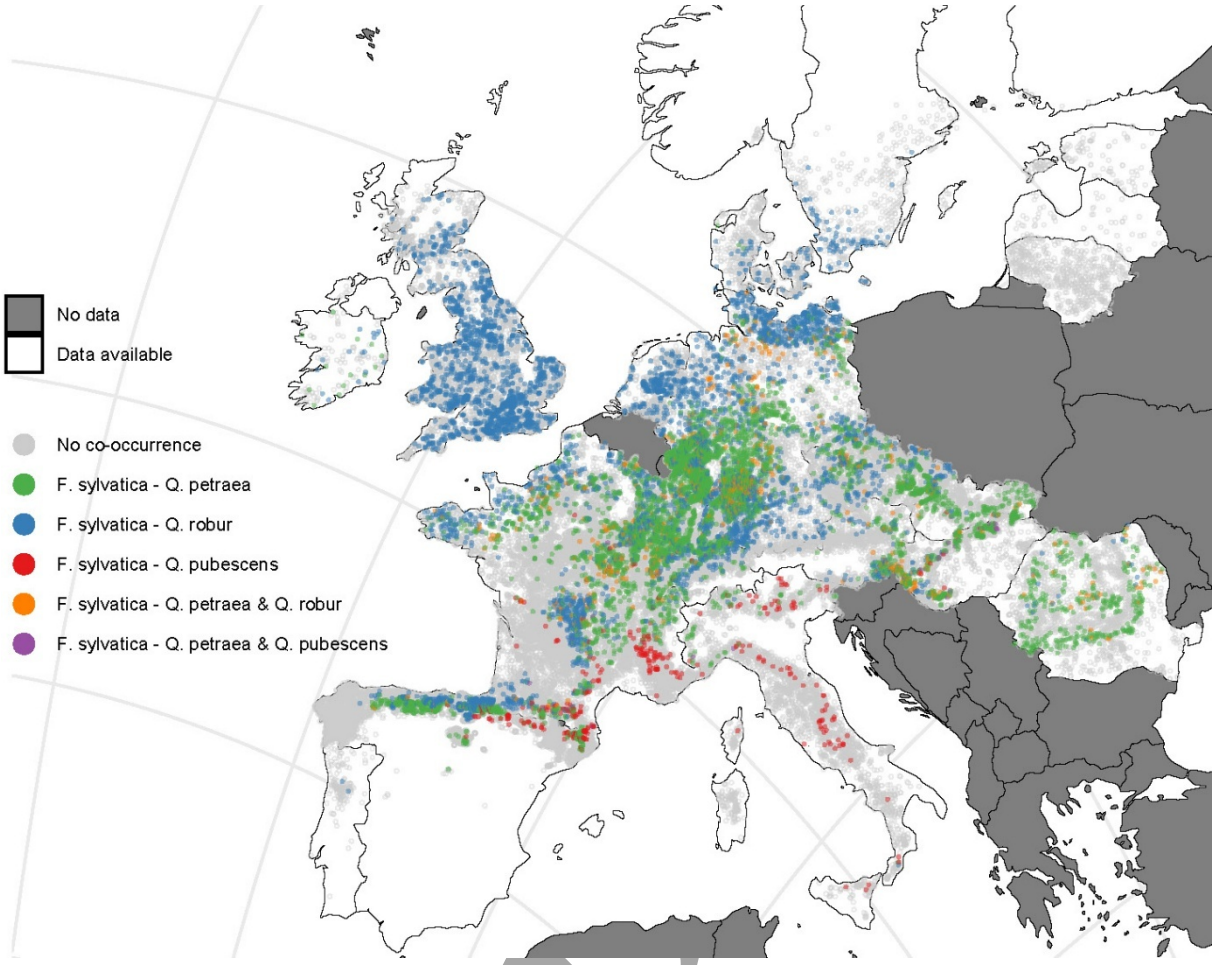


Figure 1: Map of the occurrence of beech-oak mixtures across Europe based on national forest inventories (Strona et al., 2016). The grey dots represent forest stands where mature trees (i.e., diameter at breast height > 12 cm) of either European beech (*Fagus sylvatica* L.) or oak (*Quercus petraea* (Matt.) Liebl., *Q. robur* L., and *Q. pubescens* Willd.) occur but do not co-exist within the same stand. The colored dots represent forest stands where beech and at least one oak species grow together within the same forest stand, with each color representing a different species composition (i.e., green = beech-sessile oak, blue = beech-pedunculate oak, red = beech-downy oak, orange = beech-sessile and pedunculate oaks, purple = beech-sessile and downy oaks). Mixtures between beech and all three oak species, or between beech and pedunculate and downy oaks, are not represented because they occur only in very limited numbers (i.e., n < 10). Dark grey areas represent regions for which national forest inventory data were not available.

3. Species-specific functional traits

The interactions of trees with their abiotic and biotic environments are mediated by their functional traits, which include morphological, physiological, and phenological characteristics (Lavorel & Garnier, 2002; Violle *et al.*, 2007). Species-specific functional traits and their phenotypic plasticity not only influence how trees respond to changes in environmental conditions, such as light availability, air temperature, and soil moisture, but also shape their spatial distribution and tree-tree interactions (Bussotti *et al.*, 2015; Aubin *et al.*, 2016; Anderegg *et al.*, 2018). Knowledge on the trait space occupied by different species can thus inform us about their adaptive capacity (Kretz *et al.*, 2025; Sanaei *et al.*, 2025). However, we currently lack a comprehensive understanding of the trait space occupied by beech and oak and how their functional traits change with abiotic and biotic conditions, including site conditions and tree-tree interactions in mixtures, as this knowledge remains scattered across individual studies. Here, we compare how beech and oak species differ in key functional traits related to their responses to light, temperature, and water availability to clarify their implications for performance, competition, and coexistence.

3.1. Shade tolerance and growth

Light acquisition and use are key determinants of tree survival and growth, especially during early life stages when seedlings and saplings compete for scarce light beneath forest canopies (Niinemets, 2010; Binkley *et al.*, 2013). European beech is a highly shade-tolerant species, whereas oaks are generally more light-demanding (Niinemets & Valladares, 2006; Hagemeier & Leuschner, 2019; Leuschner *et al.*, 2023a). While under prolonged high light (i.e., > 60% of light penetrating the canopy), sessile and pedunculate oak saplings can outperform height growth of beech saplings, they are outcompeted by beech under heterogeneous light (e.g., shady conditions with light flecks) or low radiation (e.g., below 15-20% under-canopy light availability) (Modrow *et al.*, 2020, 2025). These observations highlight the stronger competitiveness of beech regeneration below closed canopies compared to oaks (De Groote *et al.*, 2018; Maleki *et al.*, 2020; Jacobs *et al.*, 2022).

In sufficiently large canopy gaps, both beech and oak can rapidly gain height, reaching maximum tree heights of around 50 m in beech, 40 m in pedunculate and sessile oaks, and 25 m in downy oak (Durrant *et al.*, 2016; Eaton *et al.*, 2016; Pasta *et al.*, 2016). Mature beech trees typically form dense canopies characterized by pronounced vertical gradients in leaf traits (Bequet *et al.*, 2011; Leuschner & Ellenberg, 2017; Hagemeier & Leuschner, 2019). For

instance, sun-exposed upper canopy leaves typically show higher maximum photosynthetic capacity, leaf nitrogen content, and leaf thickness than shaded lower-canopy leaves, which often have higher chlorophyll content and specific leaf area, enhancing light capture (Van Wittenberghe *et al.*, 2012; Legner *et al.*, 2014; Scartazza *et al.*, 2016; Bachofen *et al.*, 2020). By contrast, the light-demanding oaks form more open crowns (Čermák *et al.*, 2008; Bequet *et al.*, 2011; Hagemeier & Leuschner, 2019; Leuschner *et al.*, 2023a) with smaller, thicker leaves – traits associated with warmer and drier environments (Günthardt-Goerg *et al.*, 2013; Bussotti *et al.*, 2015) – and show weaker sun-shade differentiation (Bartsch *et al.*, 2020; Leuschner *et al.*, 2023a; Deluigi *et al.*, 2026). These differences in crown morphology, foliar traits, and light requirements, coupled with contrasting tree heights, can promote more efficient canopy packing and higher stand-level light-use efficiency in beech-oak mixtures than in pure stands (Dieler & Pretzsch, 2013; Hilmers *et al.*, 2024; Deluigi *et al.*, 2026), although warmer and drier conditions may diminish or modify these advantages (Bontemps *et al.*, 2012; Sachsenmaier *et al.*, 2025).

3.2. Heat tolerance

Heat stress affects trees from the cellular to whole plant level, with impacts on growth and survival (Teskey *et al.*, 2015; Breshears *et al.*, 2021). Tree species differ widely in their tolerance to heat stress, which is commonly assessed with visual assays after heat exposure (Colombo & Timmer, 1992) or physiological metrics. A common physiological approach to quantify plant heat tolerance is to track the decline in chloroplast photochemical efficiency, one of the most heat-sensitive processes in plants (Berry & Bjorkman, 1980). In particular, the temperatures causing an initial decrease (T_{crit}) or 50% drop (T_{50}) in photosynthetic maximum quantum efficiency (F_v/F_m) are widely used (Bilger *et al.*, 1995; Murchie & Lawson, 2013; Curtis *et al.*, 2014). Across species, oaks generally have higher T_{crit}, ranging between 43-47°C, compared to 41-43°C in beech. However, with increasing temperatures, F_v/F_m tends to decline more rapidly in oaks, with T_{50} values of 47.3-53.2°C in pedunculate and sessile oaks compared with 51-55.8°C in beech (Münchinger *et al.*, 2023; Hauck *et al.*, 2025). Beech's lower thresholds for initial photosynthetic decline may be partially offset by its stronger evaporative cooling, as sustained transpiration can keep leaves cooler than air, avoiding damage (Köcher *et al.*, 2009; Salomón *et al.*, 2022; Niemczyk *et al.*, 2024; Hauck *et al.*, 2025). However, this cooling collapses under soil drought (Drake *et al.*, 2018; Kunert & Hajek, 2022; Martinetti *et al.*, 2025), a growing risk with more frequent "hotter droughts" (Allen *et al.*, 2010; Hartmann *et al.*, 2022). Such hot-drought-induced damages on beech leaves have been observed during

recent summer heatwaves in Europe (e.g., the 2018 hot-drought, Wohlgemuth et al. 2020), and have led to elevated beech mortality (Braun *et al*., 2020; Obladen *et al.*, 2021; Frei *et al*., 2022; Schiefer *et al.*, 2025).

High temperatures also affect photosynthesis, which peaks at a thermal optimum (T_{opt}), and declines at higher leaf temperatures (Yamori *et al.*, 2014; Crous *et al.*, 2022). For beech, T_{opt} ranges between 15 and 28°C (Schulze, 1970), while values between 30 and 35°C have been observed in oaks from Mediterranean (*Quercus canariensis* Willd., *Q. coccifera* L., and *Q. suber* L.) and temperate climates (*Q. robur* L. and *Q. petraea* Matt. Liebl.) (Daas *et al.*, 2008), indicating warmer optima for photosynthesis in oaks. Yet, beech can dynamically adjust T_{opt} under warmer T_{air} (e.g., Kurjak *et al.*, 2019; Deluigi *et al.*, 2025), although such plasticity appears increasingly constrained under concurrent soil drought (Fotelli *et al.*, 2000; Leuschner *et al.*, 2023b; Deluigi *et al.*, 2025).

Additionally, deciduous oaks have shown greater phenological and seasonal growth plasticity than beech, with earlier onset and longer growth duration, helping them track climate warming (van der Maaten *et al.*, 2018; Dewan *et al.*, 2020; Wenden et al., 2020; Schroeder *et al.*, 2021). Beech, in contrast, is more strongly constrained by photoperiodic control and adjusts its phenology less well to higher temperatures than oak (Vitasse *et al.*, 2009; Grossiord *et al.*, 2022). Together, these physiological and phenological differences underpin the greater heat tolerance of oak species and suggest rising competitive disadvantages for beech in mixed stands under future warmer conditions (Hanewinkel *et al.*, 2013; Zimmermann *et al.*, 2015; Kasper *et al.*, 2022).

3.3. Drought tolerance

Drought disrupts plants' hydraulic function with cascading physiological effects (Bréda *et al.*, 2006; Choat *et al.*, 2018), which are considered the main driver of tree mortality (Anderegg *et al.*, 2015; Mantova *et al.*, 2022; McDowell *et al.*, 2022). Beech is often perceived as a drought-sensitive species, due to higher vulnerability of the xylem to embolism (i.e., dissolved air expanding in the xylem, reducing its conductivity, Cochard *et al.*, 1992; Choat *et al.*, 2018; McDowell *et al.*, 2022), whereas oak species tend to be more drought-tolerant (Gil-Pelegrín *et al.*, 2017; Lobo *et al.*, 2018; Decarsin *et al.*, 2024).

Xylem vulnerability to embolism is often assessed by the stem water potential at which 50% of xylem conductivity is lost (P_{50}), with less negative values indicating higher vulnerability (Brodribb & Cochard, 2009; Choat *et al.*, 2012; Martin-StPaul *et al.*, 2014). For oaks, P_{50} typically ranges between -3.1 to -4.6 MPa in sessile oak, -1.9 to -4.7 MPa in pedunculate oak, and -2.5 to -4.8 MPa in downy oak, while less negative values (i.e., -1.9 to -3.8 MPa) have been observed in beech, consistent with its higher drought-sensitivity (Gil-Pelegrín *et al.*, 2017; Lobo *et al.*, 2018; González de Andrés *et al.*, 2021; Kahmen *et al.*, 2022; Laughlin *et al.*, 2023; Decarsin *et al.*, 2024; Schumann *et al.*, 2024). These differences align with contrasting xylem anatomy, stomatal response to drought, and rooting systems. For instance, beech is a diffuse- to semi-ring porous species, with smaller vessels (often > 50-90 µm) distributed throughout the wood ring, mostly produced after leaf expansion in spring (Schoch *et al.*, 2004; Schweingruber & Landolt, 2005). Oaks, in contrast, produce a ring-porous xylem, characterized by large vessels (often > 200 µm) concentrated in the early wood, and smaller and more diffuse vessels in the late wood (Barbaroux & Breda, 2002; Schweingruber & Landolt, 2005; Gil-Pelegrín *et al.*, 2017). In addition, ring-porous species can produce new wood before leafing to replace winter-damaged conduits (Barbaroux & Breda, 2002; Dox *et al.*, 2022).

Functionally, beech and oaks often show contrasting water-use strategies during droughts. Oaks generally show higher transpiration and photosynthesis at more negative leaf water potentials than beech (Leuzinger *et al.*, 2005; Aranda *et al.*, 2005; Fabiani *et al.*, 2022; Walthert *et al.*, 2024). To sustain the higher transpiration under water stress, the leaf turgor loss point (ψ_{TLP}, Bartlett et al., 2012; Burlett et al., 2025) is generally more negative in oaks (-1.3 to -4.7 MPa) than in beech (-1.7 to -2.6 MPa) (González de Andrés *et al.*, 2021; Kunert & Hajek, 2022; Mas *et al.*, 2023; Münchinger *et al.*, 2023; Schumann *et al.*, 2024).

In mixed stands, tighter stomatal regulation in beech during droughts may facilitate oak by maintaining higher soil water availability (Aranda *et al.*, 2005; Jonard *et al.*, 2011; Klein, 2014). However, some studies reported higher water use in beech than in oak under drought despite beech's lower intrinsic drought tolerance, likely due to its faster growth and larger canopy size (Grossiord *et al.*, 2014c; Jacobs *et al.*, 2021; Hesse *et al.*, 2024). In contrast, other studies observed more rapid and tighter stomatal regulation in pedunculate and sessile oak than in beech as soil moisture declines, indicating that oaks can also adopt conservative water use strategies (Grossiord *et al.*, 2014b; Niemczyk *et al.*, 2024). Overall, these contrasting results show that species-specific water-use responses are strongly context-dependent and shaped by the coordination of morphological and physiological traits and local environmental conditions.

Belowground traits are less well documented, but reported maximum rooting depths range between 0.2 and 2.4 m for beech and all three oaks, with a rooting depth of up to 9 m only reported for pedunculate oak (Kattge *et al.*, 2020; Tumber-Dávila *et al.*, 2022; Laughlin *et al.*, 2023; Pietig *et al.*, 2026). Still, beech can reach higher lateral root growth (0.1 to 15.7 m) than oaks (0.1 to 9.5 m across the three species) (Tumber-Dávila *et al.*, 2022). Similarly, beech and oak will primarily source water from shallow soils (0.2-0.4 m), but also dynamically shift their uptake to deeper layers under drought (Thomas, 2000; Grossiord *et al.*, 2014a; Brinkmann *et al.*, 2019; Bello *et al.*, 2019; Bachofen *et al.*, 2024; Walthert *et al.*, 2024). Yet, such plastic shifts can be insufficient to mitigate drought stress (e.g., Gessler *et al.* (2022), Martinetti *et al.* (2025)). Together, these belowground traits indicate higher intrinsic drought tolerance in oaks, likely an advantage as drought intensifies (Xu *et al.*, 2019; Zhang *et al.*, 2022b).

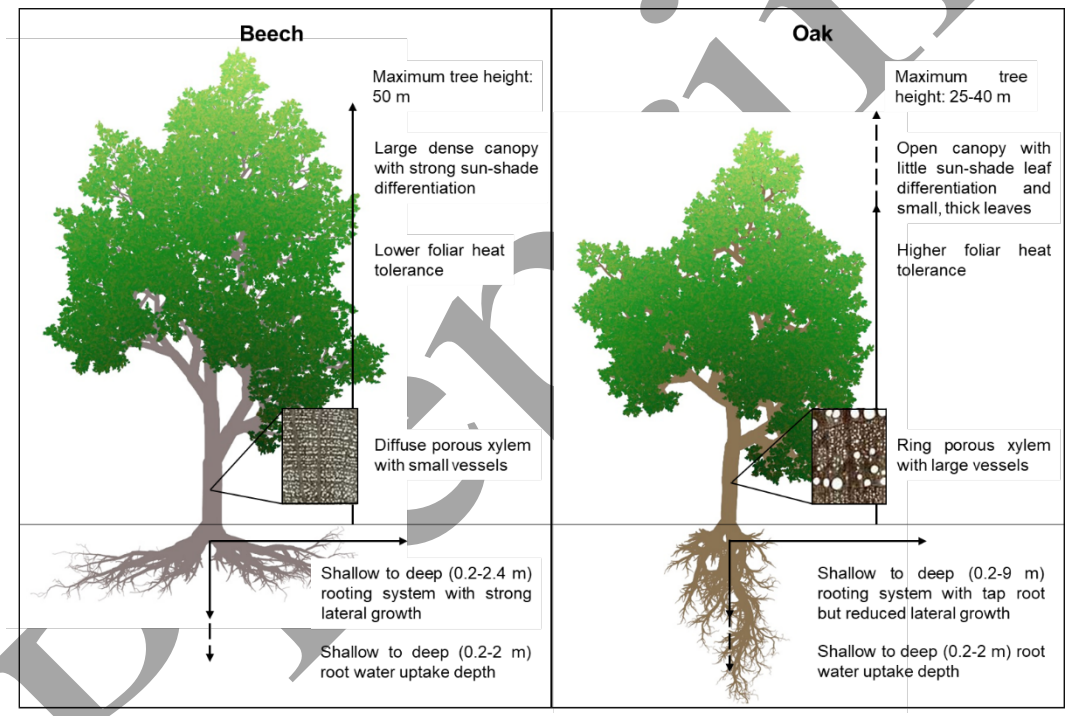


Figure 2: Simplified graphical representation of species-specific functional traits in beech (*Fagus sylvatica* L.), and oaks (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L., and *Quercus pubescens* Willd.). The oak species are described together to highlight common differences compared to European beech. Represented traits refer to trees growing in monospecific stands and may vary when growing in mixtures (see section below). Dashed arrows represent potential plastic responses in tree growth, rooting depth, and water uptake depth, as these traits are highly variable. A summary of species-specific average values of morphological features and functional traits associated with shade-, heat-, and drought-tolerance reported in the literature is listed in Table S1.

4. Tree-tree interactions in beech-oak mixtures

Functional differences between beech and oaks, such as light requirements, canopy structure, water-use strategies, and rooting depth, are expected to improve resource-use efficiency and buffer microclimate in mixed forests (Loreau, 2000; Grossiord, 2019; Ammer, 2019). Species-specific variations in these traits, however, can modulate interspecific interactions, with potentially large consequences for stand resilience and the provision of ecosystem services under warmer and drier conditions (Bussotti *et al.*, 2015; Decarsin *et al.*, 2024; Sachsenmaier *et al.*, 2025). Here, we summarize evidence on tree-tree interactions between beech and oak species in mixed stands.

4.1. Canopy packing and light-use-efficiency

A vertical canopy stratification creates microclimatic gradients that drive physiological and functional adjustments in leaf traits, impacting light-use, CO_2 assimilation, and thermal regulation (Legner *et al.*, 2014; Vinod *et al.*, 2023; Niinemets, 2023). In fully stocked, long-established mixtures of oak and beech, light-demanding oaks can only occupy the upper canopy layers due to their low shade tolerance. In contrast, the shade-tolerant beech can maintain relatively high photosynthetic capacity under low-light conditions and thus persists in lower strata (Legner *et al.*, 2014; Scartazza *et al.*, 2016; Forrester *et al.*, 2025). Only a few studies have compared functional traits between pure and mixed beech and oak stands, observing smaller and thicker leaves in beech trees growing with sessile and downy oak trees compared to pure beech stands (Didion-Gency *et al.*, 2021; Serrano-León *et al.*, 2022, Deluigi *et al.*, 2026). These findings suggest that beech trees were exposed to higher radiation and warmer conditions in mixed than pure forest stands. Consistent with these observations, studies found that despite their intrinsic lower shade tolerance, oaks were often intermixed or occupied the lower canopy layers in beech-oak mixtures, suggesting that beech often outgrows oaks in mixed forests (e.g., Jonard et al., 2011; Deluigi *et al.*, 2026). Consistent with these observations, several studies have documented faster growth and greater competitive dominance of beech when mixed with sessile, pedunculate, and downy oaks, forming taller and larger crowns that reduce light in the lower layers and suppress oak crown development and growth (Jonard *et al.*, 2011; del Río *et al.*, 2014; De Groote *et al.*, 2018; Maleki *et al.*, 2020; Deluigi *et al.*, 2026). These findings suggest that, despite differences in canopy structure, foliar traits, and light

requirements, competition can override structural complementarity, modifying canopy packing and the expected light-use efficiency gains from mixing (Dieler & Pretzsch, 2013; De Tomás Marín *et al.*, 2023; Hilmers *et al.*, 2024). However, warming and drying may reduce beech dominance and enhance oak competitiveness (Bontemps *et al.*, 2012; Mette *et al.*, 2013; Rubio-Cuadrado *et al.*, 2018; Jacobs *et al.*, 2022), potentially promoting more vertically stratified and productive mixtures, but evidence for this is currently still lacking.

In managed forest stands, the different shade tolerances of beech and oaks are also influencing regeneration approaches. European beech can be regenerated mostly naturally, with single tree selection systems and very gradual, protracted shelterwood cutting (Barna & Bosela, 2015), whereas low light conditions (< 10-20%) over longer periods in the understory typically inhibit oak regeneration and recruitment (Ligot *et al.*, 2014; Kohler *et al.*, 2020; Rubio-Cuadrado *et al.*, 2024; Modrow *et al.*, 2025). This difference threatens the persistence of oak in beech-oak mixtures. Without silvicultural interventions or other disturbances that promote oak regeneration and canopy access, oak may eventually disappear from mixed stands. Analyses of species dynamics in strict forest reserves support this pattern, showing a decline in oak trees within beech-dominated stands under past climatic conditions (Rohner *et al.*, 2012, 2013; Meyer *et al.*, 2016; Nord-Larsen *et al.*, 2019). In younger mixed stands, oak mortality increases with increasing stand basal area, leading to a continuous decrease in their proportion, though this effect is significantly weaker for dominant trees (Rohner *et al.*, 2012). To secure oak regeneration in mixed beech-oak forests following the initial establishment of naturally regenerated seedlings or after planting of oak saplings, sufficiently large canopy openings or basal area reductions are required to increase light availability below the tree canopies (e.g., > 50-60% of relative light levels) (Modrow *et al.*, 2020, 2025; Stimm *et al.*, 2021; Rubio-Cuadrado *et al.*, 2024). Such canopy openings may, in addition to active management, result from elevated tree mortality following severe drought, but even under these conditions understory thinning to reduce competition has been shown to be necessary to support oak regeneration (Lenk *et al.*, 2025). These results support an adaptive forest management approach that provides sufficient canopy openings during the regeneration phase to promote oaks and thus sustain species diversity, and bolster forest stability under climate change.

4.2. Canopy air temperature and humidity gradients

Species mixtures can also modify the air temperature and humidity in the tree canopy. Heat-tolerant oaks may better withstand warmer conditions in the upper canopy, while the more heat-sensitive beech may benefit from cooler and more humid conditions in the lower layers (Niinemets & Valladares, 2006; Hagemeier & Leuschner, 2019). Schnabel *et al.* (2025) showed recently that the higher density and structural diversity of the tree canopy layer(s) in mixtures can increase microclimate buffering. In mixtures, higher structural diversity can influence the vertical mixing of air masses, while higher canopy density reduces the penetration of sunlight and can enhance transpiration rates and air humidity, reducing vapor pressure deficit (VPD) in the lower layers, thereby lowering the transpirational water loss at the tree-level (De Frenne *et al.*, 2019; Bachofen *et al.*, 2020; Vinod *et al.*, 2023). This phenomenon has been observed in forest stands with high basal area (Zhang *et al.*, 2016; Paul-Limoges *et al.*, 2017). In contrast, low canopy packing in monocultures might increase tree susceptibility to hot and dry conditions, as observed for forests with low basal area (Song *et al.*, 2020). However, if these results can be transferred to beech-oak mixtures remains unclear, particularly if stand density is not higher in beech-oak mixtures than corresponding monocultures (Pretzsch & Biber, 2016). Recent studies have shown larger air temperature reductions of pure beech stands than beech-oak mixtures or pure oak stands along beech-oak ecotones (Hohnwald *et al.*, 2020; Leuschner *et al.*, 2023a; Deluigi *et al.*, 2026), partly contradicting expected advantages from species mixture. These effects were mainly due to higher shading and air cooling by denser beech canopies compared to more open canopies of oaks (Hagemeier & Leuschner, 2019; Gillerot *et al.*, 2022).

Taken together, these findings suggest that the capacity of mixed beech-oak stands to buffer climatic extremes strongly depends on species-specific canopy structure and stand type. Mixtures between functionally contrasting species likely do not generally provide a higher capacity to buffer temperature extremes compared to monocultures if one of the admixed species is highly shade tolerant and forms dense canopies as is the case for beech.

4.3. Water use and uptake

Differences in the timing of water use and soil depths from where water is taken up may promote niche partitioning and facilitation in mixed beech-oak forests (Loreau, 2000; Grossiord, 2019). Oaks are expected to benefit from beech's earlier drought-induced stomatal closure, which curtails beech water consumption and reduces competition for soil moisture

(Backes & Leuschner, 2000; Aranda *et al.*, 2005). Conversely, deeper-rooted oaks may access deep soil water and redistribute it upwards via hydraulic lift, boosting water availability for beech (Forrester & Bauhus, 2016; Grossiord, 2019). While these processes are often invoked to explain higher growth and stand-level productivity in beech-oak mixtures than monocultures (e.g., Jonard *et al.*, 2011; Pretzsch *et al.*, 2013b,a), direct tests – especially in mature stands – remain scarce and have yielded mixed results. For example, beech has been shown to have higher transpiration rates than co-occurring sessile and pedunculate oaks under moderate drought in mature forest stands, likely associated with larger crown sizes and higher growth rates (Jonard *et al.*, 2011; Jacobs *et al.*, 2021). In contrast, in a controlled experiment in an open-top chamber, Mas *et al.* (2023) observed higher transpiration in downy oak saplings when mixed with beech saplings under drought, due to the higher canopy leaf area of the former, underlining that canopy size plays a crucial role in trees' water use. Yet, other studies reported enhanced drought exposure of beech when mixed with sessile and downy oak under severe drought conditions, possibly due to higher soil water depletion by deeper-rooted oaks (Jourdan *et al.*, 2020; Didion-Gency *et al.*, 2021) or by more efficient soil water use by complementary rooting depth between beech and oak (Vanhellemont *et al.*, 2019). In contrast, (Martin-Blangy *et al.*, 2021) reported no significant impacts of mixture on the water use of beech and downy oak in natural mature stands. Together, these outcomes point to context dependence: interaction effects vary with environmental conditions, stand structure, and species traits.

Direct evidence for hydraulic lift in beech-oak mixtures is limited as well. Using a soil-water $\delta^{18}O$ labeling experiment in a young beech-oak forest, Zapater *et al.* (2011) observed greater isotopic enrichment in the soil near sessile/pedunculate oaks and in their xylem sap, suggesting deep-water uptake and redistribution by oaks, but no enrichment in beech xylem, suggesting little benefit to beech. Similarly, Volkmann *et al.* (2016) observed that while oak preferentially extracted water from deeper soils than beech, suggesting complementarity in water uptake, it did not enhance the relative water use of the mixture compared to the monospecific stands. These observations are in line with studies in temperate mixed forests, showing that species diversity does not always improve water-use efficiency, despite species-specific plastic responses in water uptake or rooting depth under drier conditions (Meißner *et al.*, 2013; Grossiord *et al.*, 2014a). Overall, these findings indicate that beech–oak mixtures do not inherently confer greater drought resilience, and that outcomes are site- and context-dependent. This underscores the need for more coordinated, multi-year studies in mature stands that capture full-rooting-zone dynamics, quantify species-specific water uptake pathways, and measure

469 water-use interactions during extreme drought events, ideally combining physiological
470 measurements, isotopic tracers, and belowground monitoring to directly test the proposed
471 mechanisms.

472 **Table 2:** Examples of observed beneficial, neutral, or negative tree-tree interaction effects
473 observed in mixed beech (*Fagus sylvatica* L.) and oak (*Quercus petraea* (Matt.) Liebl., *Q.robur*
474 L., *Q. pubescens* Willd.) forest stands, reported in the literature.

Tree-tree interaction	Tree species	Interaction effect	Study site	Method	Reference
Canopy packing and light-use efficiency	*F. sylvatica*, *Q. petraea*	positive for beech, negative for oak	Spain	Growth modeling from NFI data	(del Río *et al.*, 2014)
	F. sylvatica, *Q. robur*	negative	Belgium	Inferred from tree-ring analysis	(De Groote *et al.*, 2018)
	F. sylvatica, *Q. pubescens*	negative	France	Leaf functional traits along species composition gradients	(Didion-Gency *et al.*, 2021)
	F. sylvatica, *Q. petraea*	neutral	Germany	Leaf functional traits and physiology along canopy gradients	(Serrano-León *et al.*, 2022)
Canopy air temperature and humidity gradients	*F. sylvatica*, *Q. petraea*	positive	Romania	Reduction of high air temperatures by canopy cover	(Hohnwald *et al.*, 2020)
	F. sylvatica, *Q. petraea*	neutral	Belgium	Reduction of high air temperatures by canopy cover	(Zhang *et al.*, 2022a)
	F. sylvatica, *Q. petraea*	positive	Romania	Reduction of high air temperatures by canopy cover	(Leuschner *et al.*, 2023a)
	F. sylvatica, *Q. pubescens*	neutral	Switzerland	Reduction of high air temperatures by canopy cover	(Deluigi *et al.* 2026)
Water use and uptake	*F. sylvatica*, *Q. petraea*, *Q. robur*	neutral	France	^{18}O soil water labelling	(Zapater *et al.*, 2011)
	F. sylvatica, *Q. petraea*	positive for beech	Belgium	Inferred from sap flow measurements	(Jonard *et al.*, 2011)
	F. sylvatica, *Q. petraea*	positive for beech neutral for oak under drought	Germany	Inferred from tree-ring analysis	(Pretzsch *et al.*, 2013b)
	F. sylvatica, *Q. robur*	negative	Belgium	Inferred from tree-ring analyses	(Vanhellemont *et al.*, 2019)
	F. sylvatica, *Q. pubescens*	neutral	France	Inferred using ^{13}C isotopes and dendrometers	(Martin-Blangy *et al.*, 2021)
	F. sylvatica, *Q. pubescens*	negative	France	Inferred from physiological measurements	(Didion-Gency *et al.*, 2021)
	F. sylvatica, *Q. petraea*	negative, neutral under drought	Belgium	Inferred from tree-ring analysis	(Jacobs *et al.*, 2022)

F. sylvatica, *Q. pubescens*	negative	Switzerland	Inferred from physiological measurements and modeling	(Mas *et al.*, 2023)
F. sylvatica, *Q. pubescens*	negative	Switzerland	Soil water uptake depth	(Walthert *et al.*, 2024)

5. Management and ecosystem services of beech-oak mixed forests across Europe

Beech and oak play a key role in Europe, due to their high economic, ecological, and societal relevance (Durrant *et al.*, 2016; Eaton *et al.*, 2016; Pasta *et al.*, 2016). Sessile and pedunculate oaks are primarily managed to produce large-diameter roundwood, while beech is often used for energy production, and downy oak mainly for firewood because of its irregular stem form (Leuschner & Ellenberg, 2017; Unrau *et al.*, 2018; Nicolescu *et al.*, 2025). Beyond timber, beech and oak forests provide key habitats for many organisms, including specialist insects and understory plant species, and hold a significant cultural and recreational value (Felipe-Lucia *et al.*, 2018; Mölder *et al.*, 2019; Nocentini *et al.*, 2022).

Management objectives focused on timber production often conflict with biodiversity conservation, as intensive management practices can reduce structural heterogeneity and microhabitat availability (Latterini *et al.*, 2023; Uhl *et al.*, 2024; Pecurul-Botines *et al.*, 2025). A careful selection of species combinations and silvicultural practices can nonetheless help reduce these trade-offs (Felipe-Lucia *et al.*, 2018; Baeten *et al.*, 2019; Nocentini *et al.*, 2022). Knowledge on how beech-oak mixtures should be effectively managed and how different silvicultural approaches affect forest ecosystem services remains, however, limited (Bauhus *et al.*, 2017; Bravo-Oviedo *et al.*, 2018). Here, we synthetize current knowledge on three traditional and contemporary European silvicultural systems – simple coppice, coppice-with-standards, and high forests – discuss how they shape beech-oak mixtures, and assess their potential suitability under present and future climatic conditions.

5.1. Coppice forests

Coppice forests are typically even-aged stands in which all large stems are harvested at 15-25 year intervals and regenerate vegetatively from the remaining stumps or roots (Magagnotti & Schweier, 2017; Nicolescu *et al.*, 2017; Unrau *et al.*, 2018). These forests are dominated by tree species with high resprouting capacity, such as pedunculate, sessile, and downy oaks (Eaton *et al.*, 2016; Leuschner & Ellenberg, 2017; Nicolescu *et al.*, 2017). Although resprouting capacity

is often assumed to decline gradually with increasing tree age and coppice rotations, sessile oak can coppice prolifically even at 80-100 years (Pyttel *et al*., 2013) and sustain multiple rotations over 60-80 years or more, yielding 90-200 m^3 ha^{-1} of wood per rotation (Magagnotti & Schweier, 2017; Nicolescu *et al.*, 2023). Beech is less frequently managed in simple coppice systems because of its limited tolerance to repeated cutting, especially on acidic soils, though beech coppice forests persist at higher elevations in some regions, notably in Italy (Nocentini, 2009; Chianucci *et al.*, 2016; Leuschner & Ellenberg, 2017; Nicolescu *et al.*, 2017). Other tree species with strong resprouting ability, such as hornbeam (*Carpinus betulus* L., *Ostrya carpinifolia* Scop.), birch (*Betula pendula* Roth.), and ash (*Fraxinus ornus* L., *F. excelsioir* L.) are commonly coppiced, sometimes in mixed stands with oaks (Portoghesi, 2006; Nicolescu *et al.*, 2017; Bravo-Oviedo *et al.*, 2018).

Coppice forests were widespread across Europe during the 17^{th}-19^{th} centuries, providing small-dimensional materials such as firewood and charcoal, and oak bark for tanning with relatively low management and economic investment (Leuschner & Ellenberg, 2017; Magagnotti & Schweier, 2017; Unrau *et al*., 2018). Over the past century, however, many coppice forests have been abandoned, as the use of other energy sources such as gas and oil became more common and synthetic chemicals replaced oak bark for leather tanning (Becker *et al.*, 2013; Unrau *et al.*, 2018; Meyer & Ammer, 2022). Nonetheless, coppicing remains common in some European countries, such as Bulgaria, Turkey, Greece, Italy, and France, primarily for fuelwood production as a renewable energy source (Unrau *et al.*, 2018; Buckley, 2020; Latterini *et al.*, 2023). Ecologically, coppice forests are considered highly valuable, as they can host unique communities of insects, mushrooms, animals, and understory plant species adapted to the conditions created by regular coppicing, which are not found in closed forests or agricultural land use systems (Pasta *et al.*, 2016; Buckley, 2020; Nocentini *et al.*, 2022; Latterini *et al.*, 2023). Still, the low vertical stratification and temporary absence of canopy cover of these forests may limit their ability to buffer high temperatures, and potentially increase their vulnerability to hot and dry extremes under climate change (De Frenne *et al.*, 2019; De Lombaerde *et al.*, 2022). On the other hand, coppiced trees tend to develop deeper rooting systems and may increase below-ground carbon storage and drought-resistance, although empirical evidence of these effects is limited (Stojanović *et al.*, 2017; Řehořková *et al.*, 2022).

Overall, simple coppice systems appear poorly suited to sustain beech-oak mixtures. Under warmer and drier climates, they may retain relevance in regions where the cultivation of tall trees is constrained by soil drought (Grote *et al*., 2016; Stovall *et al.*, 2019), or where their

ecological and cultural value remains high, such as in mountainous beech forests (Nocentini, 2009; Manetti *et al.*, 2016). Coppice forests may also serve as transitional systems, offering opportunities through repeated disturbances to adjust species composition and facilitate the transition towards alternative silvicultural systems, such as high forests (Nocentini, 2009; Cullotta *et al.*, 2016; Manetti *et al.*, 2020).

5.2. Coppice-with-standards forests

Coppice-with-standards systems are uneven-aged stands characterized by a lower layer of regularly coppiced trees, which regenerate vegetatively from the coppiced stumps, and an upper layer of selected trees (referred to as "standards"), which originate from seeds and are grown for a longer time to provide large, valuable timber (Unrau *et al.*, 2018; Muigg *et al.*, 2020; Meyer & Ammer, 2022). In beech-oak mixtures, beech typically acts as a trainer species in the mid- and understory. The aim is to shade the stems of sessile or pedunculate oak standards, thereby preventing the development of epicormic shoots and promoting a straight, continuous stem growth, and to shade the ground to control competing vegetation and thus facilitate natural oak regeneration during the oak regeneration cut (Bauhus *et al.*, 2017; Nicolescu *et al.*, 2017; Pretzsch *et al.*, 2017). The oak standards are usually harvested when they reach a diameter of 40-80 cm in 160-240 year rotations to produce high-value timber, while the beech coppicing layer is harvested every 15-30 years for firewood (Von Lüpke, 1998; Bauhus *et al.*, 2017; Pretzsch *et al.*, 2017).

In addition to timber, these forests are highly relevant for biodiversity conservation. Besides hosting organisms associated with warm and sun-exposed environments in the coppiced layer, old oak trees in coppice-with-standards forests can host a large number of key microhabitats for various organisms, including saproxylic and phytophagous insects and mite species, enhancing forest biodiversity (Brändle & Brandl, 2001; Eaton *et al.*, 2016; Mölder *et al.*, 2019; Nicolescu *et al.*, 2025). Mature oak trees further produce large amounts of acorns during mast years (i.e., around 50-800 acorns m^{-2} every 4-8 years), which are traditionally used for pig feeding, represent a valuable food source for many birds and mammals. This silvicultural system holds an important historical relevance, as it was already used throughout the medieval period for wood- and non-wood products (Ducci *et al.*, 2015; Muigg *et al.*, 2020).

The management of beech-oak mixtures as coppice-with-standards can, however, be challenging. Beech regeneration under partially closed canopies often suppresses oak

recruitment, threatening the long-term persistence of oak standards (Petritan *et al.*, 2012; Maleki *et al.*, 2020). Maintaining oak regeneration in these forests generally requires large canopy openings or shelterwood cuts, often combined with artificial plantation, protection against ungulate browsing, and regular removal of beech trees in the understory before they reach oak canopies (Modrow 2025b, Coll 2018, Carpio 2021, Bauhus 2017). These interventions often result in higher management effort and costs, which may not be paid off if forest productivity is not increased by admixture compared to monospecific stands (Bauhus *et al.*, 2017; Mölder *et al.*, 2019). Consequently, this system is likely to persist mainly where cultural, historical, and biodiversity conservation objectives outweigh wood production goals, but seems poorly suited to maintain productive and self-regenerating beech-oak mixtures under future climatic conditions.

5.3. High forests

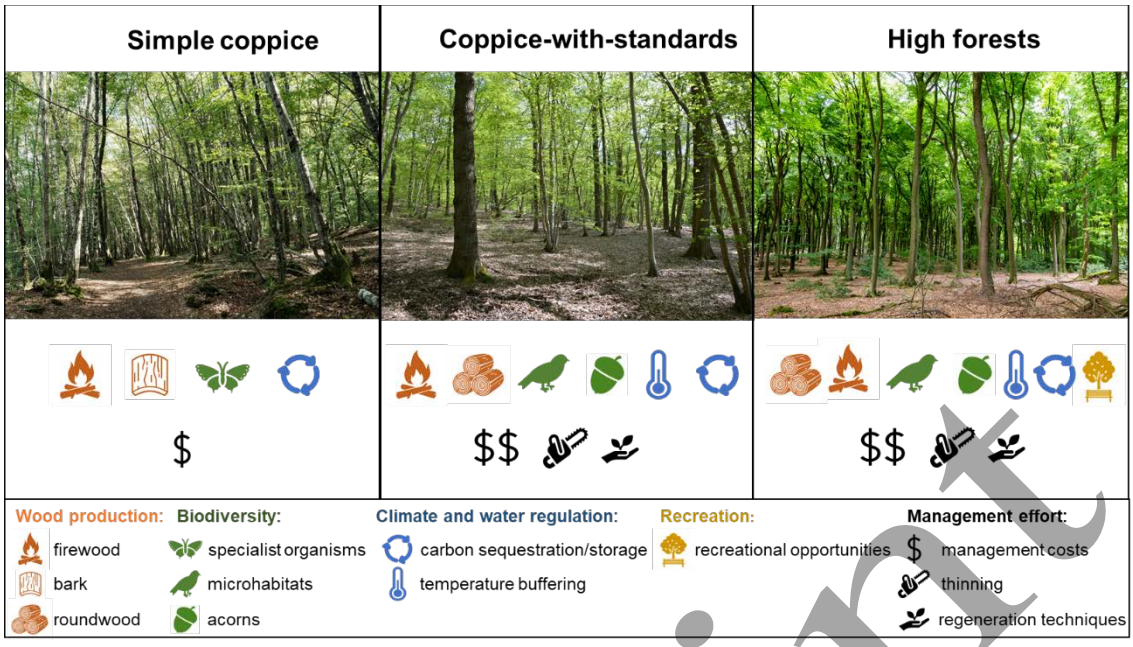
High forests consist of trees that developed from seeds and are grown to large dimensions for roundwood production (Leuschner & Ellenberg, 2017; Nicolescu *et al.*, 2017; Meyer & Ammer, 2022). The target diameter at breast height of trees selected for harvesting (i.e., crop trees) is typically 50-70 cm, achieved in 130-160 years (Leuschner & Ellenberg, 2017; Meyer & Ammer, 2022; Nicolescu *et al.*, 2025). Longer rotations have been associated with higher long-term carbon storage and wood quality than coppicing systems (Albert & Ammer, 2012; Grace *et al.*, 2014). Crop trees are typically harvested via selective cutting, where individual trees are removed from the forest stand, or group cutting, where patches of 0.05 to 0.5 hectares are cut, to limit management impacts on forest structure (Grace *et al.*, 2014; Brang *et al.*, 2014). This system aligns with the close-to-nature concept of forest management, which aims to enhance forest structural heterogeneity by maintaining low forest management intensity to increase forest multifunctionality and climate resilience (Schutz, 1999; Bauhus *et al.*, 2013).

In mixed high forests, beech may act as a trainer species or as a co-dominant canopy component (Bauhus *et al.*, 2017; Bartsch *et al.*, 2020). When acting as a trainer species, beech tree height needs to be maintained below oak canopies (e.g., 20 m, depending on the site conditions) through regular crown thinning or by removing individual large beech trees (e.g., 30-35 cm of diameter) to prevent the canopy expansion and vitality of oak from being suppressed by beech (del Río *et al.*, 2014; Bauhus *et al.*, 2017; Bartsch *et al.*, 2020; Maleki *et al.*, 2020). Removal of beech trees before reaching a certain age (e.g., 60-70 years old) could also be beneficial to

prevent seed production and thereby reduce beech natural regeneration (Genet *et al.*, 2010; Cutini *et al.*, 2015). Regeneration dynamics in high forests indeed strongly favor beech, due to its higher shade tolerance and competitive ability under closed canopies compared to oak (Ligot *et al.*, 2013; Barna & Bosela, 2015; Modrow *et al.*, 2025). Alternatively, beech may be maintained as a co-dominant component in mixed high forests, for example, on poorer, more acidic soils, where its competitive ability might be reduced (Nocentini, 2009; Bravo-Oviedo *et al.*, 2018). In these forests, crown thinning is needed to control beech growth and sustain oak development and canopy expansion, thereby maintaining forest productivity and biodiversity (Petritan *et al.*, 2012; Maleki *et al.*, 2020; Latterini *et al.*, 2023). While some studies have shown that thinning can efficiently reduce competition from neighboring trees, its effects on tree growth and forest ecosystem services in mixed forest stands remain largely unexplored (van der Maaten, 2013; Chianucci *et al.*, 2016; Antonucci *et al.*, 2021; Depauw *et al.*, 2024). Warmer and drier conditions may further reduce beech competition (Bontemps *et al.*, 2012; Jacobs *et al.*, 2022), but whether this will favor stable mixed stands is unclear.

Old oak trees in high forests can further host a wide variety of microhabitats for several organisms, associated, for example, with more than 500 different saproxylic and fungi species, and provide valuable food sources during mast years, supporting higher biodiversity (Löf *et al.*, 2016; Mölder *et al.*, 2019). High forests are, in addition, generally preferred for recreational activities, as they look more similar to natural forests (Eriksson *et al.*, 2012; Lehto *et al.*, 2025). Higher canopy cover and structural complexity in high forests may enhance temperature buffering capacity and water regulation, potentially improving climate resilience compared to coppice systems (André *et al.*, 2008; Pretzsch *et al.*, 2013b; Forrester, 2015), although empirical evidence for these effects in mature beech-oak mixtures remains limited (Pretzsch & Biber, 2016; Leuschner *et al.*, 2023a; Deluigi *et al*. 2026). Finally, higher canopy cover and structure may facilitate forest regeneration after disturbance compared to clear-cut sites, which will become increasingly important under climate change, as natural disturbances become more frequent and intense (Senf *et al.*, 2019; Aszalós *et al.*, 2022).

Overall, high forests appear more likely to remain functional under future climatic conditions. Sustaining balanced beech-oak regeneration over the long term, however, will remain challenging and depend on active and continued forest management (Bauhus *et al.*, 2017; Mölder *et al.*, 2019).



631

632 **Figure 4:** Simplified graphical representation of three main silvicultural systems for beech and
633 oak forests across Europe: simple coppice, coppice-with-standards, and high forests. Icons
634 represent the main ecosystem services (i.e., wood production in orange, biodiversity
635 conservation in green, climate and water regulation in blue, and recreation in yellow). Black
636 icons represent the management effort required for each silvicultural approach. Detailed
637 ecosystem services and management efforts are presented in the legend. Simple coppice forests,
638 unlike the other two systems, are generally dominated by one species – mainly oaks. In high
639 forests, beech can act as a trainer species, as in coppice-with standards forests, or be a co-
640 dominant species, depending on management objectives and intensity (see section 5.3.).

641

642 **6. Conclusions and future directions for research and forest management**

643 Mixed beech-oak forests play a fundamental role across Europe, providing essential ecosystem
644 services, including timber production, biodiversity conservation, climate regulation, and
645 recreation. These mixtures are also often promoted as climate-adapted systems, due to oaks'
646 overall higher heat and drought tolerance and the contrasting functional traits of these tree
647 species. These contrasting traits include light requirements, water use strategies, and rooting
648 depth, which could promote resource complementarity, improve microclimatic conditions, and
649 increase forest stability under warmer and drier conditions (Forrester & Bauhus, 2016; van der
650 Plas, 2019; Ammer, 2019). However, empirical evidence for complementary or facilitative
651 interactions between beech and oaks is inconsistent and strongly context-dependent. The

competitive dominance of beech particularly on mesic sites (del Río *et al.*, 2014; Maleki *et al.*, 2020; Jacobs *et al.*, 2021) can reduce oak establishment and growth, and potentially limit the expected benefits of beech-oak mixtures. Consistent with these observations, foresters have often highlighted the difficulty of achieving higher forest productivity (i.e., overyielding) in beech-oak mixtures compared to pure stands (Pretzsch *et al.*, 2013a; Bravo-Oviedo *et al.*, 2018).Increasing temperatures and more frequent droughts under climate change may weaken beech's competitive advantage, potentially facilitating the establishment of beech-oak mixtures (Bontemps *et al.*, 2012; Didion-Gency *et al.*, 2021; Martin-Blangy *et al.*, 2021). However, the extent of this competitive shift remains uncertain, as site conditions, stand structure, and management practices strongly influence competitive dynamics in beech-oak mixtures, suggesting that maintaining optimal proportions between these tree species in mixed stands is and will remain challenging.

Silvicultural systems further shape these dynamics. Simple coppice and coppice-with-standards systems provide high biodiversity value, supporting light-demanding and thermophilic species adapted to open conditions, but they appear poorly suited to maintain stable beech-oak mixtures. In coppice forests, oaks and other tree species with high resprouting capacity are generally favored over beech, whereas in coppice-with-standards forests high management effort is required to prevent beech from suppressing oak regeneration and growth, rendering them difficult to maintain in the long term.. Nevertheless, coppice systems may maintain relevance at the warmest and driest margins of beech-oak distributions, where the cultivation of tall, dense high forests may be increasingly constrained by drought stress, and in regions where coppice forests maintain high value for firewood production, soil protection, biodiversity conservation, or other ecological and societal objectives (Manetti *et al.*, 2016; Nocentini *et al.*, 2022). High forests may offer greater potential for maintaining beech-oak mixtures under future climates, as they provide higher compositional and structural complexity, which may enhance climate buffering and forest recovery capacity after natural disturbances, can host a large variety of organisms, and offer recreational opportunities. However, our review showed that high forests do not ensure long-term coexistence of beech and oak without active management, as low light conditions below dense canopies strongly favor beech regeneration (Rubio-Cuadrado *et al.*, 2024; Modrow *et al.*, 2025).

Appropriate regeneration techniques are thus key for climate change adaptation. While natural regeneration is often preferred over planting due to lower costs, it requires sufficiently large canopy openings and long time frames (i.e., decades) to substantially change forest composition

towards beech-oak mixtures (Bauhus *et al.*, 2017; Mölder *et al.*, 2019; Manetti *et al.*, 2020). Planting may be used to accelerate the establishment of mixed and uneven-aged stands (Bauhus *et al.*, 2017; Cordonnier *et al.*, 2018; Manetti *et al.*, 2020). For example, planting may be strategically used to introduce beech saplings once oak trees have reached pole stage, thereby reducing the negative impact of beech on oak regeneration under closed canopies, which is particularly relevant in high forests (Bauhus *et al.*, 2017). In all cases, targeted and regular silvicultural interventions and long-term monitoring will be needed to maintain species proportions and forest structure. Yet, effectiveness, costs, and ecological consequences of such interventions remain uncertain, as long-term field experiments are largely lacking (Corlett & Westcott, 2013; Manetti *et al.*, 2020).

Further research should move beyond simple comparisons of forest productivity *per se* between mixed and pure forest stands and instead focus on the mechanisms and environmental conditions that determine when species interactions are beneficial under different silvicultural systems. In beech-oak mixtures, studies should: i) identify light, soil moisture, and disturbance conditions that enable a successful oak regeneration in mixed stands; ii) assess how management practices, such as thinning, and management intensity influence tree-tree interactions and growth dynamics between beech and oak; and iii) evaluate whether structural and functional diversity in mixed stands translates into measurables gains in heat and drought tolerance and ecosystem services provision across environmental gradients. This kind of research would be particularly important towards the warmest and driest margins of beech and oak species' distributions, where climate change impacts are expected to be strongest. Long-term experimental networks and harmonized monitoring along environmental gradients and silvicultural systems across Europe are needed to better predict shift in species interactions and forest ecosystem services provision under climate change.

Finally, strengthening collaboration among researchers, foresters, and policymakers will be essential to develop, test and implement adaptive, evidence-based, and site-specific management strategies. Integrating ecological knowledge, long-term monitoring, and socio-economic considerations into forest development planning will be crucial to ensure that beech-oak forests across Europe remain resilient and multifunctional under a warmer and drier climate.

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Author contributions

JD, CB, and CG conceived and planned the research. JB and FS contributed to the conceptualization of the manuscript. JD conducted the literature review. All authors critically contributed to the manuscript writing and gave final approval for publication.

Supporting information

Figure S1: Species-specific maps of the distribution of beech, sessile oak, pedunculate oak, and downy oak in Europe based on their presence in national forest inventory plots

Table S1: Summary of species-specific values of functional traits for the selected species, based on previous studies

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