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Silver Fir (*Abies alba* Mill.): Review of Ecological Insights, Forest Management Strategies, and Climate Change Impact on European Forests

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Abstract: The silver fir (Abies alba Mill.) is among the most valuable conifers in Europe for ecological and economic reasons. In the course of history, primarily in the 20th century, its share in stands has been declining due to ill-suited management practices, especially clear-cut management, air pollution, and wildlife-induced damage. Based on recent knowledge of fir ecology and population dynamics, small-scale shelterwood and selection management have been introduced in fir stands, which have also stabilized them. Fir is an essential species for maintaining high stability and biodiversity, especially on planosols and in waterlogged habitats. Due to its shade tolerance and environmental flexibility, particularly at higher altitudes, it can coexist very well with many tree species in mixtures, which can increase the productive potential of stands. It can form stands of heterogeneous structure, ranging from single to multi-layer to selection. For its successful natural regeneration, it is essential to reduce cloven-hoofed game and thus prevent bud browsing damage. On the other hand, fir is a species relatively resistant to bark stripping and the spread of secondary rot compared to Norway spruce (Picea abies [L.] Karst.). During global climate change, fir is expected to shift to higher elevations with sufficient precipitation, while in the southern part of its natural range or at lower elevations, outside water-influenced habitats, it is likely to decline. This paper essentially reviews the description and distribution of the species, its ecological requirements, threats and diseases, habitat and stand conditions, and close-tonature forest management practices with emphasis on ongoing climate change.

Keywords: forest management; silver fir ecology; climate change impact; biodiversity; threats and diseases; regeneration practices

1. Introduction

From the ecological and economic perspectives, silver fir is one of the most significant coniferous tree species in Europe [1–6] as well as in Czechia [7–10]. Originally, fir was the most abundant coniferous tree species in Czechia; its share in the natural species composition is reported to be 19.8% [11]. In contrast to other major tree species, fir never formed unmixed stands, i.e., pure fir stands, on zonal sites [12,13]. According to Málka [14], significant changes are evident in the representation of fir throughout history—year 1200: 20%, 1600: 30%, 1800: 23%, and 1900: 10%. The increase in fir representation, up to 30%, was likely supported by more widespread grazing under deciduous trees and raking of their litter, thus improving the conditions for the germination of fir seeds [13,15–17]. In 1950, the proportion of fir in Czechia was approximately 3%, in 1970, 2.1%, and in 1998, it had declined to 0.9%. Currently, fir grows on 32,272 ha, i.e., 1.2% of the forest area of Czechia [11] and its share in forest regeneration is gradually increasing [approximately 1500 ha annually; 11]. A similar trend is also visible in other European countries.

Fir is a climax species [18] that cannot thrive at lower elevations and in warm regions (especially in the Mediterranean), as it is limited by lower precipitation [19], but it can be compensated by higher soil water content and sufficient air humidity [20]. However, fir does not grow on permanently

waterlogged sites [21]. In Northern Europe and in mountainous areas, silver fir is limited by low temperatures and late frosts that extend into the early part of the growing season [22,23].

Being an indicator of various types of air pollution [24], the distribution of fir was strongly affected by the air pollution calamity in the second half of the 20th century [8,25–27]. Synergism of air pollution with the occurrence of silver fir woolly aphid (*Dreyfusia normannianae*), balsam woolly aphid (*Dreyfusia piceae*), and poor management practices have also been reported [4,5,9,28]. A decrease in silver fir abundance is also hastened by game-induced damage through bud browsing, bark stripping, browsing, and fraying [8,29–34].

Current fir dieback is mainly attributed to climate change [5,9,27,35,36]. In particular, warm summers and recurrent drought have a significant negative impact on the health of silver fir [2,20,36–38].

This literature review of 341 studies aims to assess the role, opportunities, and risks of silver fir in European forestry. The secondary objectives focus on a detailed review of (i) species description and distribution, (ii) ecological requirements, (iii) threats and diseases, (iv) habitat and stand conditions, (v) seed production and nursery management, and (vi) close-to-nature forest management with an emphasis on the ongoing climate change.

2. Description and Distribution

The silver fir is characterized by a solid, cylindrical trunk and a conical to cylindrical, very regular crown (Figure 1). In old trees, the lateral branches overgrow the terminal and form a flattened "stork's nest" at the top of the crown. Fir grows 30–60 m tall and 1–2 m in trunk diameter. The root system is formed by a tap or even heart-shaped root with deep-reaching lateral roots, which provide stability. The bark contains resin canals, is smooth, whitish-grey, becoming longitudinally fissured, and darker grey. The wood is yellowish-white, with sharply defined annual rings, without resin canals. The annual shoots are smooth and brown with distinct dark hairs. The buds are ovate, brown, and without resin. The needles grow in two rows, covering the shoot on fruiting branches. They are 18-30 mm long, about 2 mm wide, flat, dark green above, glossy with two pale bands of stomata below, usually slightly notched at the tip, and rounded to pointed on fruiting branches. Male strobili are 2 cm long and 0.6 cm wide, greenish-yellow, primarily on the margins of the mid to lower part of the crown, at the base of the previous season's branch twigs. Female strobili are 2.5–4.5 cm long and 1–1.5 cm wide, greenish-yellow to red, borne on uppermost branches on the previous season's branch twigs. Fir cones are 10–18 × 3–5 cm, erect. Initially, the cones are greenish to bluish in color, brown when ripe, each scale with an exserted bract, usually turned down and pressed to the scales. The seed is 7-10 mm long, triangular, glossy brown, and the wing is broad and asymmetrical. Flowering in April-May, the cones ripen during September in the first year. Fir has a lifespan of 300-600 years [3,18,39–42].

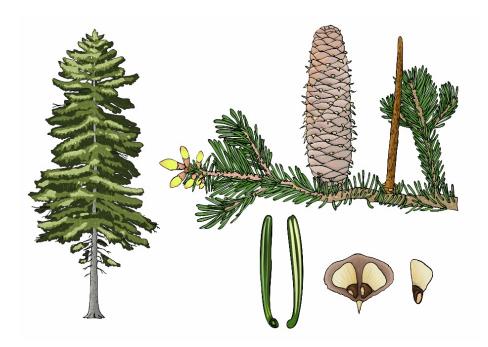


Figure 1. Tree habitus, branch with cones, needle, and scales with the seed of silver fir (Abies alba Mill.).

Silver fir grows primarily in Central and Southern Europe. Its distribution range is relatively small, divided into larger and smaller areas, but its potential range is significantly larger (Figure 2). In the south, it grows from the Pyrenees through Corsica, Southern Italy, and Macedonia to Bulgaria and Greece. Its southernmost limit is in the Southern Apennine Peninsula in Calabria, while the westernmost range closes up in the Eastern Pyrenees, where it also forms the upper boundary of the forest. Further west, there is a small isolated area in the Normandy hills of northwest France and another in central France. A more continuous distribution begins in the western foothills of the Alps in eastern France and the Jura, Vosges, and German Black Forest. The northern boundary of the fir goes through the Weser Uplands in northwestern Germany, the Thuringian Forest, the foothills of the Ore Mountains (Krušné hory), and the Giant Mountains (Krkonoše), on through the Malopolska and Lublin Uplands in Poland. It reaches its northern limit near Warsaw and in the Białowieża Forest. The eastern boundary continues into the Eastern and Southern Carpathians. Inside the Alpine system and in the Tatra Mountains, it grows sparsely. However, silver fir also occurs in the lowlands, for example in France, Poland, and Ukraine [2,3,18,25,40,42-44]. It is the leading co-dominant tree, primarily in the forest altitudinal zones 4–6 400–1200 m a.s.l.; [45]. In these typical fir habitats, it forms mixed forests together with European beech (Fagus sylvatica L.) and Norway spruce (Picea abies [L.] Karst.), characterized by a complicated internal structure, the so-called Hercynian mixtures [46–48]. Montane forests, composed of these three tree species, cover a total area of more than 10 million hectares in Europe [49].

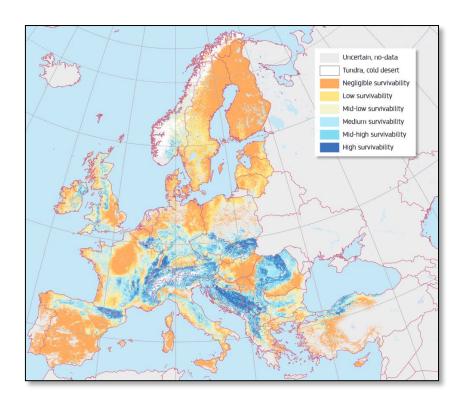


Figure 2. Map showing the maximum habitat suitability for silver fir (Abies alba Mill.) in Europe [3].

3. Ecological Requirements and Production

Abies alba prefers a predominantly oceanic temperate cool and humid climate with mild winters, ideally like the continental climate in Poland. It grows from 135 to 2900 m above sea level [39]. Firbeech forests in the central part of its distribution range are considered the optimal habitats for silver fir, i.e., to the south from Czechia, at altitudes of about 800–1200 m a.s.l., with precipitation of 1000 mm or more [40,50]. At lower altitudes, silver fir occurs in cooler and wetter basins and also on alluvial plains at the northern boundary of its range [51]. Severe and dry winters and dry, hot summers are unsuitable for fir. It is sensitive to late frosts [18,40,42,52].

The silver fir is a tree species that could benefit from the anticipated climate change, especially in terms of dispersal to higher altitudes with sufficient precipitation, except in areas with severe winters [25,47,53]. However, it has considerable moisture requirements and is one of the species with the highest air humidity requirements. The minimum precipitation varies between 500–1000 mm, the optimum is 1000–2500 mm, and the need for precipitation increases from north to south. An exception is the relatively xerophilous relict intra-alpine ecotype in the canton of Wallis (southwestern Switzerland), in an area with low annual precipitation of 400–550 mm, of which only about 270 mm comes during the summer [15,16].

The fir is known for its ability to tolerate shade for several decades [54]. Fir undergrowth can grow in heavy shade for as long as 120 years, with a height of only 1–2 m. Its light requirements are influenced by a complex of other climatic factors (heat, precipitation, soil moisture, humidity, and airflow) and soil factors. The more favorable the habitat conditions, the lower the light requirements of the fir. In contrast, at cooler, higher elevations or on drier and mineral-poor soils, even at the lower limit of its range, the light requirements of fir trees are significantly higher [15,16]. Fir grows primarily on deeper, moderately fertile to rich, moist to waterlogged soils. However, it can adapt and grow on stony or peaty soils. In some areas, its optimal habitat is limestone (Western Alps, Jura). There is no equivalent substitute for this tree species on heavier loess soils, especially on planosols at mid and higher altitudes [16,50]. In mixed forest stands, the addition of fir needles stimulates the formation of desirable forms of humus and, with regard to the penetration of root systems into deeper soil layers, especially compared to spruce, fir positively influences soil properties and stand stability [55]. In

mixtures, silver fir also positively contributes to creating and maintaining a desirable stand environment, especially considering that it can thrive as a component of the lower layer for a long time. It helps balance extremes in temperature, humidity, and airflow limitation [53].

Silver fir is a high biomass producing tree species, which is documented by data from numerous growth charts and field measurements. For example, at a mean height of the main stand of 30 m, the roundwood volume reaches 580 m³ [56]. According to the overview in Table 1, the average volume of mature fir stands ranges from 237–657 m³ ha⁻¹ and the stand basal area from 20.6–70.0 m² ha⁻¹. However, timber processors are not yet able to adequately exploit the high-quality and standard production of fir timber compared to spruce, and therefore, the produced mass is not sufficiently cost efficient. An interesting feature of the change in the timber market during the years of the bark beetle calamity in Czechia (2016–2020) is the fact that the price of fir timber in roundwood assortments has increased significantly and is currently at the same level as that of spruce [57].

Table 1. Overview of selected available publications related to silver fir (*Abies alba* Mill.) production parameters in Europe.

- Parameters in I	aurope.								
Study	Country	Altitude [m a.s.l.]	_	DBH [cm]	Height [m]	Basal area [m² ha-1]	Volume [m³ ha-1]	Density [trees ha ⁻¹]	Climate classificat ion
[58]	Bosnia and Herzegov ina	to 1078	max. 165			28.7– 45.7	274–590	588–732	Dfb
[10]	Croatia	876–978	73–76	28.4– 32.2	19.4– 22.6		227–361		Cfa
[9]	Czechia	660–710	56–146	28.9– 40.7	18.0– 26.0	43.4– 53.3	486–594	336–816	Dfb
[59]	Czechia	940– 1100	158– 189	23.0– 27.0	13.0– 15.0		450-560		Dfb
[60]	Czechia	640-800	68		29-34		333		Dfb
[10]	Czechia	660–790	63–76	25.8– 31.8	21.2– 23.6		346–398		Dfb
[61]	Czechia	330	45	18.0– 22.0	17.0– 19.0		164–372	714–1042	Cfb
[8]	Czechia	670–730	108– 126	15.4– 34.9	22.8– 37.6	20.6– 43.5	237–598	456–1624	Dfb
[62]	Italy	1200	max. 130			35.0– 45.9	336–356	1175– 1215	Cfb/Csb
[10]	Italy	944– 1324	66–75	23.0– 28.1	18.7– 25.4		220–289		Csb
[63]	Poland	337–889	40–115	15.9– 46.5	14.1– 31.5	35.5– 43.8	322–657	211–1852	Cfb/Dfb
[64]	Poland	550-600	68–78	24.6– 30.0	24.9– 25.5	27.6– 37.9	362–533	569–752	Dfb
[65]	Poland	300–725	40–150	21.0– 39.0	27.3– 31.0	34.0– 70.0		382–715	Cfb/Dfb
[66]	Poland	194	60	33.1	22.2		301	378	Cfb
[8]	Poland	520	124	34.5	35.2	43.3	591	464	Dfb
[67]	Romania	700–950	100– 130	7.6–45.0	5.8–31.6	35.0– 45.0	299		Dfb
[68]	Slovenia	850	108– 132			33.4		207	Dfb

[(0]	Ukraine	750-	04 122	36.0-	28.0-	224 FEO	Da
[69]	Ukraine	1045	94–132	48.0	30.0	324–550	Dfb

Notes: climate classification according to Köppen [70]: Cfa—humid subtropical climate, Cfb—oceanic climate, Csb—warm-summer Mediterranean climate, Dfb—warm-summer humid continental climate.

Fir is the slowest growing tree species in the first 10–15 years compared to beech and spruce, although it can tolerate the lack of light for a long time. Therefore, it can only succeed in the regeneration if it has a time lag of at least 15–20 years over other tree species that are more vigorous in their youth [71,72]. Another prerequisite for its successful growth is sufficiently differentiated stands in which fir can maintain a long crown [9,73]. Subsequently, the height increment of fir accelerates until around year 15, peaks at 30–40(–70) years or much later in unfavorable conditions, and persists for over 100 years. Volume increment peaks at around 55–65 years, i.e., relatively late [40]. As a result of climate change, a significant increase in annual volumetric increment of fir trees, from 7.2 to 11.3 m 3 ha $^{-1}$ y $^{-1}$, has been recorded in Europe from 1980–2010 [49].

Fir's ability to tolerate shading and regenerate under it makes fir suitable for multi-layer, allaged stands and for single and group mixed selection forests [4]. In mixed stands, its strengthening function against windthrow and its beneficial effect on the soil is highly valued [55,74]. This is also true in the case of the Hercynian mixture, which used to be the most common composition of natural stands at mid and mountain altitudes in Central Europe. In ravines and on scree, fir mixtures were formed, e.g., with maples (*Acer* spp.), in warmer habitats with European hornbeam (*Carpinus betulus* L.), and in poorer habitats also with Scots pine (*Pinus sylvestris* L.). Limes (*Tilia* spp.), sessile oak (*Quercus petraea* [Matt.] Liebl.), rowan (*Sorbus aucuparia* L.), or hazel (*Corylus avellana* L.) occur as subsidiary species. In the Pyrenees, it accompanies the mountain pine (*Pinus uncinata* Ramon ex DC) on the uppermost border. In other habitats, fir is usually found only as an admixed or interspersed tree species [75]. It maintains its presence here primarily due to its ability to survive in the understory for a long time or its ability to grow on alternately wet and waterlogged soils [9,13,47,76].

In forest stands, fir affects the soil mainly by the quality of litter and its relatively low decomposition rate [64,77,78]. In particular, fast-decomposing deciduous species decay within a few months (C/N ratio = 12–25), whereas it takes several years to slow decomposers, mainly conifers (C/N ratio > 40), including silver fir [79]. Spatial structure also influences soil conditions through litter [80]. The amount of litter is higher under the tree canopy than in the openings [81,82]. Different spatial structure of stands greatly influences thermal, light, and moisture conditions, and thus affects the rate of litter decomposition [83–85]. Stand gaps are characterized not only by increased light, heat, and precipitation but also by faster decomposition of organic litter [86,87] and higher nutrient concentrations in the soil solution [88]. In addition, soil heterogeneity of stands is enhanced by the cluster distribution of concentrated roots and, thus, higher water and nutrient consumption [89,90].

Generally, the success of natural regeneration, apart from ground vegetation [91], depends on the properties of the topsoil horizons [92], which is a condition for seed germination, root development, relationships with soil microflora, and the availability of water and nutrients [85]. Compared to spruce, fir is characterized by a lower acidification capacity and a higher C/N ratio [93]. Třeštík and Podrázský [94] reported a lower (54%) accumulation of forest floor humus in fir stands and significantly higher total nitrogen and calcium contents compared to spruce.

In the natural species composition, fir reached the highest proportion in the ecological series of gleysols and planosols, up to 70%. The groups of forest habitat types include (*Fageto-*) *Abietum variohumidum mesotrophicum*, *Abietum piceosum variohumidum acidophilum*, *Abietum piceosum variohumidum oligotrophicum*, *Abietum quercino-piceosum paludosum mesotrophicum*, and *Abietum quercino-piceosum paludosum oligotrophicum* [50]. In these habitats, fir formed a full spectrum of mixed stands, with beech, spruce, oaks, sycamore maple (*Acer pseudoplatanus* L.), black alder (*Alnus glutinosa* [L.] Gaertn.), silver birch (*Betula pendula* Roth.), European aspen (*Populus tremola* L.), and Scots pine [75]. It is often the main species of montane forest phytocenoses, such as silver fir and European beech (*Abieti-Fagetum*), subcontinental silver fir forests (*Galio-Abietion*), upland fir forests (*Querco-Abietetum*), and slope forests of silver fir (*Abietetum albae*) in Switzerland [95]. It also forms forest phytocenoses with spruce [*Piceetum subalpinum sphagnetosum*; 95].

As a long-lived species, fir is considered an important ecological and functional stabilizer of European forests [3]. It stabilizes soil, retains water, and is less susceptible to snow and ice damage than Norway spruce [7,96,97]. Silver fir is an essential species for maintaining high biodiversity in forest ecosystems due to its tolerance to shade, ability to survive extended periods in the understory and respond when light conditions become more favorable, plasticity to environmental conditions, and ability to coexist with numerous tree species [8,54,98].

Fir is normally the most differentiated tree species in terms of age, height, and diameter, which makes the natural forest with a higher proportion of fir trees close to a selection forest in its structure [99–101]. With a higher representation of beech at the expense of spruce, the regeneration and growth of fir is more continuous, creating a vertical and multi-layered canopy [102]. A higher spruce share creates a typical horizontal fir and spruce canopy at the optimum stage—as a consequence of the fact that the lifespan of trees is longer than the duration of their height growth [103]. The optimum stage, also characterized by stagnation of natural regeneration, usually occupies about 20% of the area of the natural forest, and its duration is expressed in the same period over the entire development cycle, i.e., about 80 years [76,103,104].

At the main level of the stand of both selection and cultural forests, we normally see a gradual rotation of the principal tree species in larger or smaller areas [99,105]. It is clear that especially in forest altitudinal zones 5 and 6, there is a gradual rotation of generations of fir, spruce, and beech in their typical stand mix at the main stand level. This is likely due to the shorter lifespan of beech and its requirements for specific light and soil conditions [46,76,103,106–108].

The interchangeability of tree species in the same stand is also seen in the context of their different light use [47]. Firs primarily use the short-wavelength blue component of the solar spectrum 400–430 nm; [109] and, according to research, are more sensitive to the lack of this component than to the overall reduction in light intensity that occurs in shaded conifer stands [75,99,110]. This fact also explains the better regeneration of firs under spruce than under fir canopy, a historically observed phenomenon [4,52,111]. Since the spontaneous interchange of these two tree species in the same stand cannot be explained by different lifespans (both tree species naturally live to the same age, on the average of 300–400 years, although some firs live up to 500 years), the different use of the components of the solar radiation spectrum is one of the causes of this phenomenon [99].

The competitive abilities of tree species in the mixture also change depending on the soil properties [112]. Acidic soils reduce the vigor of beech, and calcareous soil, the vigor of spruce. With increasing acidity and excessive soil moisture, fir and spruce establish at the beech optimum, while nitrogen-rich soils reduce conifer vigor [46]. According to Ellenberg [113], Tinner and Lotter [114], fir is more competitive than beech in locations with lower temperatures and higher summer rainfall. According to historical records, the abundant summer precipitation is more crucial for fir than low temperatures. For example, in the Insubrian Alps, palaeobotanical studies documented fir dominance that lasted for several millennia before vanishing due to human-induced forest fires. Summer precipitation reached 800 mm, and the average June temperature was 22 °C, 4 °C higher than in Central Europe [114].

In more complex layered stands, where the growth space is fully utilized, the amount and biomass production of the understory (lower story) is inversely influenced by the biomass of the main stand upper stories; [64,115–118]. Changes in the upper story, combined with canopy disturbance, are quickly reflected in a changed light regime of the understory, and, thus, in an increase in its biomass. Hence, the reduction of the canopy, whether natural or artificial, affects the structure and vigor of natural regeneration [71]. In forests of the typical Hercynian mixture of forest altitudinal zones 5 and 6, the requirements of fir, spruce, and beech for light, nutrients, and water, do not differ substantially, while light intensity plays the most important role in growth [47,119,120]. Tree species differ significantly in their ability to survive in the long term under reduced light conditions while maintaining fully functional and efficient photosynthetic processes [121]. Research indicates that fir, an extremely shade-tolerant species, has a distinct competitive advantage, especially over spruce [46,115,120]. This fact is also confirmed by the preserved montane mixed forests of the Romanian Carpathians by Stancioiu and O'Hara [117]. These studied stands lie at an altitude of 800–1300 m

a.s.l., and the age of the main stand is 70–350 years. Their results show that at low light intensity (Percentage of the Above Canopy Light, PACL < 20–35%; BA > 30 m² ha $^{-1}$), fir and beech clearly outgrow spruce, and the latter can even be eliminated from the regeneration as it develops. Under medium light conditions (PACL = 35–70%; BA = 15–35 m² ha $^{-1}$), the growth abilities of all three species are equal, while under open conditions (PACL > 80–90%; BA < 15–20 m² ha $^{-1}$), all of the three species show the same development, with the spruce tending to outgrow the other two shade-loving species [117]. Another factor is the reduction in height increment of fir under direct sunlight (PACL > 80–90%) compared to maximum growth when shaded PACL = 50–80%; [117]. The fact that strong interventions into the main stand canopy are more favorable for spruce and beech than for fir has been noted by many authors [99,115,121–124].

Numerous studies confirmed that mixed stands can have higher biomass productivity than monocultures in suitable habitats [107,125–128]. Silver fir and Norway spruce also grew faster in mixed stands than in monocultures, and their complementary effect increased with improved growing conditions, i.e., resource availability or climatic conditions [129–131]. However, an increase in complementarity and productivity can occur in these species if the interactions affect the absorption of photosynthetically active compounds by radiation or light use efficiency [126].

Changes in species composition also cause dissimilarities in growth characteristics and ideal conditions for the initial and subsequent growth of natural regeneration of tree species [71]. In the last 40–60 years, a significant decline of fir in forest stands and its gradual replacement by spruce or dynamically spreading beech has been observed, both in the Hercynian and Carpathian regions [7,8,30,132–137]. Especially in forest altitudinal zones 5 and 6, the predominance of beech regeneration over fir regeneration has been documented. In the well-preserved Dobroč Primeval Forest in Slovakia, the percentage of fir in the regeneration was around 60% in 1935, followed by a significant decline. Korpel [76] reported only a 20% share of fir in the late 1970s and 1980s. This phenomenon has been interpreted as a common substitution of tree species occurring during the development cycle in virgin forests [76,104]. However, the negative influence of game on fir regeneration was evident at the time, and as the regeneration continues to decrease in many areas, this has been assessed as an unnatural and negative development that is unlikely to be reversed naturally within the evolution of the forest stand [8,30,102,132].

4. Threats and Diseases

One of the most striking aspects of the ecology of the silver fir is its recurring decline, observed in Europe since the 1500s [111,138–140]. The rapid decline of fir in Central Europe has been associated primarily with the intensification of human activity in forests and the development of industry [141–145]. However, data on fir dieback dates from well before the mass industrial expansion of the 20th century [8,9,13,25,99,146–148]. Fir dieback and its problematic natural regeneration have been observed from the 1960s to the 1990s. The decline was first interpreted as a marginal effect of the natural range of fir [149], but in the 1970s and 1980s, fir dieback of varying intensity was observed across the entire natural range of the species [139,150]. While the exact cause of silver fir dieback has not yet been established, it is generally believed to be a combination of abiotic, biotic, and anthropogenic factors [8,96,151,152].

Very sensitive to air pollution [153,154], fir was believed to be in decline due to its subsequent stress [9,26,27,52,151,155–157]. In particular, SO₂ pollution was a critical factor in the decline of silver fir in the 20th century [151]. The worsening situation was reflected in reduced growth and increased tree mortality [5,151]. There were predictions that silver fir would eventually experience general dieback due to air pollution [158], but in the interim, SO₂ concentrations declined significantly. In Europe, SO₂ emissions peaked in the early 1980s and from that point until 1995, decreased by 50% [159,160], which triggered a rapid recovery in fir growth and vigor [26,38,161].

When the air pollution decreased, fir stands regenerate, even in the most affected areas [7,8,30,148,151]. According to Bošel'a et al. [26], Bountgen et al. [38], and Mikulenka et al. [9], this was due to the combination of air pollution reduction and an increase in temperature. Bošel'a et al. [26] cited that the most significant factors which positively affect radial growth in the four regions of the

Western Carpathians are the reduction in air concentrations of SO_2 and NO_3 and an increase in temperature in April, June, and July. Although there are differences between the areas in all four regions, a rapid acceleration of the increment in the last two to three decades was observed, reaching values between 150 and 300% compared to previous periods. Similarly, in the forests of the Sudeten system, there has been a significant regeneration of silver fir since the high annual SO_2 concentrations (30–50 μ g.m⁻³) subsided [148,162,163].

In recent years, silver fir has increased its dominance in Pyrenean forests, in some mixed forests in Spain [164,165], and in other European forests [59]. However, some studies suggest a different response of silver fir along the borders of its natural range [166]. The retreat of silver fir from warmer and drier areas has been observed in Slovenia, especially in fragmented forests and at the limits of fir's distribution range [167]. Its dieback is often attributed to climate change [27,35,36,168–171]. The negative impact of climate warming has been observed in southwestern Europe [2], chiefly in the Mediterranean region, where the decline of silver fir is related to increased aridity [161]. In particular, warm summers and recurrent drought have had a significant impact on the health of silver firs [2,36–38,172]. Also, the narrow genetic variation of silver fir in Europe may have limited its adaptability to current conditions [139,173–175].

However, pathogens and insect pests can also contribute to the loss of vitality and increase the susceptibility of fir to subsequent stress. Infestation by bark beetles (*Pityographus pityographus* Ratz.; *Pityokteines vorontzovi* Jac.; *Pityokteines spinidens* Reitt.) has been observed in southern France, which could partly explain the high mortality [176,177]. The decline of firs during the period of the ecological calamity has often been associated with the damage to fir stands by the silver fir woolly aphid (*Dreyfusia normannianae*) and balsam woolly aphid *Dreyfusia piceae*; [178,179]. In the northern Carpathians (Czechia, Slovakia), Slovenia, and Croatia, silver fir has declined due to the spread of beech and, to a lesser extent, Norway spruce, and due to the failed regeneration as a result of the cloven-hoofed game population increase [8,30,102,132,167,180,181]. The retreat of silver fir from natural fir stands, as well as from artificial regeneration, is aggravated in many locations by game-induced damage through bud browsing, bark stripping, browsing, and fraying [8,29,30,32–34,182–184]. Table 2 clearly shows the high attractiveness of silver fir in terms of bud browsing damage (49%) across Europe. Higher damage in montane forests was also recorded for rowan (57%) and sycamore (57%) compared to minimal damage in Scots pine (5%) and Norway spruce (12%).

Table 2. Overview of selected available publications related to the proportion of browsing damage (%) in selected tree species with an emphasis on silver fir (*Abies alba* Mill.).

Study	Country	Climate classification	Altitude	Fir	Beech	Spruce	Rowa n	Maple	Ash	Pine
[185]	Czechia	Dfb	450-1033	41	16	14	31	22	42	0
[186]	Czechia	Dfb	1000– 1257	8	44	0	35	64		
[187]	Czechia	Dfb	725–765	36	12	3	57	100		
[59]	Czechia	Dfb	940-1100	100	78	48	76	91		
[8]	Czechia	Dfb	520-730	88	30	9				
[102]	Czechia	Dfb	740-920	100	56	18	94			
[31]	Czechia	Dfb	420-440	53	23	25	50	34	23	
[188]	Czechia	Dfb	640-810	68	6	2	82	100		
[182]	Italy	Dfc/Dfb	900-2300	42		14				2
[189]	Italy	Dfc/Dfb	800-2500	41	15	13	46	46	39	14
[190]	Poland	Dfb	223-364	19	15			48		
[191]	Poland	Dfb	800-1600	33	1	1	40	39		
[192]	Switzerlan d	Dfc/Dfb	380-3000	6	3	1	62	29	19	
Mean				49	25	12	57	57	31	5

Notes: climate classification according to Köppen [70]: Dfb—warm-summer humid continental climate, Dfc—subarctic climate.

One of the most serious threats not only to fir stands but to all conifers is the removal of bark from the tree trunks by cloven-hoofed animals (browsing and bark stripping), which happens at a very young age. As a result of this damage, not only is the vascular cambium disrupted, but above all, the quality of the timber is compromised by secondary infestation with fungal pathogens and the development of stem rot. This is especially true for Norway spruce, whose value as merchantable timber decreases rapidly due to bark damage and subsequent decay [193–198]. In contrast, there is minimal knowledge of the effects and consequences of game-induced bark removal on silver fir. Bazzigher, Schmid [199] and Kohnle, Kändler [200] only report that bark damage in silver fir is less threatening than in Norway spruce, while also suggesting that fir timber is less susceptible to stem rot. However, neither the reasons for the increased susceptibility of Norway spruce to decay nor the mechanisms of resistance of silver fir to the spread of rot and subsequent decay are currently known. Metzler et al. [201] reported that, unlike silver fir, Norway spruce has resin canals, which may be the reason for the spread of fungal pathogens after bark damage by game. Game-induced bark damage to silver fir was partially studied in terms of histological changes by Oven and Torelli [202,203], and concerning growth and vitality by Pach [204–208], who pointed to a decrease in timber quality, reduced vitality and growth of fir trees, and the spread of rot. This rot can manifest itself in timber discoloration, a more advanced level of its development, and even the decomposition of the wood mass (so-called soft rot), which very negatively affects the mechanical stability of the affected stands [209]. Timber discoloration as the initial stage of rot can be the result of fungi, bacteria, and wood reaction to pathogens [194,210-212].

Thus, bark damage is less harmful in silver fir than in Norway spruce, and its timber is also less susceptible to stem rot [200]. Trees damaged by browsing and bark stripping are generally more vulnerable to lack of precipitation, while healthy trees are more responsive to temperature [197,213], which may play a significant role in terms of climate change. Various measures are taken in an attempt to prevent damage to forest stands by wildlife, notably methods of individual or group protection and the use of commercial repellents [214–217]. However, these short-term measures do not address the long-term problem of continuous increase in population density as well as the distribution range of wild ungulates [218,219]. These changes in the population dynamics of ungulates are driven by many factors, including changing climatic conditions [220,221].

Silver fir decay results from the spread of rot through injured bark. *Heterobasidion abietinum* infects primarily silver fir and causes stem rot, particularly in Southern Europe [222–224], where firs are often affected by drought during summer. However, in Central Europe, this fungus does not cause any tangible problems in fir, likely due to more favorable climatic conditions or to the low abundance of this fungus [223,225]. *Phellinus hartigii* occurs on silver firs with injured bark in Central Europe [226,227]; Figure 3.



Figure 3. Intensive, repeated bud browsing by game (left), earlier damage by browsing and bark stripping (middle) and subsequent infestation by *Phellinus hartigii* (right) (Photo: Stanislav Vacek).

Fir stands can also be infested by the hemiparasitic mistletoe (*Viscum album* L.), which attacks a wide range of woody plants [228–230]. This parasite and the subsequent invasion of microorganisms—such as fungi or bacteria—cause mechanical and aesthetic damage to the timber, reducing its increment and commercial value [231–234]. The greatest damage to fir trees by mistletoe occurs at lower elevations with lower annual precipitation [234].

It is also a fact that forests, including fir forests, have always been exposed to natural and anthropogenic disturbances. These play a principal role in the dynamics of forest ecosystems and influence stand structure and regeneration processes. In Europe, wind and fire are the most severe abiotic disturbances [2,235], and insect infestation is the primary driver of biotic disturbance [108]. Silver fir is relatively resistant to wind, snow, and ice storms compared to other dominant tree species, such as Norway spruce. Disturbance regimes in forests dominated by silver fir are characterized by small-scale events, such as a single tree falling, while large-scale events, such as windstorms or forest fires, are rare [236].

5. Impacts of Ongoing Climate Change on the Well-Being of Fir Trees

Ongoing climate change is currently exhibiting widespread impacts on forest ecosystems and, thus, on all forest management, which should adapt to changing conditions. Existing climate models predict an increase in average air temperatures during the 21st century, as well as an increase in the frequency of extreme weather events such as storms, floods, heat waves, and dry periods [108,237– 239]. Appropriate forest management measures include abandoning monocultures, establishing mixed stands, and promoting the cultivation of natural regeneration [240,241]. A large number of studies report positive relationships between species diversity and forest productivity [107,242], and it has also been confirmed that diversity in forest species composition increases resilience to biotic insect pest calamities [240,243]. Therefore, declining forest stands in Central Europe are often replaced by mixtures of tree species in an attempt to adapt forests to climate change [244]. Much of the Central European forest landscape is still dominated by Norway spruce despite its documented susceptibility to drought, wind, bark beetles, etc. Numerous studies from across Central Europe confirm that the area suitable for growing Norway spruce will continue to decrease with ongoing climate change [35], even at higher altitudes [245]. Compared to Norway spruce, silver fir and European beech are less susceptible to short summer droughts [246-248]. Therefore, silver fir and European beech with natural mixtures of other habitat-suitable species have been recommended in many European montane and alpine ranges in Central Europe [245,246]. However, as a result of global climate change, fir is predicted to retreat to higher elevations and northwards [249].

In the present situation, fir is not usually considered a main tree species in most European countries, nor will it be in the future, but only an interspersed or admixed species in mixed stands. In nutrient-rich and gleyed habitats of mid and higher altitudes, a slightly higher proportion of fir is expected due to its ameliorative and stabilizing properties [250]. However, in stands with a high proportion of fir, it is necessary to maintain its share through natural regeneration [9]. When establishing and maintaining its intended proportion in forests, it is imperative to have a thorough knowledge of its specific ecological requirements (especially with regard to the complicated interspecific relationships of the main tree species) and also to use silvicultural practices that ensure its vital and persistent growth and development [9,47,251]. A set of adaptation measures has to be adopted mitigating the negative impacts of climate fluctuations. The issue of forest adaptation to global climate change has long been addressed by many authors [173,244,252–255]. For example, in Czechia, the strategy of adaptation measures to global climate change in forest stands is part of the National Forestry Programme [256]. Adaptation to climate change is broadly defined as "finding solutions to and ensuring preparedness for the adverse effects of climate change, enhancing resilience, taking appropriate action to prevent or minimise the damage such effects can cause and taking advantage of any opportunities that may arise." [257]. It is a set of measures that take into account the variability of climatic conditions, aim to increase the flexibility of forest management, and reduce the risk of damage or destruction of forest stands.

In a rapidly changing environment, living organisms can choose between two strategies for survival: migration to more suitable habitats or local persistence through adaptation [258]. The third option is extinction. These potential strategies apply to trees in forest ecosystems that have limited migratory capabilities, although significant climate change makes them very relevant [259]. Tree populations begin to migrate when existing habitat conditions are unsuitable for survival [260]. Our knowledge of tree migration rates under global climate change is still limited. Yet the differences between observed migration rates and tree habitat displacement rates under ongoing climate change are considerable [261]. Among others, Feurdean et al. [262,263] estimated the maximum migration rate for early successional stages of pioneer trees such as birch, willow, or Scots pine to be 225–540 m yr⁻¹, while for climax trees such as silver fir and European beech, it ranges between 115 and 385 m yr⁻¹ depending on the mode of seed dispersal by wind or animals. Numerous climate change scenarios predict the horizontal spread of up to several kilometers and a vertical spread of up to tens of meters per year [264,265]. For these reasons, tree migration is significantly slower than the rate of forest habitat change [266]. Moreover, the significant forest fragmentation of much of Europe substantially reduces the rate of tree migration [267].

6. Seed Production and Nursery Management in the Context of Climate Change

Fertility in fir stands occurs at about 60 years and is maintained into old age. As a solitary tree, it reproduces at the age of 30 years [268]. Depending on latitude and altitude, fir trees flower from May to mid-July. Seed years occur at two-year intervals at lower altitudes, while at higher altitudes, every 3–5 years [269,270].

The cones mature from September to October. They grow on the upper third of the crown, from where, after the disintegration, the seeds are released by May of the following year [271]. Therefore, the best time to harvest cones is in September, ideally just before they fully ripen while the cones are still intact [272-275]. At this time, the cones contain 30-70% water [272,276] and the seed about 40% [277]. The harvesting period depends on the altitude and the amount of precipitation in a given year. The cones can be harvested as early as mid-August and at higher altitudes as late as October [269,278]. The harvesting period is closely related to the cone-to-seed ratio and the germination capacity of the seed. The later the harvest, the higher the cone-to-seed ratio and germination. A recurrent level of 14% is reported for fir cones [279,280]. If the cones are harvested in August, a 50% cone-to-seed ratio must be considered due to the high water content in the cones. The limit of 14% is reached when harvested just before the cone disintegrates. Standard harvesting in early August results in a coneto-seed ratio of 6-8%, and from mid-September, we reach values of 10-12% [57]. An unseasonable harvesting time is one of the vital factors that can negatively affect seed quality. Seeds are at their highest quality immediately after ripening. Fir seeds should be collected at morphological (hard) maturity, which precedes physiological maturity when the seeds can germinate [276]. Fir cones are usually collected manually by picking from standing or felled trees [281] or from seed orchards established for this purpose [282]. The best way to harvest them is to stretch tarps underneath the crowns and shake the disintegrating cones down on them. Using Czechia as an example, the expanding production of silver fir seed material points to rising demand for fir seed material in the context of an increased need for seedlings for reforestation of large clearings following the 2017–2019 bark beetle calamity [283]; Table 3.

Table 3. Production of seed material, estimated weight of seed (in kg) (cone-to-seed ratio of 10%) and average seedling yield, according to the standard of the silver fir quantity in Czechia in 2010–2022.

Year	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Productio													
n (thous.	42.1	59.0	30.5	95.3	7.7	48.6	19.5	15.2	79.0	5.9	115.7	42.7	134.5
kg)													
Seed													
amount	4.2	5.9	3.1	9.5	0.8	4.9	1.9	1.5	7.9	0.6	11.6	4.3	13.4
(thous.	4.2	3.9	3.1	9.3	0.0	4.7	1.9	1.5	7.9	0.0	11.0	4.5	13.4
kg)													
Seedling													
numbers	12.6	17.7	9.2	28.6	2.3	14.6	5.8	4.6	23.7	1.8	34.7	12.8	40.3
(mil. pcs)													

In Czechia, the trend in artificial regeneration fluctuated at 4.8% for 2010–2022. Table 2 shows that fir reproductive material can be used for the regeneration of approximately 5000 ha per year. The annual regeneration of fir in Czechia ranges from 872 to 1635 ha per year. These figures show a substantial overproduction and the supply of other EU member states with silver fir reproductive material. The productivity of stands under ongoing global climate change is highly variable across various locations in Czechia. The need for collecting high-quality reproduction material is constantly increasing [11].

Seed quality is influenced by the forest altitudinal zone, which reflects the amount of precipitation and air temperature during the growing season. The highest seed quality in Czechia was recorded in forest altitudinal zones 2 and 3 (200–500 m a.s.l.), where water-affected habitats suitable for fir are often found [284]. The germination of fir seeds, which depends on provenance and

pre-sowing preparation [285,286], is generally low, around 40% [287,288], and on the southern border of the distribution range, it is even lower, reaching only ca. 28% [289]. Bezděčková and Řezníčková [285] tested the effect of two temperature regimes (constant and alternating) on the germination of fir seeds for different time spans of stratification. However, the authors did not observe a significant effect of temperature on germination, as seeds stratified for 3 to 4 weeks at 3 °C germinated better at 20/30 °C (alternating temperature) than at 20 °C. Long-term storage of fir seeds is accomplished by gradually reducing the water content in the seeds to 9–11% and storing them at –8 to –15 °C in cooling boxes [280].

Seedlings are usually grown from substrate sowings at $pH_{(KCI)} = 6.0 \pm 0.2$ [290], while the most suitable for nursing bare-rooted seedlings are soil-based substrates, and for growing of containerized planting stock, there are the peat-based substrates [291]. To increase the quality of the planting stock and its survival rate after planting, inoculation with ectomycorrhizal fungi is recommended [292], e.g., genus Lactarius spp. [293,294]. However, sowing can also be performed on mineral soils and is generally implemented in the autumn when natural stratification occurs in the seed. If sowing is carried out in spring, e.g., to avoid spring frosts, it is essential to stratify the seed artificially. Without this step, germination is significantly reduced [295]. Fir seed is usually stratified at a temperature of 3-5 °C for 21 days [279,280]. Fir seedlings are susceptible to late frosts upon emerging from the ground, and their hardiness varies depending on provenance [296]. Furthermore, they need constant moisture and sufficient shading to maintain their physiological quality [297]. In the first year, the above-ground part usually grows to a height of 5 cm. A good quality seedling with sufficient dimensions for nursery production is rarely produced in the first year. In the second year of life, it usually grows to 8–15(25) cm [278]. The sowing rate is determined by the quality of the seed (purity and germination capacity) and the targeted maturity of the seedlings and ranges from 0.15–0.23 kg m⁻² [57].

The standard method of producing bare-rooted fir seedlings is in nurseries. Better growth and vigor of planting stock have been observed in a shaded bed [297]. Fir seedlings typically receive two, sometimes three years of nursing [298]. There are no significant losses following transplanting if all agrotechnical deadlines and precautions are observed [299]. Seedlings from the substrate and mineral soil can be plucked manually or mechanically when broadcast-sown in mineral soil. The collection period is usually March–April. In busy nursery schedules, seedling retrieval from soil can be even done in January and February in mild winters, as long as the soil is warm and there is no risk of excessive root hair damage [299,300].

The individual manual reduction of the root systems of seedlings is another salient point of the silvicultural technology for the after-cultivation of seedlings in containters. Frequently, the root systems are reduced by up to 50%. Along with the reduction in the taproot length, other roots are also shortened. The individual reduction of root systems involves both the skeletal roots and the fine fascicular roots growing from the removed parts of the root framework. This reduction prevents root deformation and inappropriate root growth after replanting the seedlings into the container and to the bed [300].

In Czechia, the spring plucking is the best option in forest nurseries. Dormant seedlings tolerate handling better, and early plucking is absolutely necessary for seedlings intended for storage. It is not advisable to pick up seedlings and saplings from frozen or excessively wet soil [301]. Before picking up, it is necessary to check the health of the planting material, i.e., to watch for the occurrence of quarantine pests, or apply chemical, cultural, and biological pest control [301,302]. This is recommended primarily for seedlings intended for storage [301], which needs temperatures just above or below freezing [303]. Early and sufficient irrigation (watering of seedlings) or treatment of above-ground parts of seedlings with antitranspirants is also recommended [301] and can increase the survival of containerized seedlings up to over 90%, as in the case of Japanese larch [304]. The roots must be protected after plucking (established, covered, and containerized) immediately after retrieval from the bed [onto a moist substrate or soft foam at the bottom of the crates; 301], possibly treated with antidesiccants [305].

The standard period for growing bare-rooted silver fir seedlings is five years, or seven years, in the case of large-sized plants [306]. In response to the accelerated need for seedlings, a revolutionary method of growing fir trees on an air cushion in a shorter time has been developed [307]. Stratified seed is sown directly into seedling trays with a small cell size (20–50 ml). After one year, the seedling is placed into a standard-size container, usually 200–330 ml, where, as a biennial seedling with an arranged root system, it reaches a height of 10–25 cm. The plantable part of the production is shipped at this age, and the remaining seedlings are kept in the containers for another year, where they usually reach a height of 20–50 cm [299].

The critical stage in growing planting stock is between picking it up from the nursery to the moment of planting. Inadequate protection from weather conditions often results in irreversible damage to seedlings, leading to death or severely reduced growth [308–310].

7. Close-to-Nature Silvicultural Methods in the Context of Climate Change

The most crucial factors for fir regeneration, its survival for advanced growths and further development are suitable habitat, light, soil, and air humidity. For the light requirements of fir, Jaworski [311] states that seedlings emerge at light intensities of 1-5% of maximum light. They require at least 5% of maximum light to survive until the following year. Up to the age of 15, optimum conditions for fir are 15-25% of maximum light. In the shade, growth is suspended, and saplings tend to form a flat crown [312]. Its emergence in the third year of life is an indicator of adequate light conditions of the regenerating stand. For the next 10 to 20 years, the height growth of the fir remains relatively low. When a height of about 50 to 80 cm is reached, illumination should be increased by slow, gradual opening of the parent stand, thus initiating height increment. The transition to full release must be slow and smooth [313]. The critical consequences of changes in the growth rhythm of trees in Saxony were addressed by Meyer [111], who searched for causes of fir dieback at the northern limit of its distribution. Informed by numerous analyses of fir trunks with normal crowns and growth dependencies based on Backman's function, Meyer derived the course of a "normal development line" [314]. He did the same for diseased and poorly growing fir trees. From the developmental line of healthy and diseased trees, he concluded that the development of all healthy trees was slower in youth than that of diseased trees with deformed crowns. This implies that fir trees in the studied same-aged stands did not experience a period of suppressed growth in their youth. Too rapidly releasing growth and even stimulating seedling growth already in the nursery alters the growth course of fir trees in the early years of development [47,315]. This presumably sets a specific growth rhythm of fir trees, whereby, as a shade tree, they respond to altered conditions. It is possible that in this way, a climax tree can become a pioneer tree, i.e., with an altered growth rhythm in youth and early maturation, but also with premature senescence and a smaller final wood mass. A violent change in the development can cause reduced resistance, increased susceptibility to diseases, and a likely change in hereditary characteristics [314].

In natural conditions, the fir can tolerate long periods of oppression without weakening their vital energy. However, firs which evolved in clear-cut forests for several generations did not experience a long-term shelter from the parent stand, i.e., changed their nature and required increased illumination from the beginning of their growth. If they are suddenly exposed to the oppression of the shelterwood for a longer period, they fail to adapt and become critically weakened [99]. Annual-ring analyses indicate that withering firs with dried-out crowns and a more pronounced decline in recent increment generally showed significantly higher diameter increment in their youth than relatively healthier firs with less weathered crowns in the same stand [148,316]. This implies a greater threat to fir trees that were released more rapidly in youth than those that were gradually thinned and experienced slower development.

In close connection with light, fir's requirements for the other component of radiation—heat—must be considered. From this point of view, fir is a relatively demanding tree species, especially when compared to spruce [99]. Because fir assimilates well in the shade, it also requires a reasonable moisture regime, as it transpires more and has a higher demand for CO₂ and water. Higher transpiration is predominantly characteristic of self-seeding firs. They transpire more than older trees

[317,318]. Therefore, its regeneration and quality growth depend not only on light but also on the soil and air humidity, and—above all—sufficient precipitation during the growing season, at least 350 to 400 mm [313]. Firs are susceptible to short-term droughts, severe winters, late frosts, and air currents [319,320]. Therefore, fir can be considered one of the most sensitive and demanding coniferous tree species because, in addition to the already mentioned requirements for light, moisture, and heat, it needs deep, nutrient-rich, loose soils with sufficient water in the upper soil layers for successful growth, preferably around springs in flat terrain, on slopes with water-holding soil, and generally on sites influenced by water [50,321,322].

Regarding silvicultural practices, fir is not suitable for the clear-cut management method with artificial regeneration, which was widespread in Central Europe in the past [73,102,152,323,324]. Contrarily, shelterwood, selection, or even border (group) management methods are suitable [4,8,187,325,326] or as underplanting under pioneer tree species in the restoration of salvage clearings [327].

Silver fir stands, especially in forests with rich structures, cannot be effectively managed without a thorough understanding of the ecological requirements of the tree species represented and their specific responses to climate change [328]. In particular, the combination of shade-tolerant tree species, fir, beech, and spruce creates good conditions for stable stand formation, even under anticipated climate change [20,329]. Yet, the optimal representation of these tree species under the given habitat conditions is crucial [251]. At the same time, their cenotic position and the morphological and physiological differences of trees of different dimensions and levels are important, which is reflected in their growth rhythms and responses to climate change [245,330–332]. In the context of climate change, and particularly, the increasing drought, fir can be expected to replace spruce in many locations [333] unless subjected to extreme climatic conditions [334]. This is because the surface root system of spruce does not allow drawing water from greater depths, as is the case for fir or beech [335,336]. Mixing different tree species in structured stands allows for more efficient use of different resources, such as water nutrients, which can ultimately reduce the stress of individual tree species and enhance the resilience of the entire stand [329,337]. Fir has locally been observed to shift to the sub levels, in both managed and unmanaged stands [8,135,136]. Dominant trees are generally considered more susceptible to drought [332]. In addition to dominant spruces, Vencurik et al. [251] also report a negative effect of drought in subdominant trees in the late summer of the current year.

From the perspective of future forest management principles, it is therefore essential to know the forest types that will be most suitable in terms of their species, age, and spatial composition under future climatic conditions [108,213,338]. On the one hand, this is very difficult to determine under the increasing pressure of rapid climate change [339]. On the other hand, forest conversion and management measures to increase the ecological stability and adaptability of forest stands have been underway for quite a long time in many places [108,187,188,340,341].

8. Conclusions

Silver fir, due to its relative resistance to abiotic and biotic factors, may play a crucial role in the future tree species composition of Central European forests compared to declining stands of Norway spruce. This greater importance is also reflected in an increasing share of fir in forest regeneration. Due to its character, shade-loving nature, and adaptability, it has great potential to fulfil both productive and non-productive forest functions in mountain areas and on water-influenced habitats at lower altitudes. Adaptive management favors the establishment of structurally differentiated mixed stands with silver fir. In close-to-nature silviculture (small-scale shelterwood and selection management methods), it is necessary to promote structural differentiation of stands and to achieve not only higher production potential but also increased stability and biodiversity of these forest ecosystems by cultivating mixed forests. In particular, silver fir, beech, and spruce represent an ideal type of mixture due to the combination of deciduous and coniferous species with different ecological requirements and different root system morphologies. However, natural regeneration and its

subsequent successful growth are impossible without the combined principles of active silvicultural and hunting management.

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