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Impact of stand structural diversity on natural regeneration and drought resilience in silver fir (*Abies alba* Mill.) dominated European mountain forests

Wpływ zróżnicowania strukturalnego drzewostanów z dominacją jodły pospolitej (*Abies alba* Mill.) na odnowienie naturalne oraz odporność na suszę w lasach górskich Europy

Doctoral thesis

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Table of contents

List of articles comprising the thesis

Article 1: **Kolisnyk, B**., Brzeziecki, B., Jankowski, P., Drozdowski, S., & Bielak, K. (2024a). Linking the quantitative and qualitative approaches to assessing tree size diversity using silver fir (*Abies alba* Mill.) stands in the Zagnańsk Forest District. Sylwan, 168, Article 12. https://doi.org/10.26202/sylwan.2024057

(Ministerial score: 70; IF: 0.5)

Article 2: **Kolisnyk, B.**, Wellstein, C., Czacharowski, M., Drozdowski, S., & Bielak, K. (2024b). Contrasting Regeneration Patterns in *Abies alba*-Dominated Stands: Insights from Structurally Diverse Mountain Forests across Europe. Forests, 15, Article 7. https://doi.org/10.3390/f15071182

(Ministerial score: 100; IF: 2.4)

Article 3: **Kolisnyk, B.**, Czacharowski, M., Bingham, L., Wellstein, C., Uhl, E., Drozdowski, S., & Bielak, K. (2025). Tree size diversity can enhance the drought resilience of *Abies alba* Mill. in the European mountain forests. Forest Ecology and Management, 589, 1–14. https://doi.org/10.1016/j.foreco.2025.122765

(Ministerial score: 200; IF: 3.7)

Summary

Impact of stand structural diversity on natural regeneration and drought resilience in silver fir (*Abies alba* Mill.) dominated European mountain forests[*]

Understanding how silvicultural systems and resulting stand structures influence forest ecosystem functioning and stability is crucial amid global change. Although notable progress has recently been made in studying mixed-species stands, uneven-aged silviculture and its effects on forest structure-functioning interactions have received comparatively less attention.

To address this research gap the presented doctoral thesis comprises three thematically related, published scientific articles, examining: (i) how different silvicultural systems (even- *versus* uneven-aged) shape tree size diversity and how it can be quantified; (ii) how tree size diversity influences natural regeneration; and (iii) how it affects the drought resilience of silver fir (*Abies alba* Mill.) in European mountain forests.

To address the formulated questions, we established a network of 139 circular research plots (0.05 ha each) across four sites located in Poland (Zagnańsk - PL1, Nawojowa - PL2), Italy (Tissens-Laurein - IT1), and Germany (Inzell - GE1), spanning a broad climatic gradient within the natural range of silver fir. The methodological framework encompassed data acquisition in both field and laboratory settings, including standard dendrometric measurements, as well as the extraction, preparation, and cross-dating of increment cores from approximately 600 trees. Subsequently, multiple metrics were calculated to characterize stand structure, climatic conditions, natural regeneration, and growth responses to drought, followed by statistical analyses to explore the underlying patterns of how these factors interact.

The first article focused on identifying a robust set of indices for the objective quantification of tree size diversity, which were subsequently used in the following papers. Fifty-four variations of distance-independent indices were evaluated based on their agreement with forestry experts' perceptual assessments of tree size diversity at site PL1, based on a structured questionnaire. Shannon diversity and evenness indices, particularly those based on tree height classes and basal area as a proxy of the share of trees in the class, as well as Kurtosis and Skewness of the diameter at breast height distribution, exhibited the strongest correlations with experts' evaluations. The indices

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were discussed from ecological and silvicultural perspectives, with practical recommendations provided for their application. The study highlights the need to bridge the gap between mathematical concepts and applied close-to-nature silviculture.

The second article examined the influence of silvicultural systems and the resulting diversity on natural regeneration. The uneven-aged stands had a higher probability of regeneration, particularly at sites with lower average annual temperatures and lower overall regeneration density (such as IT1). Higher stocking density reduced regeneration density across all species, with the exception of silver fir. The admixture of broadleaf species (mainly European beech (*Fagus sylvatica* L.)) slightly decreased regeneration density at more water-limited sites (PL1, PL2, and IT1), but significantly increased it under water-rich conditions (GE1). Notably, greater tree size diversity in uneven-aged stands promoted the progression of regeneration from juvenile to more advanced developmental stages, especially under more water-limited conditions. These findings highlight the importance of site-adapted forest management and stand structure as essential tools to support natural regeneration, which is a key process in ensuring forest sustainability.

The third article explored how tree size diversity influences the growth resilience of silver fir to drought stress, based on increment cores and a set of complementary resilience indices proposed by Lloret et al. (2011), as well as additional indices developed in this study. At more water-limited sites (e.g., PL1), as indicated by the Forest Aridity Index, greater tree size diversity improved drought resistance and stress-driven deviation from normal growth variability, while this relationship weakened (PL2, IT1) or reversed (GE1) in more humid conditions. Similarly, smaller trees performed better under drought stress in more water-limited sites, though this effect flattened or reversed with increasing climate humidity. Broadleaf species admixture and stocking density had no modifying effect on the observed patterns. These findings are consistent with the stress-gradient hypothesis, which suggests that facilitative interactions among plants become more prominent under harsher environmental conditions.

In conclusion, uneven-aged silviculture, by fostering stand structural diversification, can enhance the natural regeneration potential and improve the drought resilience of silver fir, particularly in more water-limited environments. Promoting tree size diversity can therefore be considered a strategic silvicultural tool to support forest adaptation to the ongoing climate change.

Keywords: climate change adaptation, forest resilience, growth limiting factors, mountain mixed forests, uneven-aged silviculture

Streszczenie

Wpływ zróżnicowania strukturalnego drzewostanów z dominacją jodły pospolitej (*Abies alba* Mill.) na odnowienie naturalne oraz odporność na suszę w lasach górskich Europy[*]

Poznanie zależności między zróżnicowaniem strukturalnym drzewostanów, kształtowanym przez różne sposoby zagospodarowania lasu, a funkcjonowaniem i stabilnością ekosystemów leśnych jest kluczowe w obliczu zachodzących zmian środowiskowych i społecznych. O ile na przestrzeni ostatnich dwóch dekad struktura i dynamika jednogeneracyjnych drzewostanów mieszanych były przedmiotem zainteresowania wielu badaczy, to drzewostany dwu- i wielogeneracyjne oraz ich zróżnicowanie strukturalne rzadko stanowiły obiekt systematycznych i pogłębionych badań.

Celem niniejszej pracy doktorskiej, stanowiącej cykl trzech tematycznie powiązanych artykułów naukowych, było zbadanie: (i) jak różne sposoby zagospodarowania lasu wpływają na stopień zróżnicowania wymiarowego drzew wyrażony za pomocą wybranych wskaźników ilościowych; (ii) jaki wpływ na odnowienie naturalne jodły pospolitej (*Abies alba* Mill.) mają zróżnicowanie wymiarowe drzew oraz różne warunki klimatyczne; oraz (iii) jak wspomniane zróżnicowanie wpływa na odporność tego gatunku na stres związany z suszami atmosferycznymi.

W tym celu założono sieć 139 kołowych powierzchni badawczych (każda o powierzchni 0,05 ha) w Górach Świętokrzyskich (Zagnańsk - PL1), na terenie Beskidu Niskiego (Nawojowa - PL2) oraz Południowych (Tissens-Laurein – IT1) i Północnych Alp Wapiennych (Inzell - GE1). Badane drzewostany reprezentowały gradient zróżnicowania strukturalnego (od jednowiekowych, jednogatunkowych i jednopiętrowych drzewostanów jodłowych, poprzez drzewostany dwugeneracyjne i dwupiętrowe, aż po drzewostany wielogeneracyjne i wielopiętrowe z domieszką głównie buka (*Fagus sylvatica* L.)) oraz różne warunki klimatyczne lasów górskich w Europie. Prace terenowe obejmowały standardowe pomiary dendrometryczne drzew, inwentaryzację odnowień oraz pobranie wywiertów dordzeniowych z prawie 600 drzew. W ramach prac kameralnych obliczono szereg parametrów i wskaźników charakteryzujących: zróżnicowanie strukturalne badanych drzewostanów, warunki

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klimatyczne, naturalne odnowienie jodły i innych gatunków łącznie oraz reakcje przyrostowe drzew podczas susz atmosferycznych na przestrzeni ostatnich 20 lat. Otrzymane wyniki poddano analizie statystycznej w celu poznania wzorca zależności między zróżnicowaniem strukturalnym drzewostanów z dominacją jodły oraz warunków klimatycznych na pojawianie się i rozwój odnowień naturalnych oraz odporność tego gatunku na suszę.

Pierwszy artykuł przedstawia zestaw wskaźników ilościowych opisujących stopień zróżnicowania wymiarowego drzew. Na podstawie przeprowadzonego przeglądu literatury wybrano i przeanalizowano łącznie 54 różne warianty wskaźników zróżnicowania wymiarowego, których obliczenie nie wymaga wiedzy na temat przestrzennego położenia drzew względem siebie. Otrzymane wyniki porównano z ocenami ekspertów, którzy na podstawie ustrukturyzowanego formularza zakwalifikowali każdą powierzchnię badawczą na terenie Nadleśnictwa Zagnańsk (PL1) do jednej z pięciu klas zróżnicowania strukturalnego. Najsilniejsze korelacje z ocenami ekspertów uzyskano w przypadku matematycznych wskaźników różnorodności i równomierności Shannona opartych na rozkładach pierśnicowego pola przekroju drzew w klasach wysokości, a także dwóch wskaźników statystycznych: kurtozy i skośności rozkładów grubości. Na tej podstawie, w kolejnych dwóch publikacjach, do modelowania statystycznego wykorzystano wskaźnik różnorodności Shannona oparty na rozkładzie pierśnicowego pola przekroju w 4-metrowych klasach wysokości drzew. Uzyskane wyniki przedyskutowano pod kątem ekologiczno-hodowlanym i właściwego doboru poszczególnych wskaźników w zależności od wielkości próby, celu badawczego oraz kategorii analizowanych drzewostanów. W pracy podkreślono również potrzebę wypełnienia luki pomiędzy wymiernym podejściem matematycznym oraz sztuką hodowli lasu.

Drugi artykuł prezentuje wyniki dotyczące wpływu sposobu zagospodarowania lasu i związanego z tym zróżnicowania wymiarowego, a także efektu domieszki gatunków liściastych oraz zagęszczenia drzewostanu (wyrażonego pierśnicowym polem przekroju), na prawdopodobieństwo pojawiania się odnowień naturalnych oraz ich zagęszczenie. Analizowano również zdolność odnowień do awansu z fazy nalotów do podrostów, z uwzględnieniem zróżnicowanych warunków klimatycznych. Drzewostany wielogeneracyjne o strukturze przerębowej miały wyższe prawdopodobieństwo pojawiania się odnowień naturalnych w stosunku do drzewostanów jednogeneracyjnych, szczególnie w lokalizacjach o niższych średnich temperaturach rocznych i sumarycznym zagęszczeniu odnowień (IT1). Wraz ze wzrostem zagęszczenia drzewostanu zmniejszała się całkowita liczba odnowień, z wyjątkiem odnowień jodłowych. Domieszka gatunków liściastych wpływała negatywnie na zagęszczenie odnowień w położeniach geograficznych z niższą sumą opadów (PL1, PL2 i IT1), podczas gdy w lokalizacji z znacznie większymi opadami (GE1) zanotowano odwrotną zależność. Większe zróżnicowanie wymiarowe drzew w drzewostanach o strukturze przerębowej wpływało korzystnie na zdolność awansu nalotów do fazy podrostów, zwłaszcza w warunkach, w których występują mniejsze opady (np. PL1). Otrzymane wyniki podkreślają znaczenie kształtowania zróżnicowanej struktury drzewostanów dla skutecznego pojawiania się oraz rozwoju odnowień naturalnych, a tym samym dla zapewnienia ciągłości i trwałości badanych drzewostanów.

Trzeci artykuł prezentuje wyniki dotyczące wpływu susz atmosferycznych na reakcje przyrostowe jodły. Zróżnicowanie wymiarowe drzew wpływało pozytywnie na odporność jodły na susze w warunkach większego deficytu wodnego (np. PL1). Efekt ten słabł i stawał się neutralny (PL2, IT1), a nawet negatywny (GE1), wraz z polepszającymi się warunkami pluwialno-termicznymi. Analogicznie, mniejsze drzewa charakteryzowały się wyższą odpornością na susze w porównaniu z większymi drzewami w lokalizacjach z niższymi opadami. Domieszka buka oraz zagęszczenie drzewostanu nie miały istotnego wpływu na zaobserwowane zależności. Uzyskane wyniki potwierdzają słuszność hipotezy zakładającej, że interakcje między roślinami zmieniają się - z pozytywnych (kooperacja) na neutralne lub nawet negatywne (konkurencja) - wzdłuż określonego gradientu stresu środowiskowego (*ang. stress-gradient hypothesis*).

Podsumowując, hodowla zróżnicowanych strukturalnie drzewostanów jodłowych (o budowie przerębowej) z domieszką buka sprzyja zarówno pojawianiu się i rozwojowi odnowień naturalnych, jak i zwiększa odporność tego gatunku na coraz częstsze i bardziej dotkliwe susze. Ma to szczególne znaczenie w lokalizacjach z niższymi sumami opadów. Z tego względu promowanie zróżnicowania wymiarowego drzew w drzewostanach jodłowych należy traktować jako kluczowe narzędzie hodowlane, wspierające adaptację lasów górskich w Europie do zachodzących zmian klimatu.

Słowa kluczowe: adaptacja do zmian klimatu, czynniki ograniczające wzrost, górskie drzewostany mieszane, hodowla drzewostanów różnowiekowych, odporność lasu

1. Introduction

Throughout history, forests have been an essential part of human life, providing shelter, food, fuel, and other critical resources. As human populations expanded, the demand for forest goods and services increased, intensifying pressure on forested ecosystems (Kirby & Watkins, 2015). The concept of limits to growth, introduced by Meadows (1972), postulated that unchecked economic and population growth could ultimately lead to systemic collapse due to the finite nature of Earth's resources. This principle also applies to forests, as utilizing forest resources at rates exceeding their potential recovery endangers long-term sustainability (Schütz, 1998). As early as 1713, Hans Carl von Carlowitz advocated sustainable wood use in *Silvicultura oeconomica*, introducing the term *Nachhaltigkeit*, the origin of sustainable forestry in Europe. Later, Georg Ludwig Hartig and Heinrich Cotta formalized the concept with principles of sustained yield forestry, laying the foundation for modern sustainable forest management (Hartig, 1791; Morgenstern, 2007). Their work established sustainability as a core concept in forestry for decades to come (Morgenstern, 2007).

Since then, the understanding of sustainability in forestry has broadened significantly. No longer limited to timber production, modern forestry increasingly recognizes a multifunctional perspective and the full range of ecosystem services forests provide, including regulating, provisioning, cultural, and supportive services (Bosela et al., 2024; FAO, 2024). This shift is also reflected in the growing adoption of close-to-nature silvicultural principles in recent decades (Bürgi, 2015), an approach with the century long history (Gayer, 1886; Schütz, 1998; Pommerening, 2002; Jaworski, 2018; Bernadzki, 2000), that seeks to emulate natural forest dynamics, structures, and processes while ensuring the continuous provision of ecosystem services (Larsen et al., 2022). Close-to-nature silviculture promotes minimal interventions, continuous forest cover, structurally complex mixed stands, native, climate- and site-adapted species, and the use of natural regeneration to enhance ecological resilience and the long-term stability of forest ecosystems (Schütz, 1998). Those principles are now widely institutionalized and actively promoted at the policy level, including in the EU Forestry Strategy for 2030, as part of the broader EU Green Deal (Lier et al., 2022). In practice, this shift has led to the increasing adoption of mixed-species forestry and continuous cover forestry as an alternative to clear-cutting, resulting in stands with diverse structural organizations (Larsen et al., 2022).

The increasing frequency and severity of extreme climatic events and biotic natural disturbances, including recurrent droughts across Europe, raise important questions about forest stability and the ability of current silvicultural systems to sustain provisioning of ecosystem services under increasing stress (Brodribb et al., 2020; Jankowski et al., 2024; Zhai et al., 2022). This has further strengthened the focus on the resilience and long-term functional integrity of forests worldwide (Brodribb et al., 2020).

Forest resilience is commonly defined as the capacity of an ecosystem to *resist* disturbances and to *recover* its structure and functioning following such events. In this context, resistance refers to the ability of the ecosystem to withstand adverse conditions or major disturbances without degradation. This includes not only the maintenance of physical forest structure but also the continued provisioning of key ecosystem services, including timber production and carbon sequestration. Recovery, on the other hand, refers to the ecosystem's ability to restore its functionality after disturbance, including the rate and trajectory of return to a pre-disturbance or alternative stable state (Holling, 1973; Seidl et al., 2017). A robust bank of natural regeneration plays a pivotal role in recovery by enabling the rapid restoration of forest cover and provisioning of ecosystem services, thus ensuring forest sustainability.

Structural diversity is a fundamental attribute of forest ecosystems, significantly influencing forest ecosystem resilience, which can be shaped by silvicultural interventions. It is commonly characterized by three interrelated components: spatial, species, and tree size diversity (Brzeziecki, 2002; Pommerening, 2002). Numerous ecological theories have explored how forest ecosystems respond to different silvicultural systems and the resulting stand structural diversity, particularly in terms of resilience (Dănescu et al., 2016; Seidl et al., 2017). The role of species mixing has received significant attention in recent years (Pach, 2016; Bauhus et al., 2017; Pretzsch, 2018; Pretzsch & Schütze, 2021). Although species-specific responses to disturbances vary, a broad consensus has emerged that mixed-species stands enhance ecosystem resilience by distributing risks across species with differing susceptibilities to disturbance agents such as host-specific pests and pathogens (Bauhus et al., 2017; Seidl et al., 2017). Furthermore, mixtures of species with contrasting functional traits can improve ecosystem functioning in conditions of resource scarcity through temporal and spatial complementarity and niche partitioning, both above and below ground. This increases resource-use efficiency and can contribute to forest productivity and resilience (Pretzsch, 2014, 2017, 2022). Additionally, species diversity may improve the capacity for rapid natural regeneration after disturbances by supporting heterogeneous seed banks, asynchronous masting years, and diversified microsite conditions (Wang et al., 2017).

Another important component of forest structural complexity is tree size diversity, also referred to as tree size inequality. Tree size diversity refers to the variation in tree sizes, typically diameter or height, within the nearest neighborhood (Brzeziecki, 2002; Pommerening, 2002). It reflects local competitive dynamics, but also disturbance and management legacies (Forrester, 2019). Existing silvicultural systems can produce a broad gradient of tree size diversity, which arbitrarily may be divided into three groups: (i) even-aged stands, characterized by simplified vertical structure and low tree size diversity, typically resulting from clear-cutting or uniform shelterwood fellings; (ii) two-aged or two-layered stands, with intermediate tree size diversity, either as a transitional phase in shelterwood systems or towards uneven-aged structure, but also as a stable structure maintained for functional objectives; and (iii) complex, multi-layered uneven-aged stands, where trees of different sizes and ages coexist in close proximity, resulting in high tree size diversity (Kuuluvainen et al., 2012; Nyland, 2016; O'Hara, 2014).

The effects of management systems and resulting tree size diversity on forest ecosystem resilience and functional stability remain poorly understood (Dănescu et al., 2016; Gazol & Camarero, 2016, p. 201; LaRue et al., 2023). For instance, similar to species mixtures, tree size diversity is believed to influence forest resilience to drought stress and natural regeneration dynamics through vertical and horizontal spatial clustering, resource partitioning, and complementarity among trees of different sizes (Ali, 2019; Forrester, 2019; LaRue et al., 2023). However, empirical evidence remains inconsistent, as the effects of tree size diversity on resilience and natural regeneration vary considerably by site, forest type, biome, and species (Dănescu et al., 2016). These differences are frequently attributed to how limited resources are distributed and accessed by individual trees under different growing conditions (Forrester, 2019). Those competitive dynamics are strongly influenced by species-specific life history traits and, importantly, the social position of the individual tree within the stand (Pretzsch et al., 2012). The system of competitive interactions forms feedback loops where the stand structure influences competition, and competition in turn shapes structural development (Forrester, 2019). In highly heterogeneous forests, especially those with high tree size diversity managed by emulating small-scale disturbances, these relationships become increasingly complex and difficult to quantify (Forrester, 2019). Besides, there is a lack of clear definitions and standardized methods for the quantification of tree size diversity.

While several indices exist, it remains unclear what specific structural aspects they capture, and to what extent they correspond to the qualitative assessments by forest practitioners, who often rely on personal experience and professional judgment in silvicultural decisions.

To address these knowledge gaps, this study focuses on silver fir (*Abies alba* Mill.), one of the most ecologically and economically important conifers in European mountain forests (Dobrowolska et al., 2017). Silver fir exhibits high shade tolerance, morphological plasticity, and relatively strong drought tolerance compared to other montane species such as Norway spruce (*Picea abies* (L.) H.Karst) (Vitali et al., 2017; Zang et al., 2014; Tinner et al., 2013), making it well suited to continuous cover and uneven-aged forest management systems in a changing climate. Although recent extreme events, such as the 2018 drought in Central Europe, have revealed silver fir's sensitivity to prolonged water shortage (Gbur et al., 2025; Schuldt et al., 2020). Therefore, silver fir is a suitable model species for examining how silvicultural systems and stand structure influence forest resilience and natural regeneration.

2. Research hypothesis and objectives

The central hypothesis of this study is that the resilience and functional stability of silver fir-dominated forests in European mountain regions, reflected in the natural regeneration potential and resilience to drought stress, increases along a gradient of tree size diversity, from structurally simplified even-aged stands to more complex uneven-aged stands. Furthermore, this relationship is expected to be influenced by climatic conditions and stand-level characteristics, including the admixture of broadleaved tree species and stocking density.

To test this hypothesis, the study addresses the following objectives:

1) *Quantification of tree size diversity*. To review and evaluate which quantitative indices can be used to depict tree size diversity as a continuous structural variable, to identify the specific aspects of forest structure they capture, and to assess how well these metrics correspond to forestry experts' perception of tree size diversity.
2) *Assessment of natural regeneration potential*. To explore how tree size diversity affects the natural regeneration in silver fir-dominated stands, and whether this relationship is mediated by stand-level characteristics and climatic conditions.
3) *Assessment of growth resilience under drought stress*. To assess how tree size diversity influences the growth resilience of individual silver fir trees under drought stress, and whether this relationship is moderated by stand characteristics, individual tree size, and long-term climatic conditions.

This doctoral thesis, structured as a compilation of three thematically related scientific articles, contributes to a deeper understanding of structural drivers of forest resilience and natural regeneration. It aims to support the development of ecologically informed, adaptive silvicultural strategies for maintaining forest functioning under global environmental changes.

3. Materials and methods

3.1. Study sites

To address the research objectives, a network of 139 circular research plots (each 0.05 ha) was established across four sites in Poland (PL1 and PL2), Italy (IT1), and Germany (GE1), in silver fir-dominated stands on comparable eutrophic site conditions, as defined by the Polish national forest site classification (SPHL, 2004). The selected sites span from the south-west to the north-east of the natural range of silver fir, covering a broad climatic gradient (Fig. 1).

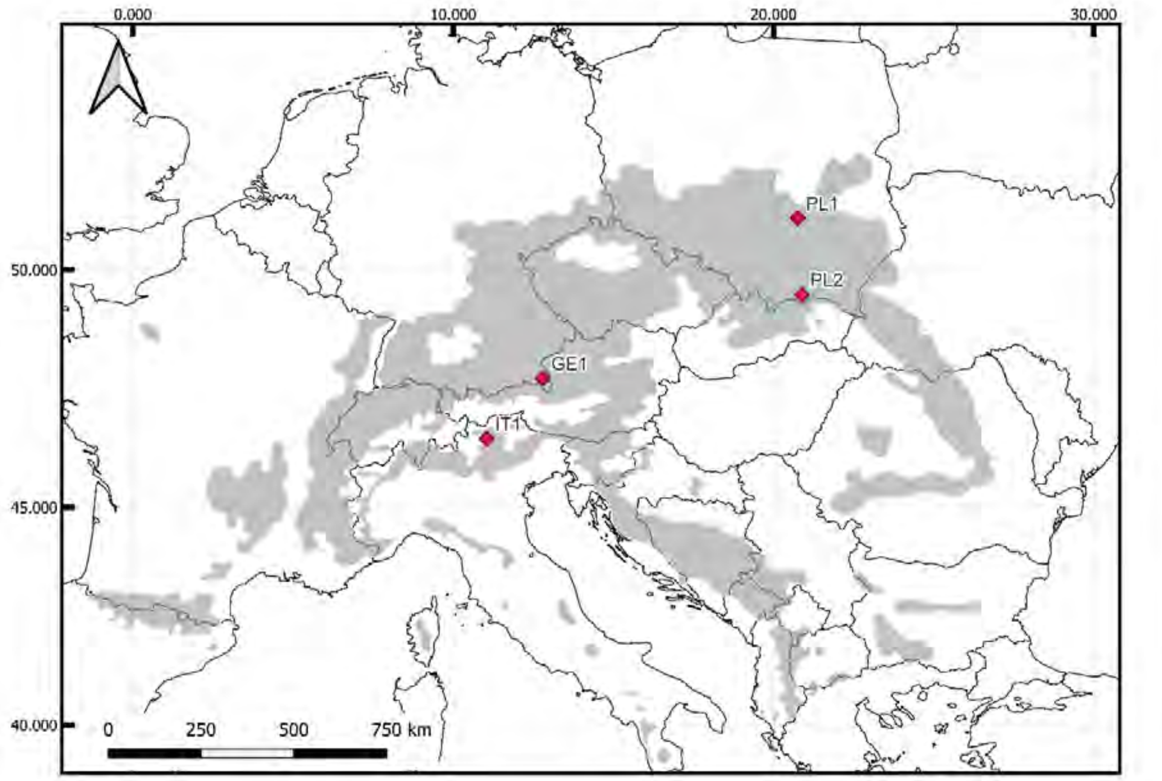

Figure 1. The location of study sites (red rhombi) and distribution of *Abies alba* Mill. in Europe (grey shaded area) (source: https://www.euforgen.org/species). Figure from article 3, Kolisnyk et al., 2025.

PL1 is located at the northeastern boundary of silver fir's natural distribution, in the Zagnańsk Forest District on the outskirts of the Holy Cross Mountains (Fig. 1). As a marginal population limited primarily by water availability, it offers a unique case to study silver fir functioning under strong environmental stress (Bronisz et al., 2010). The site is characterized by relatively low annual precipitation, warm summers, and winters often with unstable snow cover (Table 1).

In contrast, PL2 is in the western part of the Low Beskid Mountains (Fig. 1), within the eastern Carpathian Flysch zone, and is managed by the Nawojowa Forest

District (Bruchwald et al., 2015). It represents optimal conditions for silver fir growth and development, with higher and more evenly distributed precipitation and more stable temperatures due to the typical orographic influence of foothill regions. Winters are cold, usually with snow cover, while summers remain relatively cold and humid.

IT1 is located in the Tisens-Laurein region of South Tyrol, within the Southern Limestone Alps (Fig. 1). The plots are within the mountain mixed forest zone, near the upper elevational boundary of the zone, where broadleaf species are naturally constrained in growth. The site is characterized by low mean annual temperatures and strong intra- and inter-seasonal variability in temperature and precipitation. Heavy snowfall and extended snow cover in winter strongly influence local hydrology, delaying the start of the vegetation while ensuring prolonged soil moisture into the vegetation season.

GE1 is in the Chiemgau Alps, a subrange of the Northern Limestone Alps in the Bavarian Prealps (Fig. 1). This site represents a humid, water-rich environment, shaped by high annual precipitation, snowy but relatively mild winters, and thus moist summers. The research plots are located in the middle of the mountain mixed forest zone, where consistent winter snowpack and gradual spring melt play a crucial role in maintaining high soil moisture and supporting forest functioning throughout the growing season.

Table 1. The general characteristics of the study sites. Table adapted from article 3, Kolisnyk et al, 2025.

Site	Elevation	Average annual temp. (C)	Sum of annual precipitation (mm)	Stocking density (m^2 ha^{-1})	Admixture of broadleaf species (%)
PL1	320 – 400 (350)	6.7 – 9.1 (8.1)	608 – 1003 (749)	21.1 – 46.9 (34.1)	0 – 36.5 (13.0)
PL2	580 – 820 (650)	5.9 – 8.4 (7.0)	731 – 1522 (989)	31.0 – 62.9 (45.4)	0 – 58.8 (15.3)
IT1	1050 – 1750 (1320)	3.1 – 8.8 (6.8)	642 – 1336 (894)	29.8 – 90.5 (53.4)	0 – 34.3 (13.9)
GE1	820 – 1140 (920)	6.2 – 8.5 (7.6)	1471 – 2081 (1805)	40.7 – 70.1 (54.4)	0 – 35.7 (11.5)

Across all four sites, silver fir is the dominant species, but it is also the most heavily impacted by browsing pressure from ungulates, which poses a significant challenge for silviculture. The management of silver fir-dominated stands across the study sites has transitioned from clear-cutting to shelterwood and selection systems in recent decades. In PL1 and PL2, low-intensity, high-frequency single-tree selection dominates, while in GE1, foresters employ high-intensity, low-frequency interventions targeting the upper layer. IT1, due to the challenging terrain, has the lowest intervention frequency and intensity.

3.2. Experimental design and data acquisition

At each site, 34–36 circular plots with an area of 0.05 ha were established, covering two gradients: first, the gradient of tree size diversity, ranging from simple even-aged stands, through two-aged and more irregular stand structures, to structurally complex, uneven-aged forest stands; and second, the gradient of broadleaf species admixture (up to 50%), primarily European beech (*Fagus sylvatica* L.). Plots in the field were selected using a plot selection matrix (Fig. 2) to ensure that, at each site, the full range of compositional and structural gradients was represented, thus allowing the formulated objectives to be addressed. All plots at a given site were within a 15 km radius.

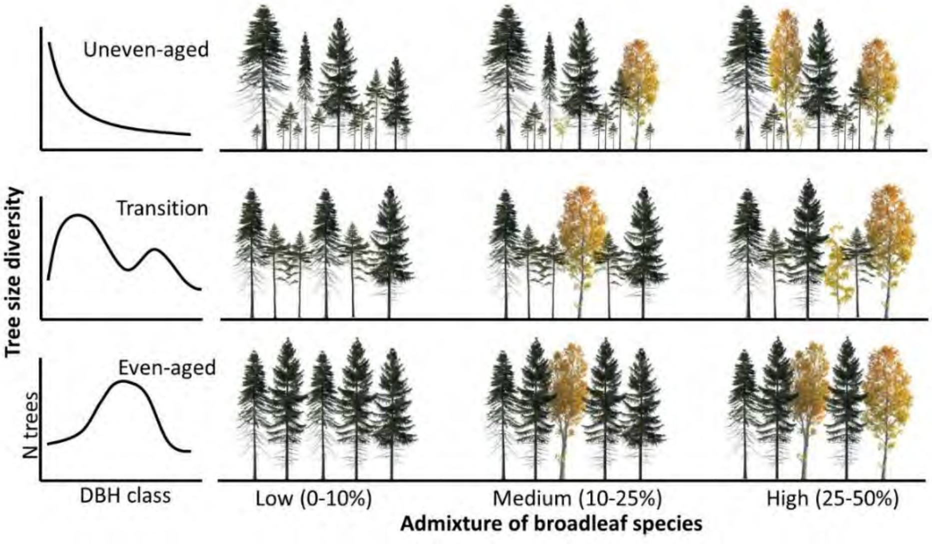

Figure 2. Plot selection matrix illustrating tree size diversity (vertical axis) and the admixture of broadleaf tree species (horizontal axis). At least three plots were established for each structural type to ensure that plots at each site represent a range of compositional and structural gradients. The DBH distribution represents the theoretical diameter at breast height distribution for each stand structural type. Figure from article 3, Kolisnyk et al., 2025.

All trees with a diameter at breast height (DBH) ≥7 cm were mapped in a three-dimensional coordinate system using FieldMap software with an Impulse LR 200 rangefinder and the high-precision MapStar Compass Module II (Institute of Forest Ecosystem Research, 2024; Tomaštík & Tunák, 2015). Standard dendrometric information was recorded, including species identity, DBH, and any visible damage (e.g., caused by wind, insects, or decay). For a subsample of selected trees from different biosocial positions and species, total tree height, height to crown base, and horizontal crown projection in the four cardinal directions were recorded. Besides, tree size diversity at PL1 was additionally assessed by forestry experts with applied and academic experience in uneven-aged silviculture, based on a structured questionnaire and a five-grade classification system.

Natural regeneration was quantified using concentric subplots. Seedlings (≥2 years old and <50 cm tall) were recorded within a 1.26 m radius from the plot center; small saplings taller than 50 cm but with DBH <2 cm were recorded within a 2.52 m subplot; and tall saplings with DBH between 2 and 7 cm were recorded in a 3.99 m radius subplot.

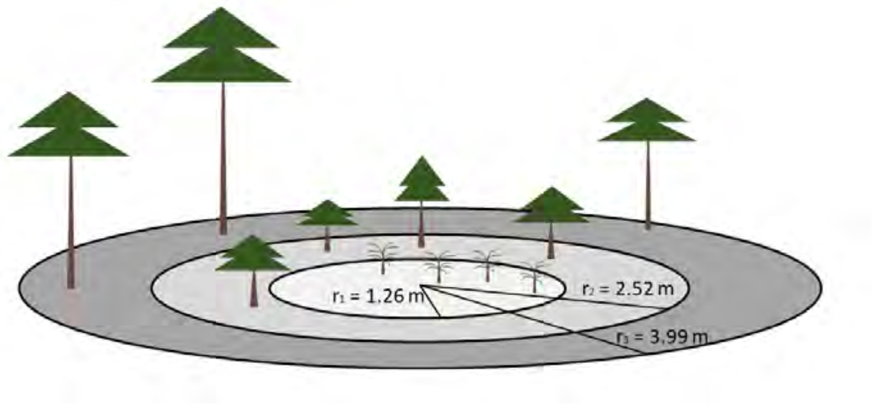

Figure 3. Schematic representation of concentric sub-plots used for natural regeneration, where r1, r2, and r3 are the radii of the sub-plots. Figure from publication 2, Kolisnyk et al., 2024b.

To assess the interannual growth dynamics of individual trees, increment cores were collected from more than 600 silver firs. In even-aged plots, 3–4 healthy trees closest to the plot center were cored. In more structurally diverse stands, 4–6 trees from different biosocial positions were selected. Cores were extracted in one direction, perpendicular to the slope, to avoid reaction wood and minimize damage due to the invasive nature of the process. Increment cores were then air-dried, glued, polished (first with 120-grit, then

800-grit sandpaper), and scanned at high resolution (1200–2400 dpi). Tree-ring widths were measured with a precision of 0.01 mm using CooRecorder (Maxwell & Larsson, 2021).

To account for elevation differences and orographic influences on local conditions, climatic information for IT1 and GE1 was sourced from the daily E-OBS gridded dataset at 0.1 degree spatial resolution (Cornes et al., 2018). For PL1 and PL2, due to the biases in E-OBS for Eastern Europe, and specifically central Poland, more locally appropriate datasets were used, including the 2 km G2DC-PL+ gridded dataset (Piniewski et al., 2021) and records from nearby climatic stations.

To address the first research objective on the quantification of tree size diversity, only data from PL1 were used. This step was essential to ensure that, prior to committing resources to fieldwork, the quantification of tree size diversity was methodologically sound and the formulated research objectives were feasible. For the second and third research objectives on the natural regeneration potential and growth resilience to drought stress, data from all sites were analyzed.

3.3. Data preparation and analysis

To structure the collected data in a coherent and logical format, two dedicated datasets were created as part of the research process. The first dataset includes plot-level information such as GPS coordinates, slope, aspect, ground and vegetation cover information (e.g., leaf litter, moss), as well as individual tree-level dendrometric data and records of natural regeneration. The second dataset comprises increment core measurements.

The majority of data processing, analysis, and visualization was done using the R programming language (R Core Team, 2022). The datasets were checked for missing values and irregular patterns. In case of uncertainty, preference was given to field verification to ensure data accuracy. To address specific research questions, collected data often had to be transformed and manipulated, including steps such as filtering, ordering, restructuring, and labeling. This was done using the dplyr and tidyverse R packages (Wickham et al., 2019, 2023). The increment cores were cross-dated and checked using CDendro software and the dplR R package (Bunn et al., 2025; Maxwell & Larsson, 2021).

Across the three articles comprising the thesis, a range of statistical methods was used depending on the specific research objectives and data structures. Generalized linear models (GLMs) and generalized linear mixed-effect models (GLMMs) were fitted using the stats and glmmTMB R packages, with various families, link functions, and optimizers used as appropriate (Brooks et al., 2024). Besides, the ccaPP R package was used to perform canonical correlation analysis with projection pursuit to address the first research objective (Alfons & Simcha, 2019). Model output tables and plots were generated using the sjPlot and ggplot2 R packages (Lüdecke et al., 2024; Wickham et al., 2025). Model diagnostics were done using the DHARMa R package (Hartig et al., 2024).

A wide range of custom R scripts was developed to support the formal analysis and visualization, including functions for accessing and analyzing climatic data, calculating complementary resilience and structural diversity indices, as well as visualization tools such as three-dimensional forest stand reconstructions. The latter has been made publicly available as the ForestVisuals R package on GitHub, and can be accessed, used, and, if needed, adapted by other researchers (Kolisnyk, 2023).

Growth resilience was assessed using complementary resilience indices proposed by Lloret et al. (2011), including resistance (Rt) and resilience (Rs). Additionally, two indices were introduced in article 3 (Kolisnyk et al., 2025), namely stress-driven deviation (SDD) and total growth response (TGR). Long-term climatic conditions were quantified using the de Martonne Aridity Index (MA) and the Forest Aridity Index (FAI) (De Martonne, 1926; Führer et al., 2011, respectively). Meteorological drought years were identified using the Standardized Precipitation Evapotranspiration Index (SPEI) for the selected period (Beguería & Vicente-Serrano, 2023).

Explicit information on the data used, data preparation procedures, and formal analyses, including full model specifications and implementation details, is provided in the individual articles.

4. Main results and general comments

Article 1: **Kolisnyk, B**., Brzeziecki, B., Jankowski, P., Drozdowski, S., & Bielak, K. (2024a). Linking the quantitative and qualitative approaches to assessing tree size diversity using silver fir (*Abies alba* Mill.) stands in the Zagnańsk Forest District. Sylwan, 168, Article 12. https://doi.org/10.26202/sylwan.2024057

Based on a state-of-the-art literature review, fifty-four variations of seven distance-independent tree size diversity indices were selected and evaluated. Expert ratings of tree size diversity demonstrated a high level of consistency, as indicated by a Cohen's Kappa value of 0.64 ($p < 0.001$). Canonical correlations between expert perceptual assessments and the calculated indices ranged from 0.26 to 0.86, highlighting substantial variability in how effectively the indices capture expert-perceived tree size diversity.

Among the evaluated indices, the Shannon diversity index, when applied to 2-meter height classes and using basal area as a proxy for class share, exhibited the strongest correlation with expert assessments ($r = 0.86$). This index effectively reflects vertical space occupancy within stands; however, it is sensitive to the class parametrization. In contrast, kurtosis and skewness of the DBH distribution, which are independent of class size parametrization, also aligned strongly with expert evaluations ($r = 0.81$ and $r = 0.79$, respectively). Several other indices incorporating basal area as a proxy of the share of the trees in the class, such as Shannon evenness, Atkinson, and Hoover indices, demonstrated moderate to strong agreement with expert perceptions. Conversely, Shannon-based indices derived from the number of trees in DBH and height classes were less robust. The LikeJ index, as proposed by Hanewinkel et al. (2014), showed the weakest correlation with expert ratings. All indices were discussed in relation to their ecological and silvicultural implications.

In structurally simplified, even-aged stands, many indices performed adequately. However, in complex stand structures, combining multiple indices, particularly those addressing different dimensions of diversity, such as inequality, distribution shape, and size variability, may be advantageous. The article presents further elaboration and a more in-depth interpretation and discussion of these findings.

Article 2: **Kolisnyk, B.**, Wellstein, C., Czacharowski, M., Drozdowski, S., & Bielak, K. (2024b). Contrasting Regeneration Patterns in *Abies alba*-Dominated Stands: Insights from Structurally Diverse Mountain Forests across Europe. Forests, 15, Article 7. https://doi.org/10.3390/f15071182

Regeneration density varied significantly across sites, with silver fir consistently dominating the regeneration layer. In GE1 and IT1, the higher elevations and harsh mountain environments contributed to a greater admixture of spruce in the regeneration layer. However, at lower altitudes, beech and hornbeam (*Carpinus betulus* L.) primarily complement silver fir in this layer.

Across all sites and developmental stages (seedlings, small saplings, tall saplings), the probability of the presence of natural regeneration was significantly higher in uneven-aged stands. A marked increase in the disparity in the probability of natural regeneration presence between even-aged and uneven-aged stands was observed with decreasing average annual temperatures. Similarly, higher stocking density was associated with reduced overall regeneration density across sites, regardless of tree size diversity. The admixture of broadleaf tree species was generally associated with a slight reduction in regeneration density (PL1, PL2, IT1), but notably increased it under the more humid environment (GE1). When examining the regeneration density of silver fir separately, the impact of broadleaf admixture was similar; however, it was not influenced by stocking density. Neither the presence of large overstory trees nor the site-level density of ungulates exhibited a significant influence on natural regeneration dynamics.

Notably, greater tree size diversity in uneven-aged stands has shown a clear positive effect on the advancement of silver fir in the regeneration layer, indicating that vertical diversification significantly contributes to the progression of silver fir from early developmental stages to more developed stages (seedlings to small saplings to tall saplings). This effect was more pronounced under more arid conditions (lower values of the Martonne index).

The presented results were interpreted from both ecological and silvicultural perspectives, with emphasis on microsite diversification, species-specific life history strategies, and the environmental conditions required for germination and the advancement of seedlings and saplings. The article presents further elaboration and a more in-depth interpretation and discussion of these findings.

Article 3: **<u>Kolisnyk, B.</u>**, Czacharowski, M., Bingham, L., Wellstein, C., Uhl, E., Drozdowski, S., & Bielak, K. (2025). Tree size diversity can enhance the drought resilience of *Abies alba* Mill. in the European mountain forests. Forest Ecology and Management, 589, 1–14. https://doi.org/10.1016/j.foreco.2025.122765

The study identified at each site the following drought stress years: GE1 (2003, 2008), IT1 (2018), PL1 (2006), PL2 (2015). We found no uniform effect of tree size diversity on the growth resilience components (Rt, Rs, SDD, TGR) across the study sites. The absence of a general pattern indicates that tree size diversity, considered in isolation, does not consistently influence growth resilience. However, when site-specific long-term water availability, represented by FAI, was incorporated into the models, a significant interaction was found for Rt and SDD. At sites characterized by limited precipitation, thus higher FAI, such as PL1, both Rt and SDD exhibited a marked positive relationship with increasing tree size diversity. Conversely, at more humid sites with lower FAI, such as GE1, this relationship was flattened or even reversed, suggesting that the positive effects of tree size diversity on growth resilience are contingent upon the prevailing climatic conditions and are more pronounced in water-limited environments.

When sequentially introduced into the base model, neither stocking density, the admixture of broadleaf tree species, nor individual tree DBH was found to be a significant mediator of the tree size diversity-resilience relationship. However, when the interaction term with FAI was added, DBH emerged as a significant predictor for Rt and SDD. In more water-limited sites, smaller trees exhibited higher growth resilience. As water availability increased, this pattern became less pronounced or slightly reversed.

The presented results were interpreted in the context of ecophysiological adaptations to prevailing growing conditions and the mode of competition. The shift from more symmetric competition under water-limited conditions to increasingly asymmetric competition with greater water availability may partially explain the observed effects of tree size diversity and individual tree size on silver fir's drought response. These findings are consistent with the stress-gradient hypothesis. The article presents further elaboration and a more in-depth interpretation and discussion of these findings.

5. Conclusions

In the context of accelerating global change and increasing ecological and societal uncertainty, the findings of this thesis emphasize the pivotal role of silvicultural systems and the resulting tree size diversity in shaping the interactions between forest ecosystem structure and functioning.

Based on the research presented, the following conclusions may be drawn:

1. Given its complexity and multifaceted nature, proper quantification of tree size diversity of forest stands requires the use of metrics grounded in solid ecological and silvicultural understanding. Indices should be selected and interpreted with consideration of sample size, management or research objectives, and environmental conditions. Future research should aim not only to develop more advanced metrics but also to bridge the gap between mathematical models, ecological traits, and the art of applied close-to-nature silviculture.
2. Uneven-aged silviculture and the resulting tree size diversity generally improve natural regeneration by increasing the probability of natural regeneration establishment and supporting their development from juvenile to more developed stages. This ensures a sustainable and robust natural regeneration bank, which is essential for maintaining a resilient forest ecosystem in the long term.
3. Tree size diversity can enhance the drought resilience of silver fir in the European mountain forests; however, its effect is influenced by prevailing climatic conditions. Specifically, higher tree size diversity is associated with greater resilience to drought stress at more arid sites. Similarly, with increasing aridity, smaller trees tend to be more drought-resistant. These findings are consistent with the stress-gradient hypothesis, which posits that facilitative interactions among plants become more prominent under conditions of increased abiotic stress.
4. The impact of broadleaf species admixture and stocking density on natural regeneration and drought resilience is highly context-dependent. Nevertheless, regulating stocking density and species composition remains an effective silvicultural tool for shaping forest structure and thus ecosystem resilience.
5. Implementing uneven-aged silviculture and increasing tree size diversity can be regarded as a strategic management tool to enhance ecosystem resilience and adapt silver fir-dominated forests to anticipated climate change.

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7. Articles comprising the doctoral thesis

Article 1: **Kolisnyk, B**., Brzeziecki, B., Jankowski, P., Drozdowski, S., & Bielak, K. (2024a). Linking the quantitative and qualitative approaches to assessing tree size diversity using silver fir (*Abies alba* Mill.) stands in the Zagnańsk Forest District. Sylwan, 168, Article 12. https://doi.org/10.26202/sylwan.2024057

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ORIGINAL PAPER

Linking the quantitative and qualitative approaches to assessing tree size diversity using silver fir *Abies alba* Mill. stands in the Zagnańsk Forest District

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ABSTRACT

Despite recent advances in understanding the structure and dynamics of mixed forests, uneven-aged forests and their inherent diversity remain underexplored. Tree size diversity, an integral component of forest structure, influences ecosystem functioning and plays a vital role in ecological modeling, monitoring, and silvicultural decision-support systems. Although a few quantitative indices exist to assess tree size diversity, it remains unclear: (i) which aspects of diversity they capture and (ii) how consistent they are with qualitative evaluations by forest experts, who base silvicultural decisions on personal perception.

To explore the relationship between quantitative and qualitative approaches, we analysed 36 circular plots in Zagnańsk Forest, Central Poland, representing a gradient from even-aged, monolayered monospecific stands to uneven-aged, mixed silver fir-dominated stands. Based on state-of-the-art literature review, we selected and evaluated 54 variations of distance-independent tree size diversity indices. Six forestry experts categorized the plots into five tree size diversity classes using a structured questionnaire.

Canonical correlation analysis revealed considerable variability in how the indices aligned with the perceptions of the experts, who showed a high degree of interrater reliability (Cohen's Kappa=0.64). Shannon diversity and evenness indices based on tree height classes and basal area, as well as Kurtosis and Skewness of the diameter at breast height distribution, exhibited the strongest correlations with experts' evaluations. Moreover, several other indices, including Shannon evenness, Atkinson, and Hoover indices, showed moderate to strong correlation with experts' qualitative evaluation.

Our results highlight the need to bridge the gap between mathematical concepts and applied silviculture.

KEY WORDS

distance-independent index, forest growth modelling, structural diversity, tree size inequality, uneven-aged silviculture

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Introduction

Since the early silvicultural advancements at the turn of the 18th and 19th centuries (Hartig, 1791; Von Cotta, 1828), forestry science and practice have predominantly relied on rotation silvicultural systems and the management of even-aged monocultures (O'Hara *et al.*, 2018). Yield tables and age-class systems, as fundamental methods for understanding forest growth and development, have proven to be versatile tools in sustainable forestry for decades (Savill *et al.*, 1997; Morgenstern, 2007). However, they have significant limitations when used to support the management of structurally complex stands, mainly due to the ambiguous definition of stand age in uneven-aged forests (Moser and Hall, 1969).

Following the landmark Rio Declaration on Biodiversity in 1992 and the Helsinki Conference on the Sustainable Management of Forests in Europe in 1993, supported by recent EU documents, including the Biodiversity (EC, 2021) and Forestry (EC, 2022) Strategies for 2030, as well as the Guidelines on Closer-to-Nature Forest Management (EC, 2023), priorities have shifted towards the management of mixed and uneven-aged stands (Franklin *et al.*, 2002; Schütz, 2002; Spiecker, 2003; Pretzsch *et al.*, 2008; Bauhus *et al.*, 2009; O'Hara and Ramage, 2013; Ammer, 2018). This shift is driven primarily by a continuously growing body of evidence on the advantages of increased alpha diversity in forest ecosystems, particularly from the perspective of risk dispersion and improved resilience to abiotic and biotic disturbances under global environmental change (O'Hara, 2014; Lafond *et al.*, 2014; Thrippleton *et al.*, 2023).

Although significant advances have been made in understanding the growth and functioning of mixed stands (Bauhus *et al.*, 2017; Bravo-Oviedo *et al.*, 2018; Pretzsch, 2018), uneven-aged silviculture and the resulting stand structural diversity have received comparatively less attention (Forrester, 2019; LaRue *et al.*, 2023). This gap stems predominantly from the complexity of silvicultural interventions required to develop and maintain uneven-aged stands (Brzeziecki *et al.*, 2021). The term 'uneven-aged' refers to a broad spectrum of tree size and spatial diversity, from relatively simple two-layered stands to highly complex structures where trees and crowns occupy multiple vertical strata (O'Hara and Gersonde, 2004). They can result from a range of management systems, such as irregular shelterwood systems, single-tree, and group selection systems (O'Hara, 2014). Even when theoretically the same silvicultural system is applied, the resulting diversity can vary significantly across ecosystems, growth-limiting factors, and, notably, the practices of individual foresters (Pommerening, 2002; O'Hara, 2014; Storch *et al.*, 2018; Camarretta *et al.*, 2020).

To improve our understanding of the complex dynamics of uneven-aged stands, there is a need for the objective quantification of the stand structure (Fig. 1). Stand structural diversity can be characterized as a combination of three facets: spatial diversity, species diversity, and size diversity (Brzeziecki, 2002; Pommerening, 2002). Spatial diversity depicts the arrangement of trees within the stand, encompassing multiple attributes of the horizontal distribution of trees, such as irregularity, clustering, spacing, and mingling (Gadow and Hui, 2001). Species diversity refers to the variety and relative abundance of tree species within a stand (Peet, 1974). Tree size diversity reflects the variation of tree sizes within a stand and inherently encompasses vertical heterogeneity and space occupancy (Pommerening, 2002; LaRue *et al.*, 2023). In the literature, tree size diversity is also often referred to as tree size inequality, size distribution, vertical pattern, and frequently structural diversity (Dănescu *et al.*, 2016; del Río *et al.*, 2016; Forrester, 2019; Zhang *et al.*, 2023).

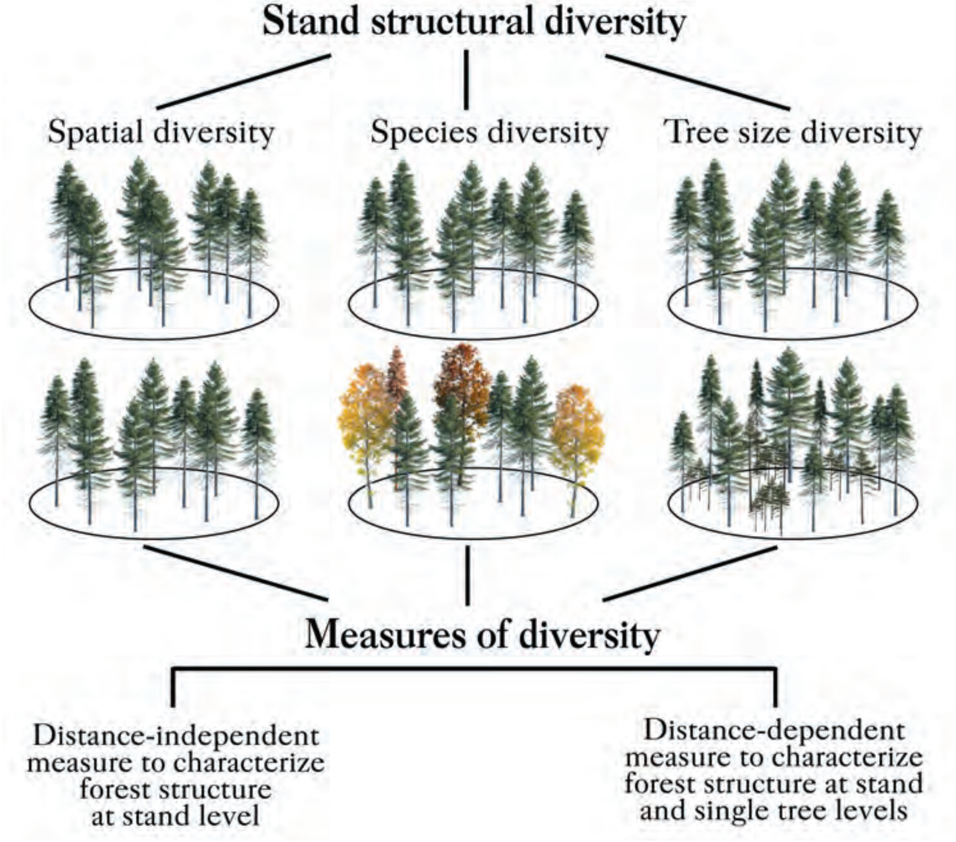

Fig. 1.
Overview of the three main characteristics of a forest stand structural diversity and the corresponding measures used to quantify it (modified from Pommerening, 2002)

In contrast to widely used species diversity metrics such as the Shannon, Simpson, or Berger-Parker indices (Berger and Parker, 1970; Peet, 1974), and distance-dependent spatial diversity measures including the Clark and Evans aggregation index or Ripley's K function (Clark and Evans, 1954; Ripley, 1976), tree size diversity represents a more intricate and less thoroughly studied aspect of forest structure (LaRue *et al.*, 2023). Furthermore, spatial diversity indices require detailed mapping, making them challenging to compute for smaller plots, while tree size diversity indices provide a more direct and distance-independent measure of realized niche occupancy (Gadow and Hui, 2001; Liang *et al.*, 2007; LaRue *et al.*, 2023). They can be effectively used with data from small-size inventory plots, which is particularly valuable given the increasing availability of national forest inventory (NFI) data (Tomppo *et al.*, 2010). Moreover, data from circular plots (*e.g.*, forest management or protection plans) are readily available to both forestry scientists and practitioners and are extensively used to assess the forest structure (Storch *et al.*, 2018; LaRue *et al.*, 2023).

Tree size diversity can be a robust predictor of forest productivity, carbon sequestration potential, and resilience and provides an easily measurable metric to guide decision-makers in maximizing ecosystem services provisioning (Dănescu *et al.*, 2016; Dybala *et al.*, 2019; LaRue *et al.*, 2023; Kolisnyk *et al.*, 2024).

A few indices have recently been utilized to quantify tree size diversity (Lexerød and Eid, 2006; Cordonnier and Kunstler, 2015; del Río *et al.*, 2016; Storch *et al.*, 2018). However, the combination of several indices is often required to capture the complex and multifaceted nature of the vertical heterogeneity of forest stands (*e.g.*, Dănescu *et al.*, 2016; del Río *et al.*, 2016). Furthermore, interpretation of the results can be challenging from an ecological perspective due to a lack of a clear understanding of how existing indices work and what aspects of forest structural diversity they depict (Zhang *et al.*, 2023).

Additionally, it remains unclear how these indices reflect forest practitioners' and stakeholders' perceptions of tree size diversity, as they often base their silvicultural decisions on personal experience and background knowledge (Bravo-Oviedo *et al.*, 2020). Discrepancies between quantitative indices and expert perception can lead to inconsistencies in how forest practitioners implement scientific advice and policymakers' recommendations.

To pave the way and bridge the gap between statistical indices and forestry experts' perceptions, it is essential to identify the optimum set of indices for an accurate description of tree size diversity. Therefore, based on a state-of-the-art literature review, we aim (i) to select distance-independent tree size diversity indices and (ii) to evaluate how the selected quantitative indices align with the qualitative evaluations of tree size diversity by forestry experts.

Materials and methods

STUDY SITE AND DATA. The empirical part of the study was conducted in silver fir *Abies alba* Mill. dominated stands in the Zagnańsk Forest District, located in the Świętokrzyskie Mountains in Central Poland. These stands represent the northeastern limit of the silver fir's distribution (Dobrowolska *et al.*, 2017; Kolisnyk *et al.*, 2024). The mean annual temperature and sum of precipitation for the last 20 years are 8.6°C and 618 mm, respectively (source: Kielce Meteorological Station).

We used a sub-sample of data from the experimental network of plots established in 2011 by the Department of Silviculture in Warsaw (Drozdowski *et al.*, 2014). We selected 36 circular plots, each 0.05 hectares in size, to cover the gradient in tree size diversity and degree of broadleaf species admixture, from even-aged, monolayered, and monospecific stands to steady-state, mixed, uneven-aged stands with highly diverse vertical structure and space occupancy (Fig. 2). The dominant tree species are silver fir, accompanied by European beech *Fagus sylvatica* L., and occasionally Norway spruce *Picea abies* (L.) H.Karst., Scots pine *Pinus sylvestris* L., and hornbeam *Carpinus betulus* L. During the recent inventory conducted in March 2022, data was recorded on species identity, tree positions in a local coordinate system, diameter at breast height (DBH), and heights for trees with a DBH of ≥7 cm. The total basal area of selected plots ranges from 21.1 to 46.9 $m^2 \cdot ha^{-1}$, with a mean of 34.1 $m^2 \cdot ha^{-1}$. The maximum DBH is 88.8 cm, with a mean DBH of 19.8 cm. The maximum and mean tree heights reach 35.0 m and 17.4 m, respectively. All plots represent similar eutrophic site conditions of the cambisol soil type formed on a loamy sand and/or loam.

STRUCTURAL INDICES SELECTION. As a preliminary step, we conducted a state-of-the-art literature review to outline the time-based current knowledge on distance-independent tree size diversity indices. The Publish or Perish software powered by the Google Scholar search engine (Harzing, 2007) was used to synthesize the literature selection. After an initial review of titles and abstracts, we performed an in-document keyword search using terms such as 'tree size diversity', 'tree size inequality', 'tree size variability', and 'structural diversity'. The indices were gathered from the literature based on selection criteria that included technical aspects, such as being published in English after peer review, and the feasibility to calculate them using readily available

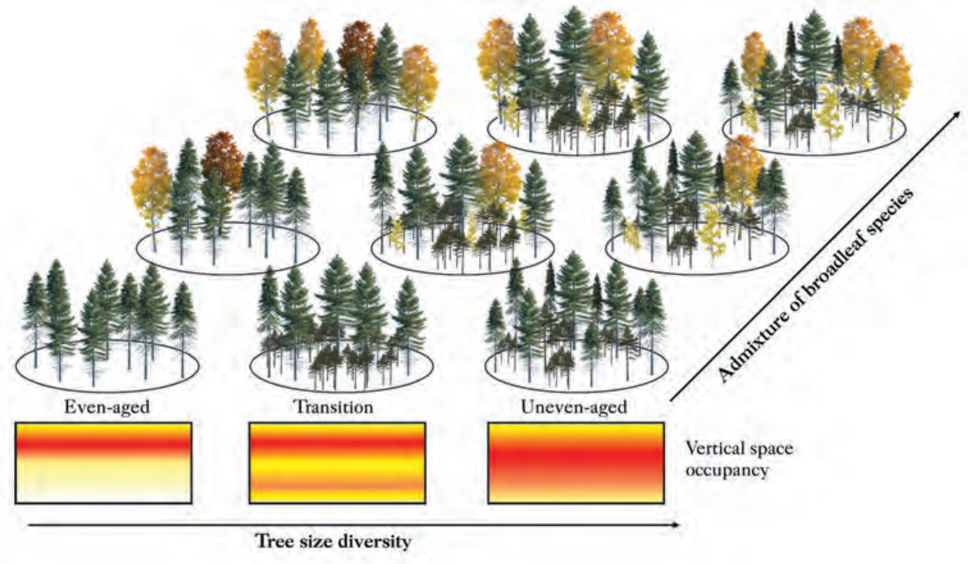

Fig. 2.

Design of the experimental network illustrating gradients of tree size diversity (x-axis) and admixture of broadleaf species (y-axis). The theoretical vertical space occupancy is represented by a yellow-to-red gradient fill, with light yellow indicating unoccupied space and red indicating fully occupied space.

records, such as standard dendrometric data from the NFI. Additionally, as a result of the snowballing approach, we selected indices from the social and economic sciences that, though not previously applied to describe tree size diversity, were subjectively identified as potentially valuable and included in this study.

A total of 7 indices were identified according to the defined selection criteria. They are presented from the most commonly used ones to those originating from the social and economic sciences but used for the first time to depict the tree size diversity.

Coefficient of variation. The coefficient of variation (CV) characterizes the degree of dispersion of a probability distribution (Manikandan, 2011). The CV is the simple ratio of the standard deviation (SD) to the mean of the sample (eq. 1 and 2):

$$CV = 100 \cdot \frac{SD_{treesize}}{\hat{x}} \tag{1}$$

$$SD_{treesize} = \sqrt{\frac{\sum_{i=1}^{n}(x_i - \hat{x})}{n-1}} \tag{2}$$

where:

x_i is the size of the i^{th} tree,
$\hat{x}$ is the mean size of the trees on the plot,
n is the total number of trees per plot.

In forestry, CV can be a useful and easy-to-calculate proxy for tree size diversity, making it widely used in the field (*e.g.*, Potvin and Dutilleul, 2009). We calculated the CV for tree height and DBH (Table 1). The calculated CV quantifies how individual tree sizes deviate from the plot mean tree size.

Table 1.

Overview of the coefficient of variation (CV), Skewness (Skew), Kurtosis (Kurt), and Gini indices (Gini), including their respective acronyms, associated tree size metrics, and statistical range (minimum, maximum, and mean values)

Acronym	Tree parameter	Index	Range
CV_DBH	DBH [cm]	CV	23.2-89.2 (62.3)
CV_H	Height [m]		13.4-51.1 (36.3)
Skew_DBH	DBH [cm]	Skew	–0.6-3.6 (1.1)
Skew_H	Height [m]		–1.3-1.4 (0.3)
Kurt _DBH	DBH [cm]	Kurt	1.7-17.8 (4.1)
Kurt_H	Height [m]		1.5-4.5 (2.6)
Gini_BA	BA [cm^2]	Gini	0.2-0.7 (0.6)
Gini_H	Height [m]		0.1-0.3 (0.2)
LikeJ index	DBH [cm]	LikeJ	0.4-6.0 (3.9)

Skewness and Kurtosis. As the CV represents the spread from the mean tree size, the Skewness index (eq. 3) shows the asymmetry of the distribution and can detect if it is tilted to the right or left from the mean. In the context of tree size distribution, if skewness is positive (right-tailed), the number of small trees is higher than the number of large trees present in the plot. Vice versa, if skewness is negative – there are more large trees.

Kurtosis (eq. 4) is also a measure of the shape of a probability distribution (Groeneveld and Meeden, 1984). While skewness describes the direction of asymmetry in a distribution, kurtosis measures the degree of flatness or peakedness (Joanes and Gill, 1998). A normal distribution has a kurtosis value of around 3 (mesokurtic), which may indicate a mix of average, small, and large-diameter trees. A kurtosis value higher than three indicates a ‘high peaked’ distribution with small tails (leptokurtic), corresponding to a stand with an abundance of trees of a given size (typically small trees in uneven-aged stands). A flattened distribution with long tails has a value lower than three, and is more typical for even-aged stands.

$$Skewness = \frac{\sum_{i=1}^{n}(x_i - \hat{x})^3}{(n-1)\cdot SD_{treesize}^3} \tag{3}$$

$$Kurtosis = \frac{\sum_{i=1}^{n}(x_i - \hat{x})^4}{(n-1)\cdot SD_{treesize}^4} \tag{4}$$

Gini index. The Gini coefficient measures the inequality among individual observations. It was initially proposed to measure the discrepancy of wealth distribution within a nation or specific geographic regions, demographic, or societal groups (Gini, 1936). It is becoming increasingly important in environmental sciences (Cordonnier and Kunstler, 2015) and has been extensively used in forestry over the last decade (Damgaard and Weiner, 2000; Binkley *et al.*, 2006). The Gini coefficient depicts how equally tree size is distributed between individuals. The simplest way to calculate the Gini coefficient from unordered data is as the relative mean difference (eq. 5). Another approach, which was used in this research (eq. 6), is to order the data by increasing tree size, as suggested by Sen (1973). The higher the value of the Gini coefficient, the greater the inequality. The theoretical range of this index is 0 to 1. Given that the Gini index is traditionally calculated based on basal area (BA) and produces results comparable to those obtained using DBH, we included the Gini index based on BA to facilitate integration and comparability with other studies.

$$Gini = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} | x_i - x_j |}{2n^2 \hat{x}} \tag{5}$$

$$Gini = \frac{\sum_{i=1}^{n}(2 \cdot l - n - 1) \cdot x_l}{\sum_{l=1}^{n}(n-1) \cdot x_l} \tag{6}$$

where:

x_i and x_j are the sizes of i^{th} and j^{th} individual trees,
l is the rank of the tree from larger to smaller,
x_l is the size of the l^{th} ranked tree.

Shannon diversity and Shannon evenness. The Shannon diversity index (ShD) was developed to measure the entropy in text strings (Shannon, 1948); however, it found its application in numerous fields of applied sciences. ShD is extensively used in natural sciences to describe diversity accounting for the number of groups of individual observations and their relative abundance (Summerville *et al.*, 2003; Senbeta *et al.*, 2007; Sharashy, 2022). In forestry, the Shannon index is mainly used to describe species diversity (Zeller and Pretzsch, 2019), although some applications concerning general plant size and specifically tree size diversity can also be found in the literature (Liang *et al.*, 2007; Brzeziecki *et al.*, 2018; Sharma *et al.*, 2020). The generalized formula is based on the proportion/share (p_i) of observed individuals in the selected group or class to the total across all classes (eq. 7). While the ShD index is aimed at quantifying entropy (in the case of tree size diversity in vertical profiles), the Shannon evenness index (ShEv, eq. 8) determines how evenly observed objects are distributed across classes (Heip and Engels, 1974).

$$ShD = -\sum_{i=1}^{N} p_i \cdot \ln(p_i) \tag{7}$$

$$ShEv = \frac{ShD}{\ln(N)} \tag{8}$$

where:

N is the number of classes,
p_i is the proportion of trees in the i^{th} class.

We calculated Shannon's Diversity (ShD) and Shannon's Evenness (ShEv) indices using DBH classes of 4 cm and 8 cm, as well as height classes of 2 m and 5 m (Table 2), with the first height class being (0, 10 m) and (0, 6 m), respectively (Fig. 3). The proportion (p_i) for each class was determined based on the number of trees (N), the sum of basal area (BA), or the tree height (H) within a given DBH or height class.

Similarity to the J-shaped distribution. Hanewinkel *et al.* (2014) proposed the LikeJ index to quantitatively characterize the forest structure of uneven-aged stands based on the DBH distribution. The index is designed to reflect the degree of similarity to a reverse J-shaped distribution (Kerr, 2014), explicitly accounting for the proportion of small and large trees and the DBH class with the highest tree density (Fig. 4). The scoring system for LikeJ was originally parameterized using the model by Schütz (1975), developed for the municipal forests of Couvet. Detailed calculation steps and the scoring system for LikeJ are outlined in Hanewinkel *et al.*, (2014). Nonetheless, LikeJ has been applied in other studies (*e.g.*, Dănescu *et al.*, 2016) without reparameterization for site-specific conditions. Likewise, in our study, we applied the LikeJ index without adaptations to the scoring system.

Table 2.

Overview of the calculated variations for the Shannon's Diversity (ShD) and Shannon's Evenness (ShEv) indices, including their respective acronyms, associated tree size classes, and statistical range (minimum, maximum, and mean values)

Acronym	Size class	p_i	Index	Range
ShD_DBH4_Ntrees	DBH 4 cm	N	ShD	1.4-2.4 (1.9)
ShD_DBH8_Ntrees	DBH 8 cm	N		1.0-1.8 (1.4)
ShD_H2_Ntrees	height 2 m	N		1.6-2.5 (2.1)
ShD_H5_Ntrees	height 5 m	N		0.9-1.8 (1.4)
ShEv_DBH4_Ntrees	DBH 4 cm	N	ShEv	0.7-1.0 (0.8)
ShEv_DBH8_Ntrees	DBH 8 cm	N		0.5-1.0 (0.8)
ShEv_H2_Ntrees	height 2 m	N		0.8-1.0 (0.9)
ShEv_H5_Ntrees	height 5 m	N		0.7-1.0 (0.9)
ShD_DBH4_BA	DBH 4 cm	BA	ShD	1.7-2.5 (2.1)
ShD_DBH8_BA	DBH 8 cm	BA		1.1-1.9 (1.6)
ShD_H2_BA	height 2 m	BA		1.4-2.2 (1.9)
ShD_H5_BA	height 5 m	BA		0.7-1.5 (1.3)
ShEv_DBH4_BA	DBH 4 cm	BA	ShEv	0.8-1.0 (0.9)
ShEv_DBH8_BA	DBH 8 cm	BA		0.7-1.0 (0.9)
ShEv_H2_BA	height 2 m	BA		0.6-0.9 (0.8)
ShEv_H5_BA	height 5 m	BA		0.5-1.0 (0.8)
ShD_DBH4_H	DBH 4 cm	H	ShD	1.7-2.5 (2.1)
ShD_DBH8_H	DBH 8 cm	H		1.2-1.9 (1.5)
ShD_H2_H	height 2 m	H		1.6-2.4 (2.2)
ShD_H5_H	height 5 m	H		0.9-1.7 (1.4)
ShEv_DBH4_H	DBH 4 cm	H	ShEv	0.8-1.0 (0.9)
ShEv_DBH8_H	DBH 8 cm	H		0.7-1.0 (0.9)
ShEv_H2_H	height 2 m	H		0.8-1.0 (0.9)
ShEv_H5_H	height 5 m	H		0.6-1.0 (0.9)

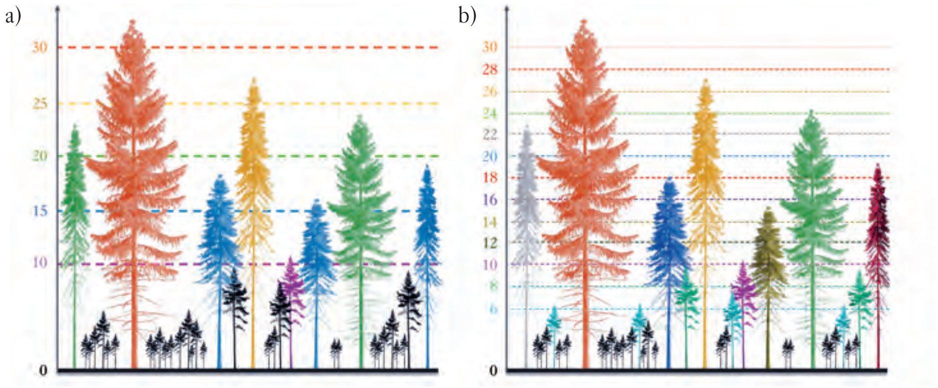

Fig. 3.

Visualization of the selected height classes with intervals of (a) 5 m and (b) 2 m. Each color represents a distinct height class, with trees categorized accordingly within a defined height interval

Atkinson index. Like the Gini coefficient, the Atkinson index was initially proposed to measure income inequality (Atkinson, 1970; Duclos and Araar, 2007). Furthermore, unlike Gini, Atkinson can determine which part of the distribution is a decisive contributor to observed inequality (eq. 9). The strength of the inequality aversion can be adjusted by choosing the correct weight parameter (ε), that allows to place higher values on the disparity in a specific part of the distribution (Table 3). A weight value closer to 1 makes the Atkinson index more sensitive to any changes in the lower part of the distribution; closer to 0 is more sensitive to changes in the upper part of the distribution (Allison, 1978). Despite the ability of the Atkinson index to adjust the inequality aversion parameter, which seems helpful in forestry for measuring tree size diversity, we could

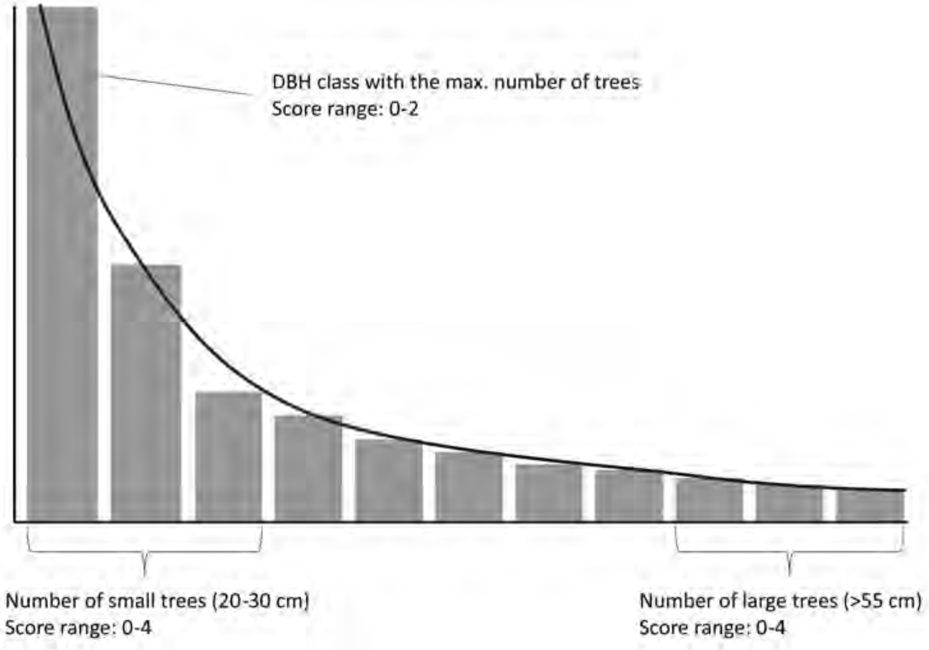

Fig. 4.
Visualization of the scoring system for the LikeJ index after Hanewinkel et al. (2014)

Table 3.
Overview of the calculated variations Atkinson indices (Atkin), including their respective acronyms, associated tree size metrics, ε parameter, and statistical range (minimum, maximum, and mean values with an accuracy to three decimal places)

Acronym	Tree parameter	*ε parameter*	Range
Atkin_BA_01	BA [cm^2]	0.1	0.009-0.116 (0.060)
Atkin_BA_25		0.25	0.023-0.261 (0.145)
Atkin_BA_5		0.5	0.049-0.438 (0.274)
Atkin_BA_75		0.75	0.075-0.552 (0.384)
Atkin_BA_1		1	0.104-0.626 (0.474)
Atkin_H_01	height [m]	0.1	0.001-0.013 (0.007)
Atkin_H_25		0.25	0.002-0.034 (0.017)
Atkin_H_5		0.5	0.005-0.069 (0.034)
Atkin_H_75		0.75	0.007-0.106 (0.051)
Atkin_H_1		1	0.010-0.143 (0.068)

not find any implementation example in this sector. By weighting either end of the distribution, we can check which (distribution of small or large trees) is more significant to explain experts' perception of tree size diversity.

$$Atkinson_{\varepsilon}=\begin{cases}1-\frac{1}{\hat{x}}\left(\frac{1}{n}\sum_{i=1}^{n}x_i^{1-\varepsilon}\right)^{\frac{1}{1-\varepsilon}} & \text{for } 0\leq\varepsilon<1\\ 1-\frac{1}{\hat{x}}\left(\prod_{i=1}^{n}x_i\right)^{\frac{1}{n}} & \text{for } \varepsilon=1\end{cases} \tag{9}$$

where:

ε is an inequality aversion parameter.

Hoover index. The Hoover index is another measure developed originally to quantify income inequality. While the mathematically similar ShD index measures the equality of distribution, the Hoover index focuses on the proportion of total income that would need to be redistributed to achieve an equal distribution (Hoover, 1936; Coulter, 2019). Although we could not find any application of the Hoover index to describe tree size diversity, there is potential for it to be implemented in this field. The classes and proxies we used to calculate the Hoover index are the same as those for the Shannon index (cf. Table 2 and 3). In contrast to the ShD index, the lower the value of the Hoover index (*Hv*), the greater the tree size diversity:

$$Hv=\frac{1}{2}\frac{\sum_{i=1}^{N}|Y_i-\hat{Y}|}{\sum_{i=1}^{N}Y_i} \tag{10}$$

where:

$\hat{Y}$ is the mean tree size or number of trees per class,

Y_i is the cumulative size or number of trees per ith class.

Expert evaluation. Six experts (four forest scientists and two practitioners) were engaged to evaluate tree size diversity. One practitioner is directly involved in managing the forests where our research network is located, and the second manages and plans silvicultural operations for stands with comparable growing conditions. All forestry scientists are directly involved in researching forest structure-functioning interactions in Poland.

The questionnaire included a 5-point scale to assess the tree size diversity of forest stands based on a visualization of the stand, photographs, and the DBH distribution (Fig. 5).

1) Even-aged monolayered stands.
2) Even-aged stands with a small vertical diversity and several trees in a second layer.
3) Two-aged stands with the presence of trees in both layers.
4) Uneven-aged stands with the dominance of trees in a few classes.
5) Steady-state uneven-aged stands with highly diverse vertical structures.

To ensure the reliability of the questionnaire and address potential bias stemming from the small sample of respondents and the imbalance between practitioners and scientists, inter-rater reliability was evaluated using Cohen's Kappa Single Score Intraclass Correlation, which measures the degree of agreement among raters (Warrens, 2015).

We used canonical correlation analysis with projection pursuit to evaluate the agreement between experts' grades and the tree size diversity indices (Alfons *et al.*, 2016). This method is based on defining projection directions through each data point and testing all possible combinations of weights assigned to the individual expert grade to find the highest correlation between the set

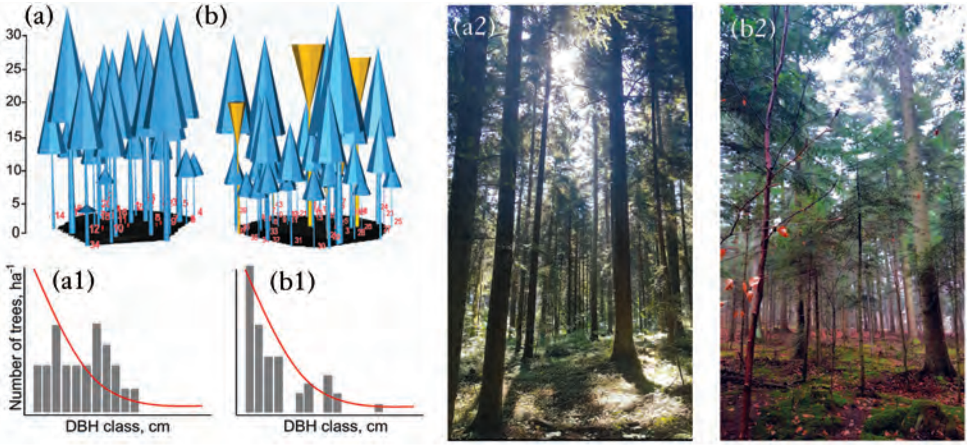

Fig. 5.

An example of visual information provided to experts is showcasing even-aged (a, a1, a2) and steady-state uneven-aged stands (b, b1, b2). The 3D stand visualizations (a and b) use simple geometric shapes with colors denoting different species. DBH distribution (a1 and b1) is parametrized in 4 cm classes, and the theoretical negative exponential curve (red line) illustrates the steady-state uneven-aged structure. Photographs (a2 and b2) offer additional perspectives on stand structural diversity.

of experts' perceptions and the tree size diversity index. Spearman's correlation was used as the correlation functional to maximize, with robust standardization to mean and standard deviation (Alfons *et al.*, 2016). The *ccaPP* R package version 0.3.3 was used for this analysis (Alfons and Simcha, 2019).

Results

Indices and their variability. The quantitative values (mean, minimum, and maximum) for the first four structural indices (CV, Skew, Kurt, Gini, and LikeJ) are shown in Table 1. For the stands analysed, all indices calculated for tree DBH were greater than for height, indicating a higher relative range and variability in the tree diameter. For example, in the case of even-aged stands of silver fir, the coefficient of variation was only about 13% and 23% for height and diameter, respectively. Skewness and kurtosis also confirmed a wide range of structures in our dataset. The values close to or below zero of the above indices represent stands characterized by low size differentiation. In contrast, the highly positive values indicate the most complex stands, including those with the largest trees in our dataset. The Gini coefficient was much more sensitive to basal area than to height. This index clearly indicates the greater size tree inequality in the stand with its higher values. LikeJ index varied from 0.4 up to 6.0 for the even-aged stands and most complex structures, respectively (Table 1).

In the case of the Shannon's Diversity (ShD) index, as might be expected, the values obtained for the narrower classes (4 cm and 2 m) were generally higher than those for the wider classes (8 cm and 5 m) (Table 2). For this index, both the range and mean values did not differ significantly between the diameter and height parameters, nor did the results for number of trees, basal area and height. A similar pattern was observed for the Shannon's Evenness (ShEv) index. However, the results obtained for this index exceed values of 0.5, indicating a relatively high tree size diversity even in the case of even-aged silver fir stands. Furthermore, the ShEv mean values were quite similar (0.8-0.9) and close to the maximum tree size diversity indicated by value 1.

The results for the Atkinson index are shown in Table 3. The index values were positively correlated with the ε parameter, *i.e.*, the higher the ε parameter, the higher the value of the Atkinson index. For the exact value of the ε parameter, the Atkinson index values for basal area were significantly higher than those for tree height.

The values of the Hoover index are presented in Table 4. All calculation variants gave very similar results in terms of the values, both for DBH and height classes, as well as for number of trees, basal area or tree height. However, this index is very sensitive to relatively small differences in the values obtained (Fig. 8).

AGREEMENT RATE BETWEEN EXPERTS' EVALUATIONS AND SELECTED TREE SIZE DIVERSITY INDICES. There was a high degree of consistency in the expert ratings of tree size diversity, as evidenced by relatively stable standard deviation values across the entire gradient (Fig. 6). A slightly higher deviation from the mean was observed in transition structures. The Cohen's Kappa value of 0.64 with the p-value<0.001 indicates a statistically significant substantial level of agreement among the experts (McHugh, 2012).

Canonical correlations between the experts' perceptual evaluations and the calculated tree size diversity indices ranged from 0.26 to 0.86, with a mean of 0.58, indicating considerable variability in how well these indices represent tree size diversity as perceived by the experts (Fig. 7). Notably, the ShD and ShEv indices, when calculated based on the height classes and BA as a proxy of tree distribution within defined classes, showed the strongest correlations exceeding 0.65. For instance, ShD_H2_BA is at the top of the correlation matrix (Fig. 7-8), as it has the highest correlation (0.86) with expert assessments.

Skewness and Kurtosis indices, when based on tree radial size, are strongly aligned with expert perceptual evaluations. Kurt_DBH and Skew_DBH have correlations of 0.81 and 0.79, respectively. In contrast, CV based on DBH shows a moderate to strong canonical correlation of 0.69.

The Hoover index, which had not been previously used to assess tree size diversity, had strong correlations above 0.7 when applied to height classes and BA (Hv_H5_BA, Hv_H2_BA). Similarly, the Atkinson index, when calculated for BA (Atkin_BA_75, Atkin_BA_01, Atkin_BA_25, Atkin_BA_5, Atkin_BA_1), showed moderate correlations above 0.65. In contrast, when applied to tree heights (Atkin_H_75, Atkin_H_01, Atkin_H_25, Atkin_H_5, Atkin_H_1), the Atkinson index demonstrated weak correlations below 0.4. The LikeJ index performed the

Table 4.

Overview of the calculated Hoover index used in the study, along with the corresponding class types (DBH or height), class size range, and proxy used to represent the sum of trees in each class

Acronym	Size class	Y_i	Range
Hv_DBH4_Ntrees	DBH 4 cm	N	0.1-0.5 (0.3)
Hv_DBH8_Ntrees	DBH 8 cm		0.2-0.6 (0.4)
Hv_H2_Ntrees	Height 2 m		0.2-0.4 (0.3)
Hv_H5_Ntrees	Height 5 m		0.0-0.5 (0.3)
Hv_DBH4_BA	DBH 4 cm	BA	0.1-0.4 (0.3)
Hv_DBH8_BA	DBH 8 cm		0.1-0.4 (0.2)
Hv_H2_BA	Height 2 m		0.3-0.6 (0.4)
Hv_H5_BA	Height 5 m		0.2-0.5 (0.4)
Hv_DBH4_H	DBH 4 cm	H	0.1-0.4 (0.3)
Hv_DBH8_H	DBH 8 cm		0.1-0.4 (0.3)
Hv_H2_H	Height 2 m		0.1-0.4 (0.2)
Hv_H5_H	Height 5 m		0.0-0.5 (0.2)

least effectively and has the lowest correlation with experts' grades among all the indices assessed (Fig. 7).

All indices examined in this study require a proxy for tree size or the proportion of trees within defined classes. The indices based on the tree radial size (DBH and BA) and height classes strongly aligned with expert perception of the tree size diversity. Of the top ten indices in the correlation matrix (Fig. 7, 8), nine were based on radial size, either representing tree size or the proportion of trees within defined classes. Five of the top ten indices utilized height classes,

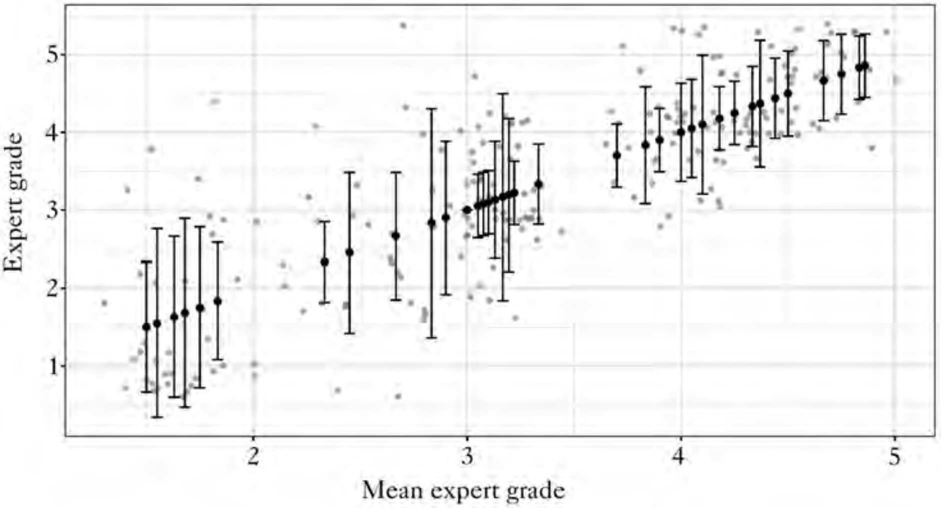

Fig. 6.

Distribution of individual expert grades (on a scale from 1 to 5) in relation to the mean plot grade for 36 study plots

Black points with error bars indicate the mean and standard deviation of the expert grades for each plot. Grey points, with jitter (random noise) applied for better visibility, represent the grades assigned by individual experts.

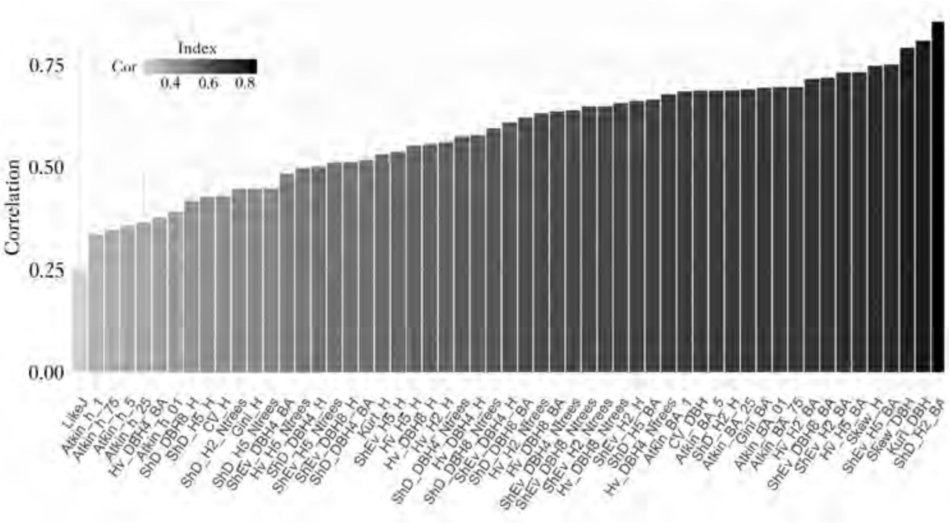

Fig. 7.

Selected tree size diversity indices ranked based on their canonical correlation to the experts' perceptual evaluation with class size (2 m *vs.* 5 m) showing minimal influence on performance, while one index employed 8 cm DBH classes. In contrast, DBH classes, tree counts, and the sum of tree heights per class generally exhibited weak to moderate success in discrete class-based indices.

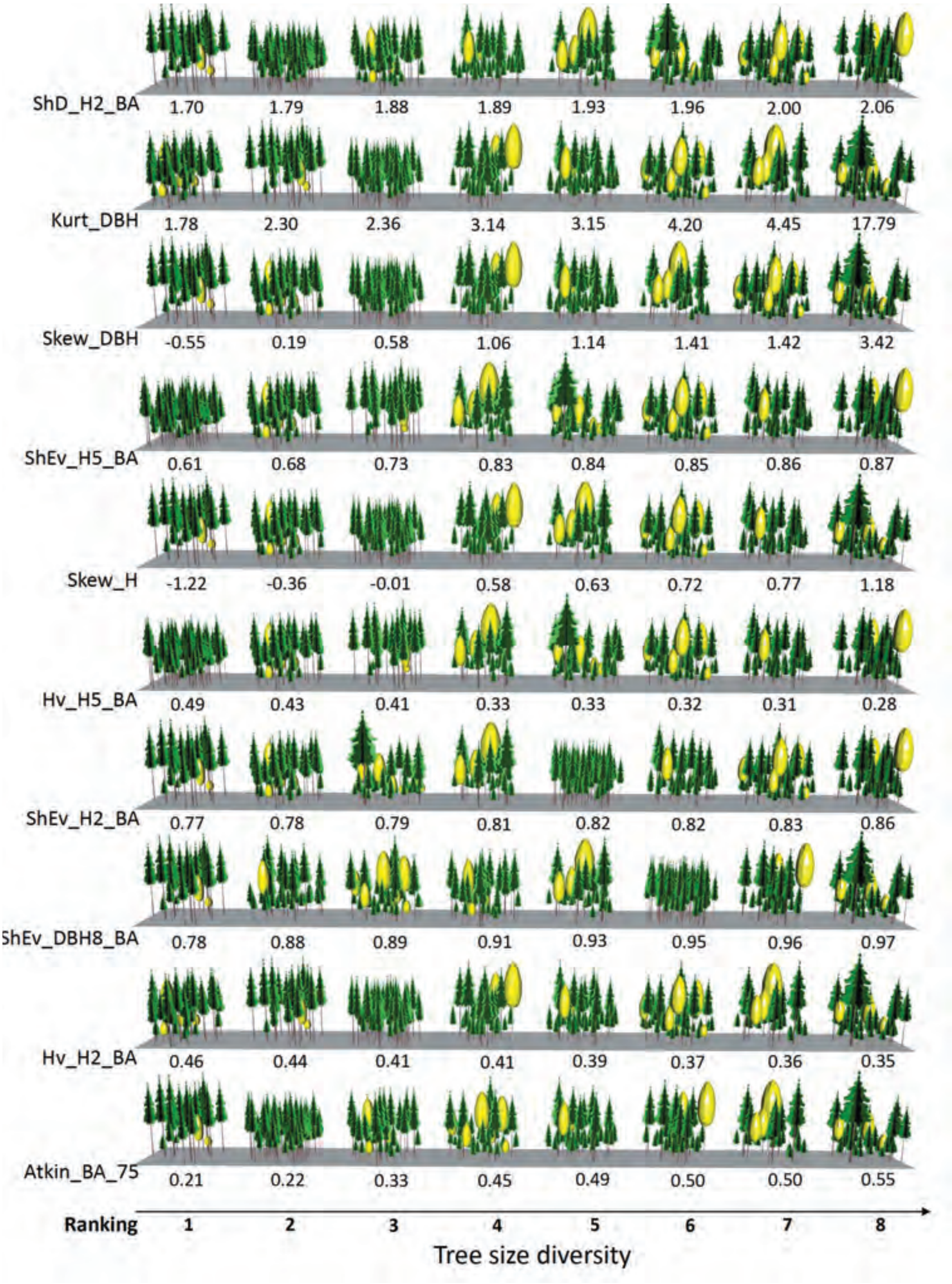

Fig. 8.

The visualization of eight randomly selected plots, ordered by increasing tree size diversity as measured by the top ten indices selected based on their correlation with expert perceptions. Hv_H2_BA and Hv_H5_BA are presented in descending order.

Discussion

Increasing importance of stand structure quantification. There has been a change in European silvicultural practices toward higher alpha diversity by increasing tree size diversity in the nearest neighborhood (Gadow *et al.*, 2012), with foresters often relying on their beliefs to achieve this goal. While qualitative assessment depends on foresters' experience and level of expertise, they can still provide a sound understanding of tree size diversity (Frey *et al.*, 2019). Consolidation of objective quantification and expert qualitative assessments can facilitate the integration of scientific research and forest management. Interestingly, several indices calculated in this study using small-size circular plots showed a strong correlation with experts' assessments of tree size diversity (Fig. 7). These indices capture different but interrelated dimensions of what foresters perceive as tree size diversity, such as size inequality, distribution, and dispersion. Each index has specific strengths and limitations that must be considered for accurate quantification of diversity (Lexerød and Eid, 2006; Motz *et al.*, 2010). The subsequent sections discuss these features and limitations from the silvicultural perspective. Furthermore, we explore the behavior of selected indices and their influence on the relationship between quantitative and qualitative assessments of tree size diversity.

Distribution dispersion and shape metrics: cv, skewness and kurtosis. The CV, skewness, and kurtosis are particularly effective with diverse datasets and limited sample sizes due to the lack of parametrization (Yusoff and Yap, 2012; Schillaci and Schillaci, 2022) and are frequently used to quantify tree size diversity (Bohn and Huth, 2017; Ali, 2019). However, despite the long tradition of use, CV may not fully capture the intricate complexity of certain forest structures. For instance, CV overestimates tree size diversity in stands with distinct upper and lower canopy layers, as it measures dispersion relative to the mean (Schillaci and Schillaci, 2022). Thus, CV may be useful to differentiate simple and more complex structures, but it will not provide a complete overview of the gradient of the tree size diversity.

Skewness quantifies how tree size values scatter from the mean, while kurtosis quantifies the concentration of tree sizes around specific values. In uneven-aged stands, which are characterized by a high density of younger generations and the presence of overstory trees, size values often cluster around smaller values below the mean, leading to positive and significant skewness and kurtosis. However, the clustering, either below or above the mean, can also be influenced by the presence of 'outliers' within an otherwise uniform distribution. A notable example in forestry is retention trees, which are left standing in the forest to improve biodiversity. Although retention trees contribute to overall diversity, skewness, and kurtosis indices may inadequately represent their impact on tree size diversity. Since skewness and kurtosis show the specific aspects of tree size distribution, depending solely on them may provide a limited view of overall tree size diversity. For instance, a plot ranked 8th in ShD_H2_BA, characterized by a high degree of space occupancy, is only ranked 4th for skewness and kurtosis (Fig. 8). Thus, we recommend using distribution dispersion and shape metrics, in combination, as a set of complementary indices to fully understand stands with the complex forest structure.

The Gini coefficient as a measure of tree size inequality. Like CV, skewness, and kurtosis, the Gini coefficient is non-parametric. It provides values on a closed range (Cordonnier and Kunstler, 2015) and shows moderate agreement with expert assessments, as reflected by a canonical correlation of 0.69. In forestry sciences, the Gini coefficient applied to individual tree BA is one of the most frequently used as a measure of tree size diversity (Peck *et al.*, 2014; Cordonnier and

Kunstler, 2015; Pach and Podlaski, 2015; Bourdier *et al.*, 2016; Pretzsch and Hilmers, 2024). However, the Gini coefficient primarily depicts inequality in tree sizes rather than offering a complete picture of the tree size diversity gradient. Similarly, to skewness and kurtosis, the presence of a single dominant tree with an exceptional size or a sparse upper layer can disproportionately increase the Gini value, limiting a more nuanced understanding of tree size diversity across the whole gradient.

SHANNON DIVERSITY, EVENNESS, AND HOOVER INDICES: THE CRUCIAL ROLE OF PARAMETRIZATION. The ShD indices, especially those based on smaller height classes (*e.g.*, ShD_H2_BA), demonstrate significant potential for characterizing tree size diversity as perceived by experts, which is reflected by the robust canonical correlation with experts' grades (Fig. 7). These indices capture the entropy of tree distribution across height classes (Jost, 2006), thereby reflecting the vertical space occupancy within forest stands. Even though ShD indices have frequently been used in the past to describe tree size diversity (Young *et al.*, 2011; Dănescu *et al.*, 2016; Sharma *et al.*, 2020), challenges arise when using ShD indices to compare diversity across biomes and growing conditions, as disparities in maximum tree size affect the number of size classes and potentially misleading results in favor of sites with larger trees. To address this, ShEv indices may offer an alternative (see also del Río *et al.*, 2016). Indices such as ShEv_H5_BA, ShEv_H2_BA, and ShEv_DBH8_BA, which include height or DBH classes and BA as a proxy for tree share, effectively capture tree size diversity as perceived by experts (Fig. 7). However, ShEv indices may show reduced sensitivity to tree size diversity changes in uniform stands as they prioritize the evenness of distribution over the number of occupied classes. For example, a 50-year-old even-aged pre-mature stand is ranked 5th and 6th out of 8 for ShEv_H2_BA and ShEv_DBH8_BA, respectively (Fig. 8), indicating above-average values for these indices. Although trees are distributed across only a few adjacent DBH and height classes, they remain abundant in all of them, which results from self-thinning law, with an age-progressive mortality rate in fully stocked even-aged stands (Trifković *et al.*, 2023).

Although not previously used for study tree size diversity, Hoover indices can be used as well in this context. Hv_H5_BA and Hv_H2_BA provide moderate correlations with experts' grades, which is comparable to the best-performing ShEv indices. Hoover indices are less dependent on the maximum tree size compared to ShD indices and are less affected by the evenness of distribution within adjacent size classes than ShEv indices. Simply, Hoover indices account for the amount of redistribution of trees across all size classes needed to achieve an equal distribution across classes, with the potential for such redistribution increasing as the number of size classes increases. However, Hoover indices may underestimate tree size diversity in two-aged stands where there is minimal variance within layers but significant differences between layers, especially with relatively large size classes. In practice, such stand structures can be formed as a result of intensive crown thinning, which removes dominant and suppressed trees and facilitates natural regeneration (Olson *et al.*, 2014; Dagley *et al.*, 2023).

To some extent, all of the discrete class-based indices rely on the premise that trees are evenly distributed across classes in structurally diverse forests. However, it may not hold true across varying ecosystems, species, or, importantly, size classes and the proxies used to estimate the proportion of trees in each class (Fig. 9). For instance, indices based on tree counts within DBH or height classes (*e.g.*, Morgenroth *et al.*, 2020) underestimate size diversity in steady-state uneven-aged stands with a negative exponential diameter distribution. These indices give higher values when trees are evenly distributed across size classes, failing to reflect the inherent inequality in space required for trees of different sizes. Our research demonstrates that using height classes

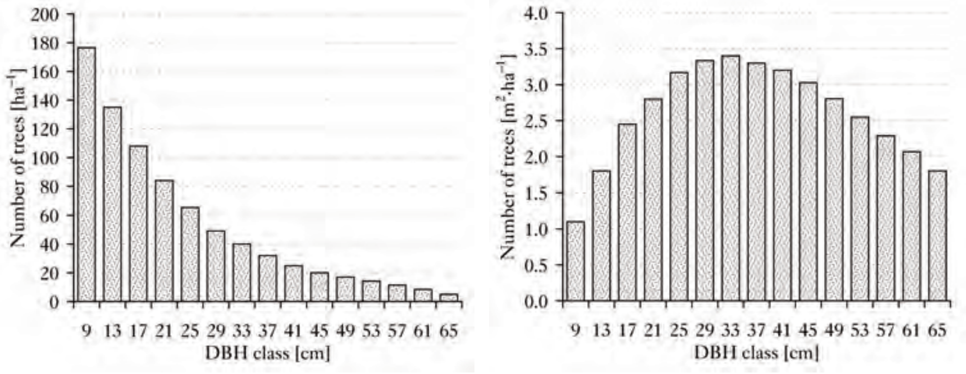

Fig. 9.

The distribution of the number of trees and the sum of basal area per ha across 4 cm DBH classes for a theoretical steady-state uneven-aged forest in the Zagnańsk forest district with a *q* factor of 1.28 (Drozdowski *et al.*, 2014)

instead of DBH classes improves the correlation of the ShD index with the qualitative evaluation of tree size diversity. However, while DBH is measured for all trees during forest inventories, height measurements are typically restricted to a sub-sample of trees due to their greater time demands. The effectiveness of tree size diversity indices based on predefined classes depends on their parametrization, particularly the criteria used to define the size classes. Thus, careful consideration of parametrization is essential for ensuring accurate, silviculturally and ecologically meaningful assessments of tree size diversity.

EXPLORING THE UNTAPPED POTENTIAL OF THE ATKINSON INDEX AND THE ROLE OF THE AVERSION PARAMETER. Regardless of the chosen ε parameter, the Atkinson index applied with BA demonstrates a moderate correlation (0.68-0.69) with experts' perceptual evaluations of tree size diversity, with the highest correlations observed when ε is either relatively large (0.75) or small (0.1). With a larger *ε* value, the Atkinson index becomes more sensitive to the distribution of smaller trees and less to the presence and distribution of large trees, which are key features of uneven-aged stands. Vice versa, when ε is small, the index places more weight on larger trees. The robust correlation observed at both ends of the ε parameter range indicates that experts' perception of tree size diversity is influenced by both, the distribution of smaller and larger trees, underlining that these aspects are not mutually exclusive. The distributions of smaller and bigger trees are not mutually exclusive but are strongly interlinked. For instance, the presence of large trees significantly impacts both the establishment and survival of the younger generation. While large trees are the source of seeds, they can also exert a strong influence on regeneration development through light limitations, as they cast shade that restricts the growth and survival of the understory (Larsen *et al.*, 1997; Curtin *et al.*, 2020; Kolisnyk *et al.*, 2024). This, however, introduces a degree of uncertainty in selecting the appropriate ε parameter, as it must be carefully selected for each application, leading to similar parametrization challenges described in the use of discrete class-based indices.

CRITICAL CONSIDERATIONS OF THE LIKEJ INDEX. While the LikeJ index is potentially an accurate tool to depict the tree size diversity, it does not demonstrate significance in the correlation with experts' perception (canonical correlation of 0.25). The main reason is that we purposely kept the LikeJ index without adapting the scoring system to our specific growing conditions. This decision was made because the existing literature already employs this index without adjustments for local conditions (Dănescu *et al.*, 2016). Recognizing that the LikeJ index is the most susceptible to parametrization pitfalls is crucial. Even with adjustments to local growing conditions, LikeJ cannot be used to compare plots across different sites, as it relies on specific numerical inputs and fine-tuning, which introduces subjectivity. Developing a unique scoring system for each site is labor-intensive and requires a high level of expertise.

LIMITATIONS OF THE STUDY. A main limitation of this research is the low number of respondents contributing to the questionnaire compared to other studies (*e.g.* Frey *et al.*, 2019). However, we believe that limiting the number of respondents to those actively involved in the management and research of the complex stands gives us a high expertise advantage. Our findings show that selected forestry experts exhibit a high degree of consistency in their perceptions of tree size diversity; thus, increasing the number of raters with a similar level of knowledge likely would not significantly alter the overall conclusions.

Another constraint is the focus on a single site. Nonetheless, the experimental network in Zagnańsk Forest is particularly valuable due to the proximity of stands with the same species composition, varying structures, and a well-documented management history, which provides a unique opportunity to analyse structural diversity.

Additionally, although Motz *et al.* (2010) suggest that some spatially explicit indices may be accurately estimated in fixed-radius circular plots, we restricted our study to distance-independent indices to avoid edge effects and ensure the usability of selected indices across varying plot sizes and conditions (Lilleleht *et al.*, 2014).

Conclusions

This study explores the relationship between the qualitative and quantitative measures of tree size diversity, emphasizing the importance of understanding tree size diversity indices in their application, as they reflect different aspects of stand structure.

The Shannon diversity index, based on height classes and basal area as a proxy for tree share within classes, representing vertical space occupancy, showed the strongest correlation with expert evaluations. However, its effectiveness, like other indices using predefined classes, depends on the parameterization of size classes, which requires cautious application.

In contrast, the kurtosis and skewness of the DBH distribution, which also demonstrated a strong alignment with expert assessments, are not affected by parameterization, making them versatile across different sample sizes and scales. These indices capture specific aspects of size distribution and should be used as mutually complementary measures or interpreted carefully. Several other indices, including Shannon evenness, Atkinson, and Hoover indices, showed moderate to strong correlation with experts' evaluations and were examined from both ecological and silvicultural perspectives.

Indices must be cautiously selected and interpreted based on sample size, research or management objectives, and growing conditions. To better address different aspects of tree size diversity in uneven-aged stands characterized by complex structures, combining multiple indices may be appropriate (*e.g.* Shannon index based on the height classes with Kurtosis and Skewness of the DBH distribution). Future research should focus not only on developing more sophisticated metrics but also on further bridging the gap between mathematical models, ecological traits, and applied silviculture. This integrated approach will advance forestry science in both theoretical and practical terms, supporting sustainable forest management and enhancing resilience to environmental challenges.

Authors' contributions

B.K. and K.B. – conceived and designed the study and developed the methodology; B.K. – performed analysis and drafted the original manuscript. All authors contributed to the review and editing of the original manuscript. All authors have read and agreed to this version of the manuscript.

Conflicts of interest

The authors declare no conflict of interest.

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STRESZCZENIE

Ilościowe i szacunkowe metody oceny stopnia zróżnicowania wymiarowego drzew na przykładzie drzewostanów jodłowych *Abies alba* Mill. w Nadleśnictwie Zagnańsk

Współczesna hodowla lasu przywiązuje dużą wagę do kształtowania drzewostanów mieszanych oraz drzewostanów o strukturze przerębowej. O ile na przestrzeni ostatnich 20 lat wzrost, struktura i dynamika drzewostanów mieszanych były przedmiotem zainteresowania wielu autorów, to drzewostany o budowie przerębowej oraz ich zróżnicowanie wymiarowe rzadko stanowiły obiekt systematycznych i pogłębionych badań. Tym niemniej zróżnicowanie wymiarowe, obok zróżnicowania gatunkowego i przestrzennego, stanowi jeden z najważniejszych aspektów zróżnicowania strukturalnego drzewostanów (ryc. 1). Znajomość tego aspektu jest istotna ze względu na poprawne modelowanie procesów ekologicznych przebiegających w lasach, monitorowanie ich rozwoju oraz budowę komputerowych systemów wspomagania decyzji hodowlanych. W literaturze przedmiotu opisano wiele ilościowych wskaźników oceny stopnia zróżnicowania wymiarowego drzew w drzewostanie, ale ich efektywność i czułość rzadko były przedmiotem pogłębionej analizy i porównania z ocenami szacunkowymi dokonywanymi przez ekspertów. W niniejszej pracy przyjęto 2 cele: (i) zbadanie szeregu ilościowych wskaźników opisujących stopień zróżnicowania wymiarowego drzew w gradiencie zróżnicowania strukturalnego – od jednowiekowych, jednogatunkowych i jednopiętrowych drzewostanów jodłowych, poprzez drzewostany dwugeneracyjne i dwupiętrowe, aż po drzewostany wielogeneracyjne, wielogatunkowe i wielopiętrowe (ryc. 2); (ii) porównanie otrzymanych wyników ilościowych z wynikami oceny szacunkowej dokonanej przez ekspertów z zakresu zagospodarowania lasów, którzy podejmują określone decyzje hodowlane na podstawie subiektywnych odczuć i przekonań.

W pracy wykorzystano dane z przeprowadzonej w 2022 r. inwentaryzacji standardowych parametrów biometrycznych drzew (średnica, wysokość, gatunek) na 36 stałych powierzchniach kołowych o wielkości 0,05 ha, reprezentujących opisany gradient strukturalny. Położone były one w swoim bliskim sąsiedztwie (maksymalna odległość między skrajnymi powierzchniami wynosiła 4 km) na terenie Nadleśnictwa Zagnańsk (leśnictwo Adamów). Na podstawie przeglądu literatury wybrano i przeanalizowano 54 różne warianty wskaźników zróżnicowania wymiarowego,

których obliczenie nie wymaga znajomości przestrzennego położenia drzew względem siebie (tab. 1-4; ryc. 3 i 4). Następnie 6 ekspertów zakwalifikowało każdą powierzchnię do jednej z 5 klas zróżnicowania strukturalnego, korzystając z odpowiednio ustrukturyzowanego formularza (ryc. 5): klasy 1. i 2. obejmowały drzewostany jednowiekowe i jednopiętrowe oraz jednowiekowe ze sporadyczną domieszką drzew w niższej warstwie drzewostanu; klasa 3. reprezentowała drzewostany dwugeneracyjne i dwupiętrowe; klasy 4. i 5. obejmowały drzewostany wielogeneracyjne, o strukturze zbliżonej do przerębowej oraz budowie w pełni przerębowej (znajdujące się w stanie równowagi demograficznej). Wyniki wskazują na zróżnicowaną czułość i przydatność uwzględnionych wskaźników do ilościowej oceny stopnia zróżnicowania wymiarowego drzew (ryc. 6-8). Z kolei wyniki badań ankietowych odznaczały się dużym podobieństwem, czego wyrazem była wysoka wartość stopnia wiarygodności międzyosobniczej respondentów (współczynnik Kappa Cohena = 0,64) (ryc. 6). Wartości współczynników korelacji kanonicznej pomiędzy ilościowymi wskaźnikami strukturalnymi i wynikami szacunkowej oceny ekspertów były bardzo zróżnicowane: wahały się w zakresie 0,26-0,86 (ryc. 7). Najsilniejsze korelacje z ocenami ekspertów uzyskano w przypadku matematycznych wskaźników różnorodności i równomierności Shannona opartych na rozkładach pierśnicowego pola przekroju drzew w klasach wysokości, a także 2 wskaźników statystycznych: kurtozy i skośności rozkładów grubości. Wskaźniki Atkinsona i Hoovera, zaczerpnięte z nauk społecznych, wykazały nieco mniejszą przydatność. Małą przydatnością w drzewostanach o strukturze przerębowej odznaczały się standardowe wskaźniki różnorodności i równomierności Shannona oparte na rozkładach zagęszczenia drzew w klasach grubości (ryc. 7). Najniższą korelację osiągnął wskaźnik LikeJ (ryc. 7). W przypadku drzewostanów o uproszczonej strukturze wiele wskaźników wykazuje efektywność, natomiast w drzewostanach o strukturze przerębowej można korzystać zamiennie z wyżej wymienionych wskaźników matematycznych i statystycznych, reprezentujących nieco inne aspekty zróżnicowania wymiarowego drzew (ryc. 8 i 9).

Wyniki wskazują na potrzebę właściwego wyboru ilościowych wskaźników zróżnicowania wymiarowego drzew w zależności od wielkości próby, celu badawczego oraz kategorii analizowanych drzewostanów. Przyszłe badania powinny koncentrować się nie tylko na opracowywaniu bardziej złożonych wskaźników, lecz także na wypełnieniu luki pomiędzy wymiernym podejściem matematycznym oraz sztuką hodowli lasu.

Warsaw, 02.06.2025

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Kolisnyk, B., Brzeziecki, B., Jankowski, P., Drozdowski, S., & Bielak, K. (2025). Linking the quantitative and qualitative approaches to assessing tree size diversity using silver fir (Abies alba Mill.) stands in the Zagnańsk Forest District. Sylwan, 168, Article 12. https://doi.org/10.26202/sylwan.2024057

my individual contribution constitutes the major part of the work presented in this publication, including the conceptualization and design of the study, development of the methodology, performance of the analysis, drafting of the original manuscript, and the review and editing of the final version.

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my individual contribution involved the final review and editing of the manuscript.

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my individual contributions included securing research funding, conceptualisation of the study, data collection, as well as reviewing and editing of the manuscript.

Kamil Bielak

Article 2: **Kolisnyk, B.**, Wellstein, C., Czacharowski, M., Drozdowski, S., & Bielak, K. (2024b). Contrasting Regeneration Patterns in *Abies alba*-Dominated Stands: Insights from Structurally Diverse Mountain Forests across Europe. Forests, 15, Article 7. https://doi.org/10.3390/f15071182

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forests

MDPI

Article

Contrasting Regeneration Patterns in *Abies alba*-Dominated Stands: Insights from Structurally Diverse Mountain Forests across Europe

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Abstract: To maintain the ecosystem resilience to large-scale disturbances in managed forests, it is essential to adhere to the principles of close-to-nature silviculture, adapt practices to the traits of natural forest types, and utilize natural processes, including natural regeneration. This study examines the natural regeneration patterns in silver fir (*Abies alba* Mill.)-dominated forests, analyzing how the stand structure—tree size diversity, species composition, and stand density—affects the regeneration. We analyze the data from four sites in Poland, Germany, and Italy, employing generalized linear and zero-inflated models to evaluate the impact of the management strategies (even- vs. uneven-aged) and forester-controlled stand characteristics (structural diversity, broadleaf species admixture, and stand density) on the probability of regeneration, its density, and the developmental stages (seedling, small sapling, and tall sapling) across a climatic gradient. Our results indicate a significantly higher probability of regeneration in uneven-aged stands, particularly in areas with lower temperatures and lower overall regeneration density. The tree size diversity in the uneven-aged stands favors advancement from juveniles to more developed stages (seedling to sapling) in places with higher aridity. A denser stand layer (higher stand total basal area) leads to a lower density of natural regeneration for all the present species, except silver fir if considered separately, signifying that, by regulating the stand growing stock, we can selectively promote silver fir. A higher admixture of broadleaf species generally decreases the regeneration density across all the species, except in a water-rich site in the Bavarian Alps, where it had a strong positive impact. These findings underscore the complex interactions of forest ecosystems and provide a better understanding required for promoting silver fir regeneration, which is essential for a close-to-nature silviculture under climate change.

Keywords: uneven-aged silviculture; mixed stands; ecosystem resilience; silver fir; sustainable forest management

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1. Introduction

The continuity of forest cover is a key element of sustainable forest management and strongly depends on the effective tree regeneration resulting from the successful completion of a series of interconnected events. Any disruption in the sequence of these events can lead to the failure of the entire process, which is highly undesirable in places where the socio-ecological role of forests is incredibly high [1,2]. Mountain forests serve as primary buffers on slopes, playing a crucial role in protecting against soil erosion, water runoff, avalanches, landslides, and torrential floods. The integrity of mountain forests is crucial for their ecological functioning as habitats for wildlife and biodiversity hotspots. Mountain forests also play an increasingly important role in the provisioning of social functions like places for tourism and connectivity with nature in today's fast-paced world [3]. While the idea of protecting these forests through strict protection or minimal interventions is widely recognized by society, the reality is ominously different.

The current state of the European mountain forests is largely shaped by human activity and timber demands. Global warming-driven changes will further alter this landscape significantly, yet the demand for timber will persist, making the strict protection of large areas unfeasible. A notable example is the widespread Norway spruce (*Picea abies* (L.) Karst.) dieback in monodominant, monolayered plantations, which have replaced the mostly naturally diverse mixed mountain forests. There is a pressing need to restore these ecosystems to their "pre-management" diversity and support the species adversely affected by human activities. It is essential to develop sustainable management practices based on uneven-aged silviculture principles to promote a continuously high level of ecosystem functioning to satisfy the growing demand for timber and non-timber ecosystem services [4–7].

Silver fir (*Abies alba* Mill.), one of the species impacted by the artificial expansion of Norway spruce, could reclaim its place in the European mountain forests. More resilient to warm climates and drought than spruce [8], silver fir thrives in the montane zone and is found even in the flatlands in Poland and Ukraine [9,10]. Alongside European beech (*Fagus sylvatica* L.), it is extremely shade-tolerant and can be classified as a competitive stress tolerator, making it well-suited for uneven-aged silviculture [11–13]. The continuity and the demographic stability of silver fir-dominated forests hinge on a robust bank of natural regeneration. Recent decades have witnessed a decline in mature silver fir stands, but also in the natural regeneration layer at some places, even often despite the presence of sufficient seed production [14]. The key issues include suboptimal microsite conditions and stand characteristics, but also browsing by ungulates [15,16].

Paluch and Jastrzębski [14] observed the highest regeneration in the pure fir stands, with the regeneration reducing in the mixed stands as the proportion of silver fir decreased. Similarly, Dobrowolska [17] emphasized that the increase in the fir percentage in a stand correlates with enhanced regeneration quantity and height increments. While a higher percentage of silver fir in a stand composition appears to be beneficial for the regeneration quantity in the short term, long-term issues like allelopathic auto-intoxication in pure silver fir stands are well-documented [18]. Furthermore, Paluch and Jastrzębski [14] found that the survival rate of the fir regeneration in nearly mono-specific stands (90% of silver fir) with an admixture of Norway spruce, European beech, and Scots pine (*Pinus sylvestris* L.) was higher than in pure fir stands. However, the benefits offered by the admixture of other tree species might not be sufficient to offset the reduced seed availability.

The impact of the stand-level tree size diversification on the success of forest stand regeneration remains ambiguous. It is posited that uneven-aged stands exhibit greater resilience to disturbances such as windthrows at the stand level, enabling rapid regeneration. This resilience is attributed partly to the presence of multiple layers, particularly the understory, as well as to the existing regeneration [19]. Hence, as the introductory step to our research, we would like to confirm whether uneven-aged silver fir-dominated stands show a higher self-regeneration capacity compared to even-aged stands, which is gauged by the likelihood of seedling and sapling emergence to ensure forest continuity and maintain the demographic balance of silver fir under varying climatic conditions. Thus, our first hypothesis (H1) is that the probability of regeneration (for all the species and specifically for silver fir) is higher in uneven-aged stands than in even-aged stands (Figure 1, H1). Following the verification of the first hypothesis, we aim to explore in detail how the structural (tree size diversity) and compositional (admixture of broadleaved tree species) characteristics of uneven-aged stands (i.e., stands with at least two age classes or layers) influence the density of regeneration, focusing particularly on silver fir. Hence, our second and third hypotheses (H2) posit that improved stand characteristics (increased tree size diversity, admixture of broadleaf tree species, and reduced total basal area) positively influence the total density of natural regeneration (Figure 1, H2) and (H3) increase the influence the density of regeneration, focusing particularly on silver fir. Hence, our second and third hypotheses (H2) posit that improved stand characteristics (increased tree size diversity, admixture of broadleaf tree species, and reduced total basal area) positively influence the total density of natural regeneration (Figure 1, H2) and (H3) increase the dominant developmental stage of natural regeneration (seedlings, small saplings, and tall saplings) of silver fir (Figure 1, H3). The presence of large overstory trees is considered to be a good forestry practice, leading to increased biodiversity and other socio-ecological functions. For instance, in Poland, a minimum of five large trees per hectare should remain [20]. Considering that large trees can also produce an excessive amount of seeds and are not inherent in the tree size diversity, we are interested in whether the (H4) presence of large overstory silver fir trees contributes to a higher density of silver fir regeneration (Figure 1, H4). Understanding how silver fir at the youngest age responds to different management strategies and stand characteristics, which foresters can influence, is vital for active protection and sustainable management.

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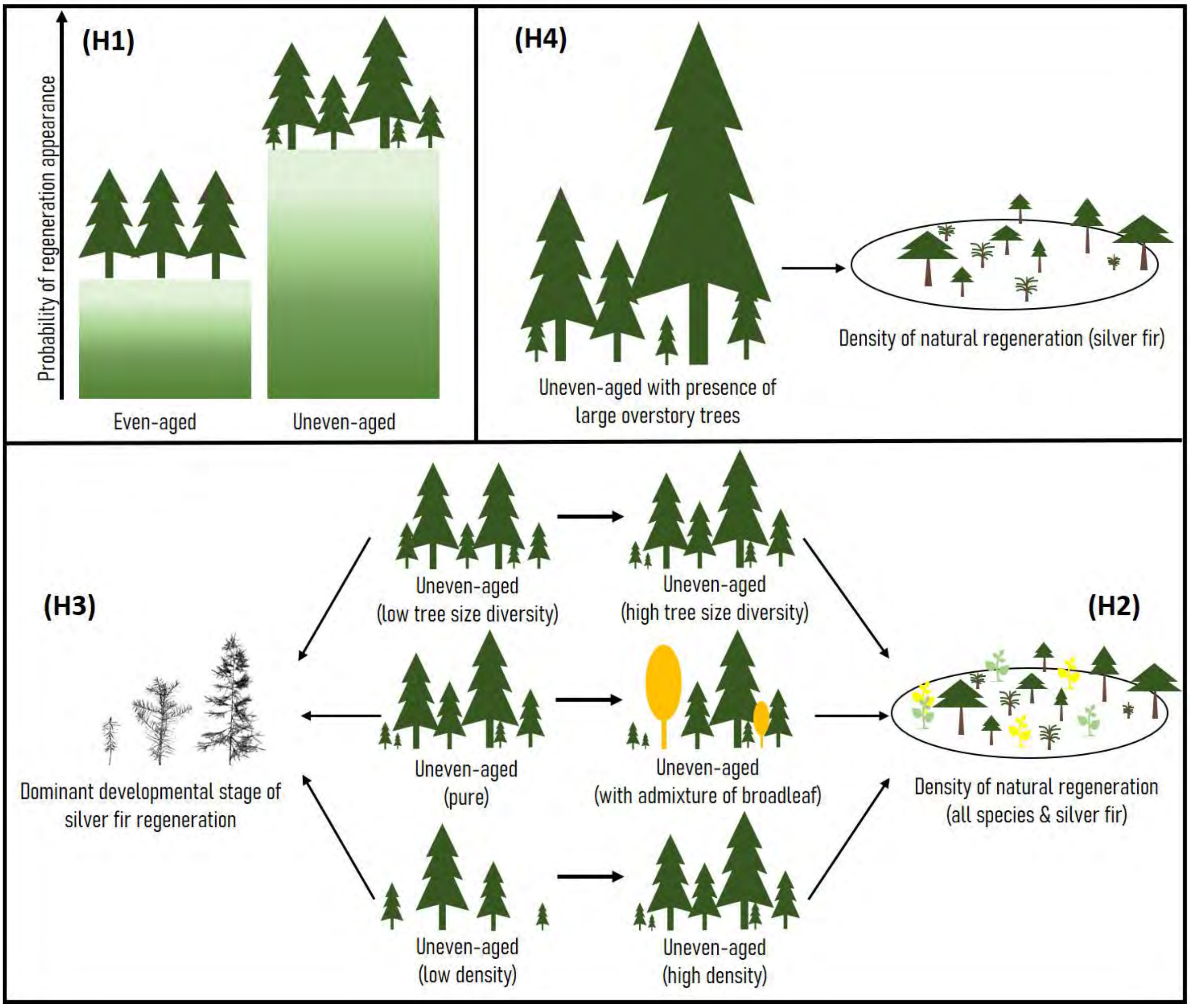

Figure 1. Schematic representation of formulated hypotheses (H1–H4).

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2. Materials and Methods

2.1. Research Area

The study was conducted across four sites in Poland, Germany, and Italy, covering a wide climatic gradient and a large part of the silver fir natural range (Figure 2; Table 1).

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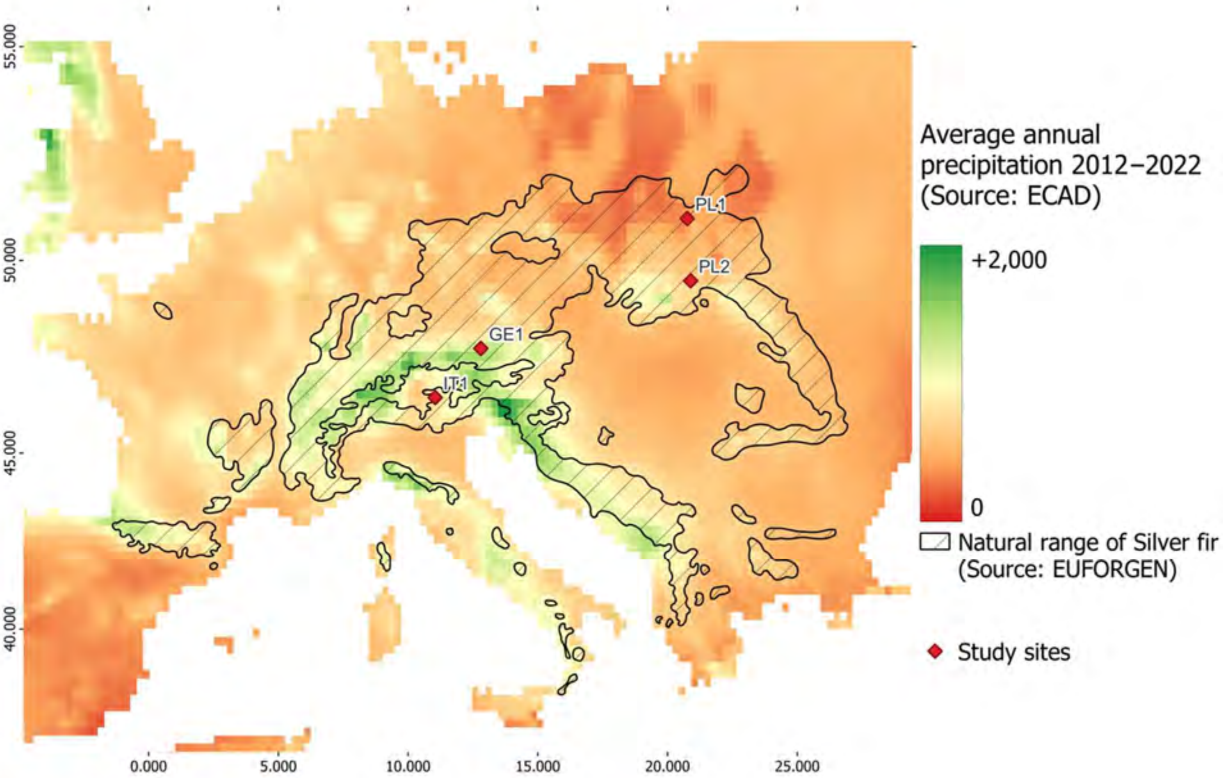

Figure 2. Map showing the locations of the study sites, natural range of silver fir (source: European Forest Genetic Resources Programme, EUFORGEN), and average annual precipitation for the period 2012–2022 (source: European Climate Assessment & Dataset, ECAD [21]).

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Table 1. The general characteristics of the research sites.

Site	Elevation	Average Annual Temp. (°C) *	Sum of Annual Precipitation (mm) *	Total Basal Area (m² ha⁻¹)	Admixture of Broadleaf Species (%)
Tissens-Laurein, Italy *(IT1)*	1060–1750 (1320)	3.1–8.8 (6.8)	642–1336 (894)	29.8–99.5 (53.4)	0–34.3 (13.9)
Inzel, Germany *(GE1)*	820–1140 (920)	6.2–8.5 (7.6)	1471–2081 (1805)	40.7–70.1 (54.1)	0–35.7 (11.5)
Zagnansk, Poland *(PL1)*	320–400 (350)	7.3–9.8 (8.7)	531–816 (685)	21.1–46.9 (34.1)	0–36.5 (13.0)
Nawojowa, Poland *(PL2)*	580–820 (650)	8.1–10.5 (9.4)	702–1087 (902)	31.0–62.9 (45.4)	0–58.8 (15.3)

* For IT1 and GE1, climatic grid data from ECAD with a resolution of 0.1 degrees were used. For PL1 and PL2, due to the tendency of ECAD E-OBS data to underestimate precipitation in central Poland, data from the nearby local climatic station in Bartków for PL1 and Nowy Sącz for PL2 were used. Climatic data are a product of the last 20 years.

Table 1 is located in the Zagnańsk Forest District, within the Małopolska Upland, on the outskirts of the Świętokrzyskie Mountains range. This district marks the northeastern boundary of the silver fir's distribution, presenting a unique opportunity to study the marginal populations facing environmental stress and explore regeneration dynamics at the species' range limit [22]. The second site (PL2) is in the Nawojowa Forest District, situated in the western part of the Low Beskid Mountains. This area lies on the east of the Carpathian flysch, featuring a geological formation of alternating sandstone and shale layers, and is a part of the Sądecki Beskids [23]. Contrary to Zagnańsk, Nawojowa provides optimal conditions for fir growth and development, serving as an uninterrupted habitat for silver fir.

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IT in the Tisens-Laurein region is nestled within the Southern Alps in South Tyrol, Italy. IT1 experiences heavy snowfall during the winter, leading to prolonged snow cover that significantly affects local hydrology and ecosystem dynamics. Plots in IT1 are located in the mountain mixed forest zone, close to the upper boundary, as evidenced by the limited vertical growth of broadleaf species (Figure S1). Lastly, the site in Inzel (GE1), situated in the Bavarian Alps, Germany, is an exceptionally water-rich area (Table 1) with pre-Alpine climatic conditions marked by distinct seasonal changes. Cold winters with steady snowfall and mild, moist summers define the climate, with snowpack playing a crucial

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2.2. Data Collection

At each site, 34–36 circular plots were established, with an area of 0.05 hectares, using Field-Map technology [24], to have at least 3-4 replications for each stand type (Figure 3). By having 3-4 replications per stand type, we ensure that our dataset is robust, captures the variability within each type, and meets the minimum requirement for regression analysis. These plots span a gradient from simple, pure, even-aged to complex, mixed, uneven-aged silver fir-dominated forest stands, with the fir constituting ≥ 40% of the stand's basal area. For even-aged stands, a pair of pre-mature (40–80 years old) and mature (80–120 years old) were included per site. The admixture tree species predominantly include European beech and Norway spruce. The research plots are distributed across stands with varying tree size diversity and admixtures of broadleaf tree species (Figure 3; Figure S2). The positioning of plots within each site is random and confined within a maximum 10 km radius.

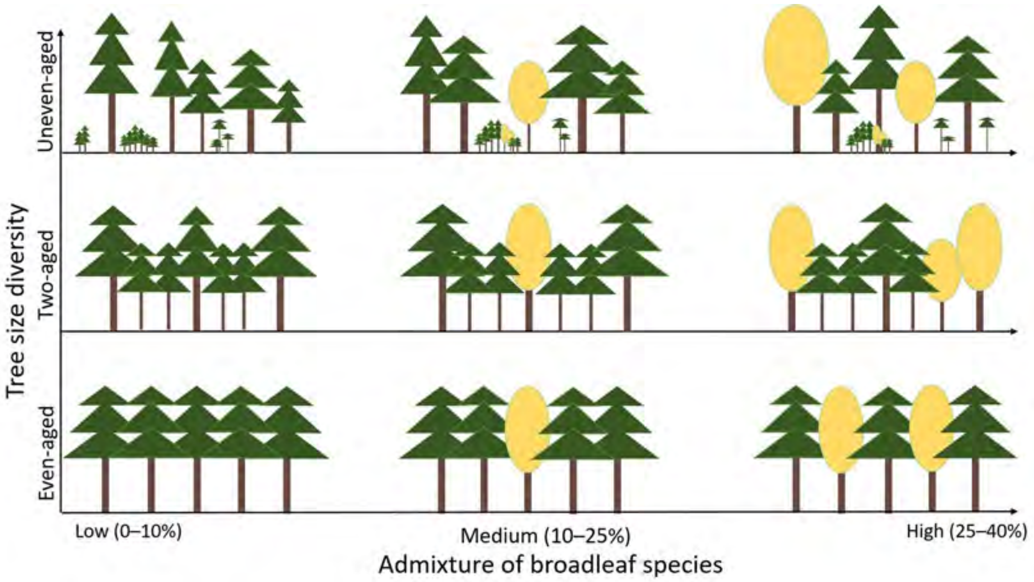

Figure 3. Plot selection matrix, including tree size diversity (vertical axis) and admixture of broadleaf tree species (horizontal axis). This design was used for plot selection purposes in the field to ensure that, at each site, plots equally cover compositional and structural gradients. All plots were used to answer H1; plots classified as transition stage and uneven-aged were used to answer H2–H4.

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All trees larger than 7 cm in diameter at the breast height (DBH) within the plots were mapped in a 3D local coordinate system. Following standard dendrometric measurements were performed, including DBH in mm, species identification, and documentation of any significant damages (such as wind breakage, decay, and beetle damage). For selected trees, additional measurements were taken, including total height, height to crown base—the height to the lowest living branch forming the continuous crown—and crown projection in four directions. Height curves were fitted to estimate the heights of the non-measured trees (Figure S1).

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Natural regeneration was measured within concentric subplots. In the first subplot, with a radius of 1.26 m, seedlings aged 2+ years and under 50 cm in height (after seedlings) were recorded, with the total count of seedlings per species noted. The second concentric plot, with a radius of 2.52 m, focused on small saplings taller than 50 cm but with a DBH of less than 2 cm (after small saplings). The third subplot, with a radius of 3.99 m, included ments were performed, including DBH in mm, species identification, and documentation of any significant damages (such as wind breakage, decay, and beetle damage). For selected trees, additional measurements were taken, including total height, height to crown base—the height to the lowest living branch forming the continuous crown—and crown projection in four directions. Height curves were fitted to estimate the heights of the non-measured trees (Figure S1).

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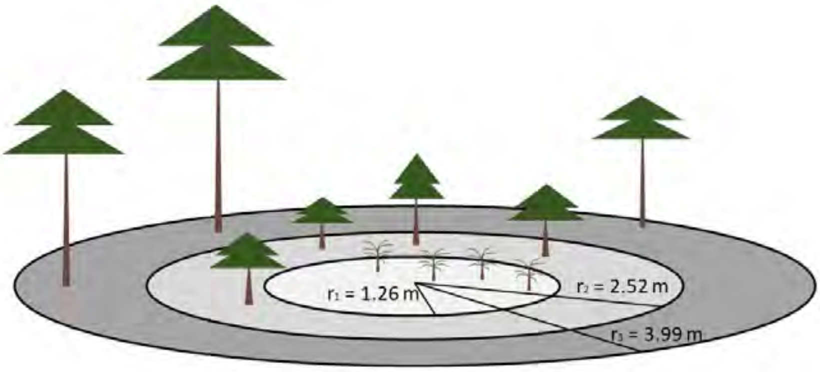

Figure 4. Schematic representation of concentric subplots for natural regeneration, where r_1, r_2, and r_3 are the radiuses of the subplots.

Figure 4. Schematic representation of concentric subplots for natural regeneration, where r₁, r₂, and r₃ are the radiuses of the subplots.

2.3. Tree Size Diversity and Admixture of Broadleaf Tree Species

To address H1, the initial classification of forest stands into even-aged and uneven-aged was performed directly in the field and later validated by measuring age at breast height (from increment cores) to mitigate bias. The number of even-aged plots per site was around 10–12. To answer hypotheses H2–H4 and to numerically describe the continuous tree size diversity, we used the Shannon diversity index (ShD) with the 4-m height classes and the sum of the basal area (BA) of all trees larger than 7 cm per class as a proxy of the class share. For instance, in class (4,8], we summed up the basal area of all trees taller than 4 m but equal to or shorter than 8 m and used it as a proportion of trees in the class (4,8]. The generalized formula is based on the proportion of observed objects in the selected class to the total across all classes (Equation (1)).

$$ShD = -\sum_{i=1}^{N} p_i \times \ln(p_i) \tag{1}$$

where

- N is the number of classes;
- p_i is the proportion of trees in the i-th class.

Subsequently, to facilitate comparison across different locations, the Shannon diversity index values were normalized to a 0–1 scale, with each site's diversity score divided by the maximum observed value for the site. The share of broadleaf tree species within each plot was determined by calculating the proportion of the total BA represented by broadleaf species.

2.4. Developmental Stage of Fir Regeneration

To estimate the dominant developmental stage (DS) of silver fir regeneration (seedling, small sapling, and tall sapling) within each plot, we employed a straightforward approach (Equation (2)) based on the adjusted formula of the weighted mean [25].

$$DS = \frac{1 \times \text{seedling} + 3 \times \text{small saplings} + 5 \times \text{tall saplings}}{\text{density all stages}} \tag{2}$$

where

- seedlings, small saplings, and tall saplings represent the per hectare density of silver fir regeneration in each respective developmental stage;
- density of all stages denotes the total density per hectare of silver fir regeneration across all developmental stages;
- 1, 3, 5—weights that signify the increasing importance of saplings with increasing developmental stage.

This approach was selected to provide a simple yet effective representation of the predominant developmental stage of silver fir regeneration across the plots. The weighting scheme (1, 3, 5) was empirically tested against an alternative conventional scheme (1, 2, 3) that is typically the first choice for such purposes. The results showed that the DS calculated with weights 1, 3, 5 produced residuals that were more favorable for the fitted model's performance. Specifically, the residuals with the 1, 3, 5 weighting scheme were smaller and more uniformly distributed, indicating a better fit and more accurate representation of the predominant developmental stages.

2.5. Climatic Data

To account for climatic differences between regions, we utilized different data sources. For IT1 and GE1, climate grid data from ECAD E-OBS were used, featuring a high resolution of 0.1 degrees with daily resolution [21]. However, for PL1 and PL2, data from the Bartków and Nowy Sącz climatic stations were used due to the observed tendency of ECAD E-OBS data to underestimate precipitation in central Poland.

To more accurately assess the impact of precipitation and temperature on natural regeneration processes, we calculated the mean de Martonne aridity index for the last 20 years [26] as a product of these two variables (Equation (3)). The lower the Martonne index, the more arid the climate is.

$$Martonne = \frac{P}{T+10} \tag{3}$$

where

- P—annual *sum of* precipitation in millimeters;
- T—average annual temperature in degrees.

2.6. Density of Ungulates

Ungulates, particularly red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.), play a significant role in shaping forest ecosystems through browsing habits, often favoring more palatable tree species such as silver fir. This interaction can lead to changes in forest composition. Despite similar average densities of red deer across Poland, Italy, and Germany, their spatial distribution within these countries shows distinct patterns. In Poland and Germany, red deer are relatively uniformly distributed, with some areas of concentration, while, in Italy, about 75% are found in the central and eastern Alps [27–29].

Data on ungulate populations were sourced locally due to the lack of uniform data across different regions. For site IT1, red deer density data were obtained from the Autonomous Province of Bolzano—South Tyrol, Department of Forestry Services, Office for Wildlife Management. The mean density of red deer per hectare over the past 10 years was calculated from this source. Similarly, for sites PL1 and PL2 in Poland, data on red and roe deer densities over the previous 10 years were provided by the Zagnansk and Nawojowa forestry districts, respectively. In Germany, for site GE1, official red deer density data were unavailable; instead, data systemized by Suzanne T. S. van Beeck Calkoen [30] were used. To estimate the red deer density in GE1, two points from [30] nearest to the GE1 study site were selected, and the distance-weighted mean was calculated.

2.7. Statistical Analysis

2.7.1. Probability of the Regeneration

To test the first hypothesis, a logistic regression analysis was performed using the glm function from the "stats" package as part of the core R [31], with the binomial distribution family and logit link, focusing on binary outcomes of the probability of regeneration influenced by two predictors, namely structure type (even/uneven-aged) and site (Equation (4)). Due to the presence of regeneration on all the plots, and thus the insignificance of the data from GE1 for this regression, they were not used. Variables explaining climatic differences were not found to be significant.

$$log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \times Structure + \beta_2 \times Site \tag{4}$$

where

- p denotes the probability of the regeneration (all species);
- coefficients β_0, β_1, and β_2 correspond to the intercept and the effects of the two predictors on the log odds of the event, respectively;
- Structure—structure type (even/uneven-aged);
- Site—study site.

Following, a second logistic regression was fitted, with the probability of silver fir regeneration as a dependent variable, mean annual temperature and stand structure (even- and uneven-aged) as dependent variables, and site as a random effect using the data from all sites.

$$log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \times Structure + \beta_2 \times Temp + \alpha_{Site} \tag{5}$$

where

- p denotes the probability of the regeneration (silver fir);
- coefficients β_0, β_1, and β_2 correspond to the intercept and the effects of the two predictors on the log odds of the event, respectively;
- Structure—structure type (even/uneven-aged);
- Temp—mean annual temperature for the last 20 years;
- α_{Site}—random intercept for each site.

2.7.2. Regeneration Density

To answer the second hypothesis of our research using the "glmmTMB" R package version 1.1.9 [32], we fitted two zero-inflated (ZI) models with the truncated negative binomial distribution (TNB), chosen to address overdispersion and an abundance of zero observations (Table 2). Despite the final similarity in our case, in contrast to two-step models, ZI models assume that there are two kinds of zeros in the data: structural zeros and zeros that occur as the result of the count process. The ZI models simultaneously calculate the probability of an excessive amount of structural zeros (a logit model for the ZI part) and, in the case of the TNB, only the count model for non-zero data [32]. A simultaneous ZI model was selected over the classic hurdle model to check whether count zeros are crucial for the model or not without drastically changing the computation behind it (negative binomial distribution vs. truncated negative binomial).

Table 2. Overview of ZI models' components and variables used and tested for the regeneration density; those tested and not included were found to be statistically insignificant.

Component	Variable	Description	Part of the Model/Model
		Model 1 *—all species	
Dependent Variable	Density_all_ha	The density of natural regeneration of all species per hectare	

Table 2. *Cont.*

Component	Variable	Description	Part of the Model/Model
Fixed Effect	Martonne	Martonne aridity index	Main Model and ZI Part
Fixed Effect	Admixture_broad	Admixture of broadleaf tree species	Main Model and ZI Part
Fixed Effect	TBA	Normalized by maximum total BA of living trees per hectare	Main Model
Interaction Term	Site × Admixture_broad	Interaction between site and admixture of broadleaf tree species	Main Model
Random Effect	Site	The factor for grouping plots by site	Main Model
		Model 2—silver fir	
Dependent Variable	Density_fir_ha	Density of natural regeneration of silver fir per hectare	
Fixed Effect	Martonne	Martonne aridity index	Main Model and ZI Part
Fixed Effect	Admixture_broad	Admixture of broadleaf tree species	Main Model
Interaction Term	Site × Admixture_broad	Interaction between site and admixture of broadleaf tree species	Main Model
Random Effect	Site	The factor for grouping plots by site	Main Model
		Tested variables that were not included	
	Tree_size_div	Tree size diversity expressed as the normalized Shannon diversity index	Models 1 and 2
	Ungulates_density	Density of the ungulates by site	Models 1 and 2
	Admixture	Admixture of tree species other than fir by species	Models 1 and 2
	TBA	Normalized by maximum total BA of living trees per hectare	Model 2

* For model 1, the bootstrapping was applied with 1000 iterations using “stats” base R package [31].

2.7.3. Dominant Developmental Stage of Silver Fir Regeneration

To answer the third hypothesis, we evaluated the Gamma and Inverse-Gaussian distributions within the framework of generalized linear models (GLMs) to accommodate the right-skewed nature of our response variable using the same “stats” base R package [31]. The choice of an appropriate link function was crucial for linearizing the relationship between predictors and the response variable. To this end, we explored a variety of link functions, including the identity, logarithmic, inverse, square, square root, and beta distribution functions. The selection of the optimal model was based on minimizing the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC), and also considering the normality of the simulated residuals. This process led us to select the GLM with a Gamma distribution paired with a log link function as the best-fitting model (Table 3).

Table 3. Table of GLM components and variables used and tested for the regeneration-dominant developmental stage.

Component	Variable	Description
Dependent Variable	DS	Dominant developmental stage (DS) of silver fir regeneration
Fixed Effect	Martonne	Martonne aridity index
Fixed Effect	Tree_size_div	Tree size diversity expressed as the normalized Shannon diversity index
Interaction Term	Martonne × Tree_size_div	Interaction between site and tree size diversity
Random Effect	Site	A random intercept for each site
	Tested variables that were not included	
	Admixture_broad	Admixture of broadleaf tree species
	TBA	Normalized by maximum total BA of living trees per hectare
	Ungulates_density	Density of the ungulates by site

2.7.4. Presence of Large Overstory Trees

To answer our last hypothesis (H4), we initially defined a criterion for what constitutes an overstory tree, describing an overstory tree as any tree reaching at least 80% of the height of the tallest tree within a given site. The influence of these overstory trees on regeneration density was then analyzed using a binary variable (0 for absence; 1 for presence).

3. Results

3.1. Probability of the Regeneration Appearance

The regeneration density of all the species exhibits considerable variation across the sites, with silver fir consistently emerging as the dominant species in the regeneration layer. In GE1 and IT1, the mountain environment and higher elevations contribute to a greater share of spruce within the regeneration layer. Conversely, at lower altitudes, beech—and hornbeam only in PL1—predominantly complement the regeneration layer (Figure 5).

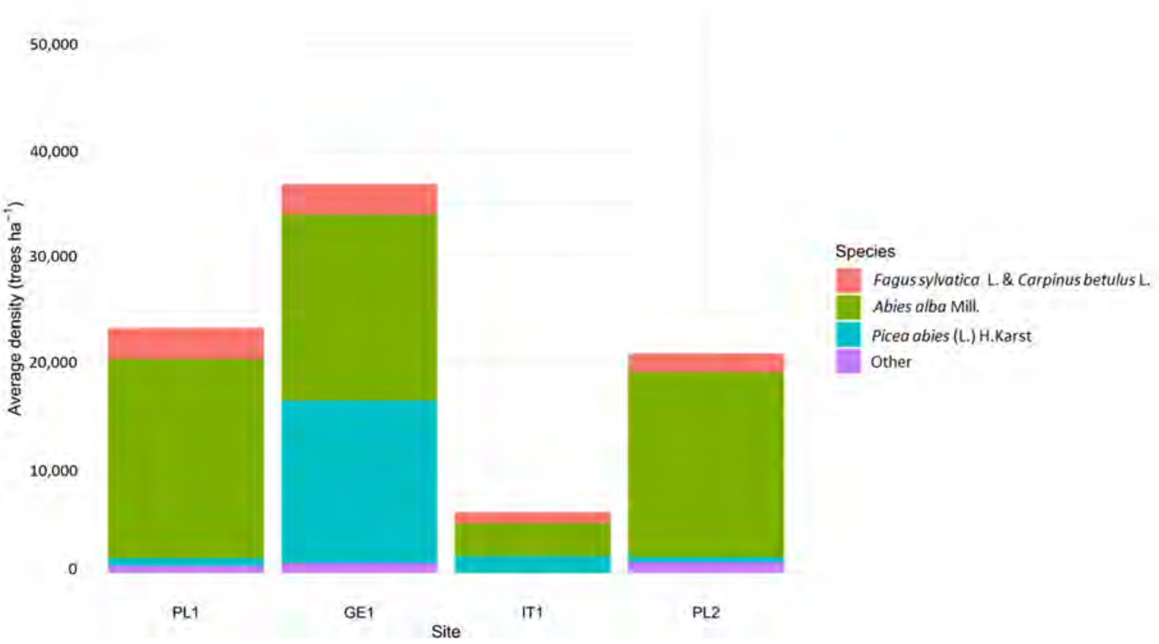

Figure 5. Comparison of the mean natural regeneration densities by species across four sites.

Figure 5. Comparison of the mean natural regeneration densities by species across four sites.

The likelihood of regeneration across various plots, regardless of the developmental stages (seedlings, small saplings, and tall saplings) and species involved, was significantly higher in the plots managed under uneven-aged forestry practices (Table 4; Figure 6). We observed a consistent trend where the probability of fir regeneration decreased, as well as a widening disparity between the even- and uneven-aged stands with a decrease in the average annual temperature (Figure 6). This trend was especially notable in IT1, where the average annual temperature and the overall density of regeneration were significantly lower compared to the other sites (Figure 5, Figure 6). Similarly, a difference in the regeneration of all the species between the even- and uneven-aged stands was observed. However, for all the species, the influence of the average annual temperature on the regeneration appeared to be insignificant.

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Table 4. Logistic regression summary on the influence of forest structure on the likelihood of regeneration (all species and fir) across four sites.

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	Regeneration Presence					
Predictors	**All Species**			**Silver Fir**		
	Odds Ratios	***CI***	***p***	***Odds Ratios***	***CI***	***p***
(Intercept)	3.75	1.14–16.95	**0.047**	0.00	0.00–0.69	**0.037**
Structure [Uneven-aged]	6.91	2.09–26.26	**0.002**	3.42	1.29–9.06	**0.014**
Site [IT1]	0.13	0.02–0.51	**0.007**			
Site [PL1]	1.75	0.26–14.62	0.568			
Temp				2.43	1.16–5.08	**0.018**
Random Effects						
σ^2				3.29		
τ$_{00}$				0.42 $_{\text{Site}}$		
ICC				0.11		

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Random Effects						
σ^2					3.29	
τ_{00}					0.42 $_{\text{Site}}$	
ICC					0.11	
N					4 $_{\text{Site}}$	
Observations		105			139	
R^2 Tjur		0.252			0.255/0.340	

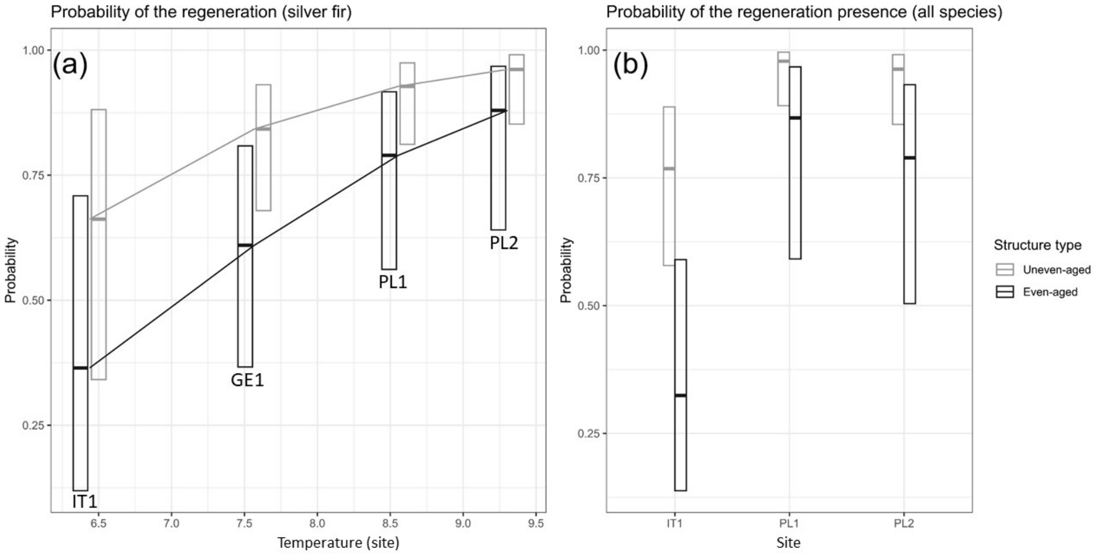

Figure 6. The probability of the regeneration for silver fir (**a**) and all species (**b**) in even- vs. uneven-aged stands across four sites and temperature gradients, with horizontal lines representing predicted values and boxes confidence intervals. Two solid lines connecting predicted values depict the trend of increased regeneration probability with increasing temperature.

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3.2. Regeneration Density

Across all the sites, higher total basal area (TBA) is associated with a decrease in the density of natural regeneration of all the species regardless of the tree size diversity and the presence of a broadleaf species admixture in the stand layer (Figure 7). Interestingly, while the inclusion of broadleaf species generally tended to slightly (but statistically significantly, Tables S1 and S2) decrease the density of the natural regeneration in places with a higher aridity index (PL1, PL2, and IT1), it notably increased the regeneration density in water-rich GE1 (Figure 7).

When considering solely silver fir regeneration, the findings diverge slightly. The density of silver fir regeneration does not appear to be influenced by TBA. Yet, similar to the overall trend, an increasing admixture of broadleaf species is associated with a decrease in the silver fir regeneration density in PL1, PL2, and IT1, whereas, in GE1, with a lower aridity index (high water sufficiency), it is associated with a significant increase (Figure 8).

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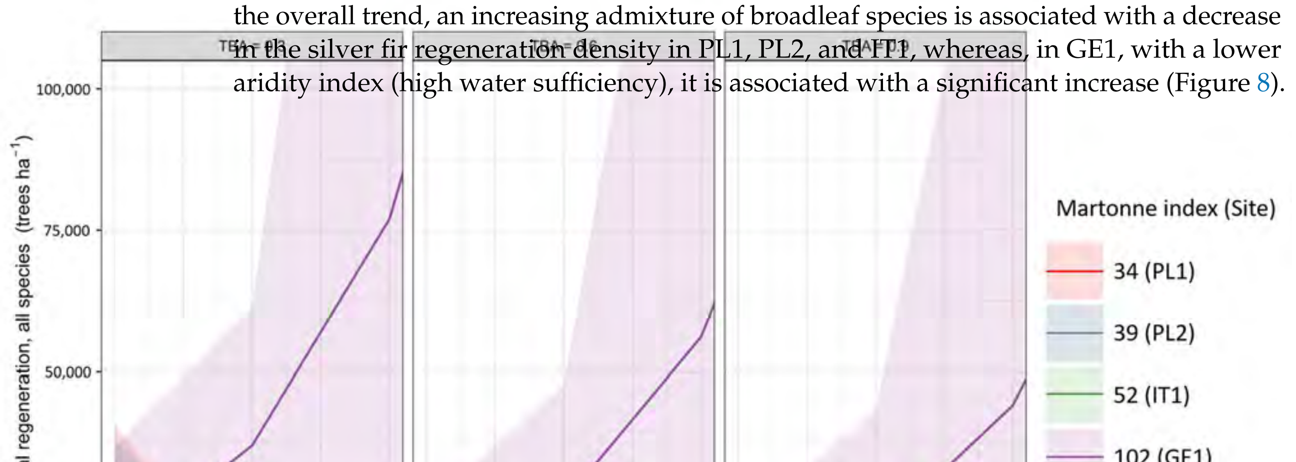

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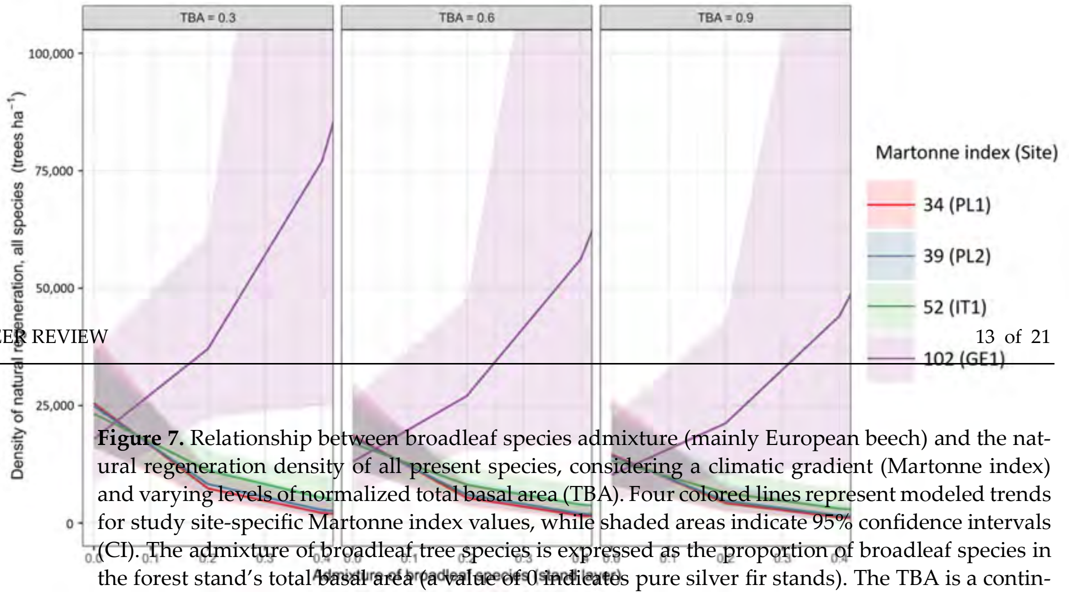

Figure 7. Relationship between broadleaf species admixture (mainly European beech) and the natural regeneration density of all present species, considering a climatic gradient (Martonne index) and varying levels of normalized total basal area (TBA). Four colored lines represent modeled trends for study site-specific Martonne index values, while shaded areas indicate 95% confidence intervals (CI). The admixture of broadleaf tree species is expressed as the proportion of broadleaf species in the forest stand's total basal area (a value of 0 indicates pure silver fir stands). The TBA is a continuous variable, with values close to 1 indicating maximum stand density in our plots. The selected TBA levels were chosen to cover the range of the parameter. Note that factors contributing to the relatively wide CI include high inherent variability in natural regeneration data, sample size, model complexity, and data range. Overlapping CIs may appear as a different color.

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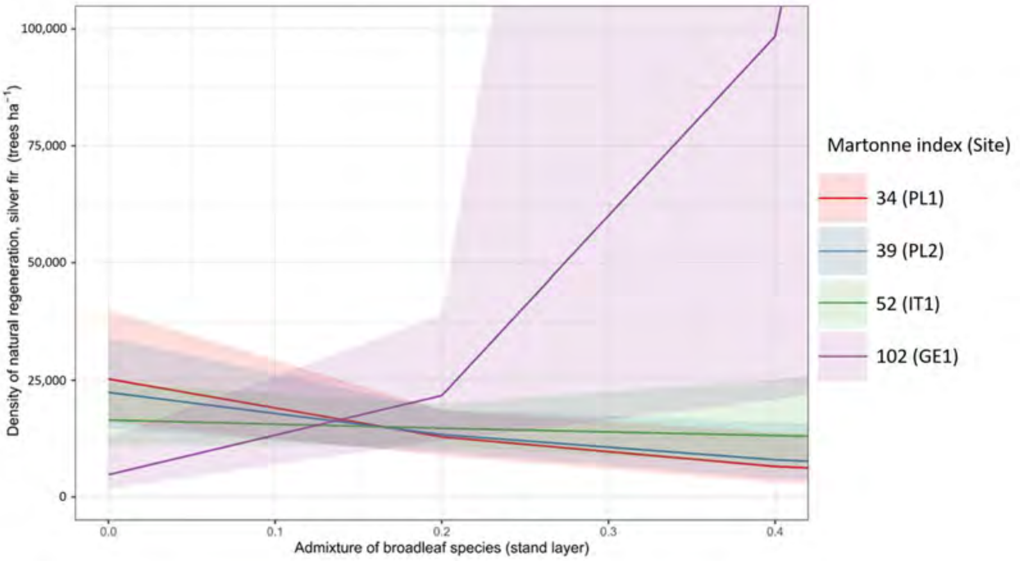

Figure 8. Relationship between broadleaf species admixture (mainly European beech) and the natural regeneration density of silver fir, considering a climatic gradient (Martonne index). Four colored lines represent modeled trends for study site-specific Martonne index values, while shaded areas indicate 95% confidence intervals (CI). The admixture of broadleaf tree species is expressed as the proportion of broadleaf species in the forest stand's total basal area (a value of 0 indicates pure silver fir stands). Note that factors contributing to the relatively wide CI include high inherent variability in natural regeneration data, sample size, model complexity, and data range. Overlapping CIs may appear as a different color.

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3.3. Dominant Developmental Stage of Silver Fir Regeneration

The tree size diversification has demonstrated a clear positive impact on the advancement of silver fir in the regeneration layer, indicating that vertical diversification significantly contributes to the progression of silver fir from the early growth stages (seedlings) to more developed stages (saplings) (Table 5; Figure 9). Notably, neither the TBA nor the admixture of broadleaf tree species within the stand layer has a discernible effect on the

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Table 5. GLM summary on the influence of forest tree size diversity on the DS of silver fir.

Predictors	**sqrt(DS)**		
	Estimates	***CI***	***p***
(Intercept)	0.96	0.68–1.35	0.813
Martonne	1.00	1.00–1.01	0.185
Tree_size_div	2.19	1.31–3.68	**0.003**
Martonne × Tree_size_div	0.99	0.98–1.00	**0.035**
Random Effects			
σ^2	0.07		
$\tau_{00\ \mathrm{Site}}$	0.01		
ICC	0.07		
N_{Site}	4		
Observations	77		
Marginal R^2/Conditional R^2	0.119/0.179		

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N_{Site}	4		
Observations	77		
Marginal R^2/Conditional R^2	0.119/0.179		

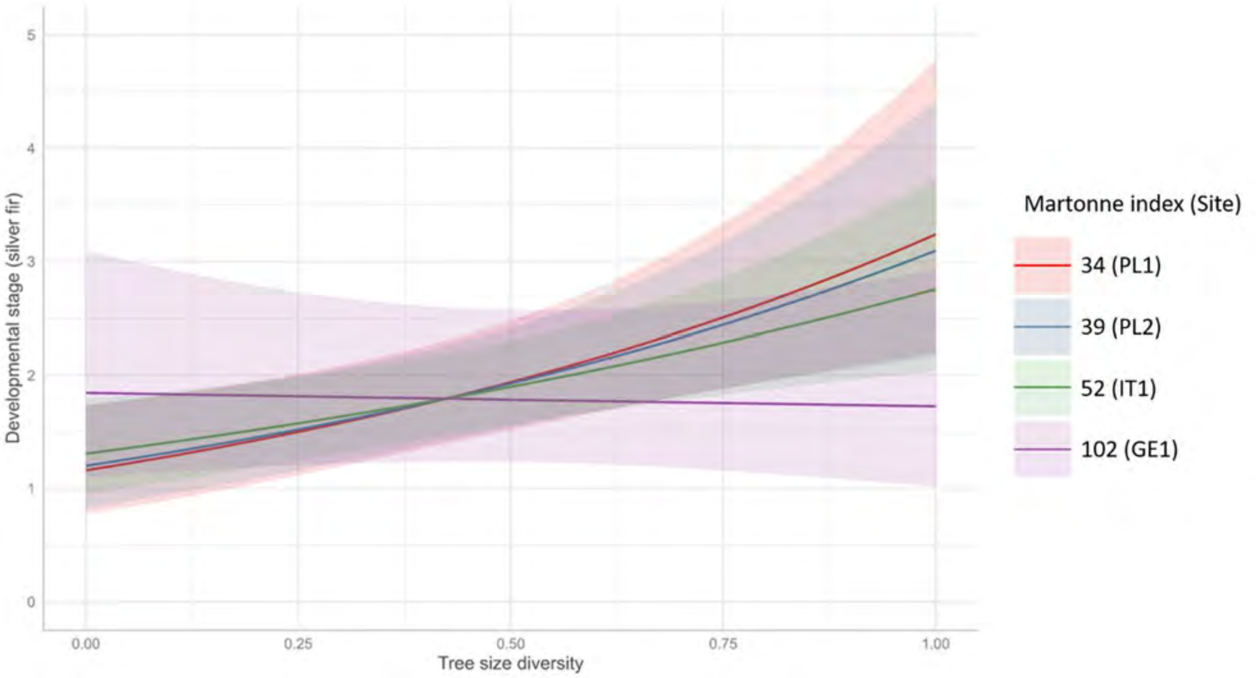

Figure 9. Relationship between tree size diversification in uneven-aged stands (only stands with two or more age classes), expressed as the Shannon diversity index (showing how diverse trees are in terms of size in the stand layer) and the dominant developmental stage of silver fir natural regeneration across a climatic gradient (Martonne index). The dominant developmental stages of natural regeneration range from 1 (predominantly seedlings) to 5 (predominantly tall saplings), indicating the advancement of natural regeneration. Four colored lines represent modeled trends for study site-specific Martonne index values, while shaded areas indicate 95% confidence intervals (CI). Note that factors contributing to the relatively wide CI include high inherent variability in natural regeneration data, sample size, model complexity, and data range. Overlapping CIs may appear as a different color.

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4. Discussion

4.1. The Likelihood of Regeneration Success—To Be or Not to Be?

The principle of fostering a robust bank of natural regeneration is anchored in the objective of establishing a resilient ecosystem capable of maintaining a stable level of ecosystem services provisioning, species demographic equilibrium, and prioritizing natu-

4. Discussion

4.1. The Likelihood of Regeneration Success—To Be or Not to Be?

The principle of fostering a robust bank of natural regeneration is anchored in the objective of establishing a resilient ecosystem capable of maintaining a stable level of ecosystem services provisioning, species demographic equilibrium, and prioritizing naturally favored species [33–35]. This is especially critical in the face of large-scale disturbances, which have become more frequent during the last decade [36]. Creating favorable conditions for the rapid restoration of ecosystem functioning by carefully selecting a forest management approach is paramount, even more so under the challenges posed by climate change [37,38].

Our findings support the implicit idea, resonating in numerous publications, e.g., [39–41], that uneven-aged stands are more likely to undergo natural regeneration than even-aged stands with a simplified vertical structure and closed canopy. This holds for all the species collectively and specifically for silver fir. Moreover, the disparity in the regeneration probability between the even-aged and uneven-aged stands is more pronounced for all the species than for silver fir alone (Figure 6).

For the germination of most forest tree species' seeds, three fundamental conditions are required: sufficient water, oxygen, and an optimal temperature range [42]. However, for the successful establishment and survival of regenerations beyond their first years, the substrate and the level of light availability become critical factors [43,44] in addition to the possible disturbance by browsing. Different species employ diverse life strategies and follow distinct recruitment patterns, resulting in varying resource requirements. Consequently, the environmental heterogeneity at the stand level, especially concerning the light availability, microsites, and soil conditions that partly arise from small-scale disturbances of uneven-aged forestry, is creating multiple niches for varied species regeneration [45,46]. The uneven-aged silviculture primarily involves modulating the competition for light across the forest's vertical profile, including the natural regeneration layer [19]. The increased light availability facilitates more optimal conditions through enhanced solar radiation reaching the forest floor, creating a favorable environment for regeneration development in general. For instance, Scheller and Mladenoff [47] compared the even-, uneven-aged, and old-growth forests in terms of the understory plant communities, including the regeneration of wooden plants. Scheller and Mladenoff [47] found that the understory species richness was lower in old-growth forests compared to even-aged forests, and, most importantly for us, lower in even-aged stands compared to uneven-aged stands, and attributed the difference to the available light and deadwood debris.

Certain tree species, including silver fir, can derive benefits from the limited light under the horizontally closed canopy of even-aged stands and degraded microsite conditions. Such trees experience reduced competition from other tree species in the regeneration layer, shrubs, and grasses [48]. Particularly in their early developmental stages, seedlings of extremely shade-tolerant species exhibit a remarkable degree of tolerance. Despite the minimal photosynthesizing area, which restricts growth, the small silver fir seedlings under the canopy can maintain their current stage for an extended period of time [49]. A study conducted in Comelico (Italian eastern Alps) in Norway spruce–silver fir stands showed that, in the gap system, the fir saplings were more abundant in the understory and less in the gaps, as compared with spruce [50]. Furthermore, even though the age structure of the regeneration in the gap showed that most of it appeared after the formation of the gap, saplings taller than 2 m were predominantly already present at the moment of the gap harvest [50], underscoring the importance of the understory presence for a rapid post-disturbance recovery. However, the advantage gained from the reduced competition does not outweigh the benefits derived from light availability. In even-aged stands, natural regeneration predominantly remains at the seedling stage, with the saplings that manage to develop often exhibiting a suboptimal "silvicultural" quality mainly due to insufficient light (Figure S2).

In addressing the rhetorical question of whether natural regeneration is more viable in uneven-aged stands, our research affirms its feasibility. Following this, we focused on identifying the forester-controlled stand characteristics only within the class of uneven-aged stands that could further enhance natural regeneration.

4.2. The Complexity of Choice: The Impact of Stand Density and Tree Size Diversity on the Natural Regeneration

We found that the tree size diversity does not affect the regeneration density, suggesting that any level of diversification in the vertical profile, which enables increased light penetration to the forest floor and/or improved microsite conditions, is sufficient to create an optimal environment for seed germination and the initial establishment of regeneration. Further diversification, even with improved microsite conditions and the availability of light, is not needed at the early developmental stages. However, as seedlings grow and progress and the demand for resources increases, a higher stratification in the vertical profile could theoretically partition the competition not only for light but also for other resources [46,51]. This provides a window of opportunity for seedlings to grow and develop, thus enhancing the average developmental stage of fir regeneration. This is supported by our findings that, in IT1, PL1, and PL2, where the main resource of competition is most likely water, the average developmental stage of regeneration increases with increasing tree size diversity, whereas, in the water-rich GE1, the tree size diversity appears to have no significant effect. While the quantity of regeneration may not increase, its quality, in terms of being in a more advanced developmental stage, improves, potentially enabling faster post-disturbance recovery. Moreover, reducing the TBA significantly boosted the density of all the species, although it did not notably influence the silver fir density alone. Thus, when the goal is to promote the natural regeneration of silver fir, selecting the locally optimal stand density emerges as an effective strategy.

The process of formation and further management of stands with high tree size diversity, such as those managed under the renowned "Plenterwald" system, is recognized for its complexity, time-intensive nature, and associated initial costs [52–55]. The maintenance and stable functioning of these systems necessitate frequent interventions [19,56]. While on a long-term scale such practices have proven to be economically viable in regions with well-developed infrastructure and accessible terrain, the feasibility of frequent interventions becomes questionable in remote areas with less developed infrastructure or challenging terrain [57–59]. In these contexts, in practice, foresters often resort to the less frequent single-tree selection system or shelterwood, creating simpler stand structures like two-layered stands [60]. Nevertheless, the critical question persists: do the advantages of an improved regeneration developmental stage, which acts as a form of ecological insurance for the quick recovery of ecosystem functions, outweigh the extra costs in areas where frequent management actions are economically demanding? This question, while beyond the scope of our current research, opens the field for further research.

4.3. Influence of Broadleaf and Conifer Interplay on the Natural Regeneration

The impact of species mixtures on the natural regeneration patterns of tree species is a topic of ongoing research within forest ecology, reflecting a limited understanding of this area. The high level of uncertainty in this field is often linked to the complexity of forested ecosystems, especially those characterized by a high level of diversity, which leads to increased entropy in terms of microsite conditions [61–63]. Generally, the introduction of broadleaved species at the stand level is observed to decrease the density of silver fir regeneration, with a belief that low levels of admixture might positively influence the fir regeneration density [14,17]. However, the threshold at which the benefits of improved microsite conditions offset the drawbacks of a reduced seed source remains ambiguous. Our findings in places with a comparatively higher aridity index (PL1, PL2, and IT1) align with the commonly observed trend: a small but overall reduction in the density of silver fir regeneration within stands dominated by fir. Contrary to expectations, the situation significantly diverged with increasing water availability (GE1). The GE1 is characterized by the presence of large overstory fir trees, which can produce a substantial amount of seeds and potentially offset the drawbacks of a reduced number of seed sources. Yet, our models failed to confirm our H4 and such a relationship in general. The possibility of allelopathic effects or soil acidification influencing the regeneration patterns was considered unlikely given the long history of mixed stand management in this region. We assume that the distinct outcomes observed in GE1 are predominantly the result of unique local climatic conditions, signifying that the climate plays a crucial role in shaping the impact of species mixtures on regeneration. This underlines the complexity inherent in forest ecosystem dynamics and emphasizes the need for continued research to elucidate these complex interactions with greater clarity and precision [64–66].

4.4. Influence of Ungulates on the Regeneration of Silver Fir

Our study found no significant impact regarding the differences in ungulate density and thus browsing pressure on the regeneration success, density, and developmental stage of silver fir and other tree species. This is not in line with the expectations based on previous case studies that have consistently demonstrated that ungulates preferably browse silver fir trees [51,67]. The presence of red deer has been specifically linked to changes in the regeneration composition, heavily affecting silver fir regeneration.

The role of the ungulates in silver fir regeneration dynamics is complex and influenced by multiple other factors [68]. The differences in data sources and methodologies to estimate the ungulate density and the resulting browsing pressure contribute to high uncertainty, potentially explaining the discrepancies with previous studies. The broad spatial and temporal scale has inherent high variability; thus, more precise long-term local observations of ungulate density and direct measures of ungulate browsing (including control plots without browsing) are needed to fully understand the natural regeneration and wild game interplay.

5. Conclusions

Keeping our initial goal in mind, it is fitting to conclude with recommendations for foresters from the perspective of natural regeneration. **(1) Adopt uneven-aged silviculture:** silver fir-dominated forests, when managed under an uneven-aged system, possess an advanced self-regeneration capacity expressed as a higher probability of regeneration compared to even-aged stands. **(2) Balance the tree size diversity:** while adding more tree size diversity to these uneven-aged stands helps silver fir progress to more advanced developmental stages, it does not boost the overall density of regeneration, which leads us to an important consideration: the need to balance the ecological benefits of enhanced regeneration quality against the required frequent interventions that are crucial to increasing and maintaining a high level of tree size diversity. **(3) Moderate the broadleaf species admixture considering specific growing conditions:** including an admixture of broadleaved species into uneven-aged stands in places with a higher aridity index (PL1, PL2, and IT1) results in the reduced density of the natural regeneration of all the species and silver fir specifically. This reduction is statistically significant, although it is negligible in absolute terms. To avoid soil degradation and allelopathy, reaching an equilibrium between the negative and positive effects of the admixture of broadleaf tree species and maintaining a sensible proportion of broadleaf species to favor silver fir regeneration are crucial. This is also important when we consider places with water abundance (GE1), where we noted a significant increase in the natural regeneration density with increasing admixture. **(4) Retain large overstory trees:** large overstory fir trees did not significantly enhance the density of the fir regeneration. However, given the critical role these trees play in ecosystem functioning and biodiversity conservation, the fact that their presence does not detract from the quality and density of the natural regeneration underlines the importance of retaining them in some places. **(5) Use the stand density as a tool to promote desired species:** the total BA played a crucial role in boosting the density of all the species, even though it was not significantly influential for silver fir separately. In scenarios where promoting silver fir natural regeneration is a key objective, regulating and carefully selecting the locally appropriate stand density appears to be a suitable tool. Furthermore, considering the importance of the findings, we would like to underline that there is room for further research that incorporates direct measures of light availability and ungulate browsing.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15071182/s1, Figure S1: Height curves for selected species groups across four sites; Figure S2: Even-aged, monospecific stand (left) and uneven-aged, mixed stand (right); Table S1: Zero-inflated models' summary on the relationship between broadleaf species admixture and natural regeneration density of silver fir and all species across four sites and different levels of the normalized TBA; Table S2: Zero-inflated models' summary on the relationship between broadleaf species admixture and natural regeneration density of silver fir across climatic gradient and different levels of the normalized TBA.

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Supplementary Materials

Table S1. Zero-inflated models' summary on the relationship between broadleaf species admixture and natural regeneration density of silver fir across climatic gradient and different levels of the normalized TBA.

Predictors	**Density_all_ha**		
	Incidence Rate Ratios	CI	p
	Count Model		
(Intercept)	50129.27 ***	10072.58 – 249483.72	**<0.001**
Martonne	1.00	0.97 – 1.02	0.761
Admixture broad	0.00 ***	0.00 – 0.16	**0.005**
TBA [sqrt]	0.32 **	0.13 – 0.82	**0.017**
Martonne Ã— Admixture broad	1.10 **	1.02 – 1.19	**0.016**
(Intercept)	2.47	2.00 – 3.25	
	Zero-Inflated Model		
Martonne	0.95 ***	0.93 – 0.97	**<0.001**
	Random Effects		
σ^2		0.75	
τ_{00} Localization		0.31	
ICC		0.30	
N Localization		4	
Observations		93	
Marginal R^2 / Conditional R^2		0.163 / 0.411	

* *p<0.1;* ** *p<0.05;* *** *p<0.01.*

Table S2. Zero-inflated models' summary on the relationship between broadleaf species admixture and natural regeneration density of silver fir across climatic gradient and different levels of the normalized TBA.

	Density_fir_ha		
Predictors	***Incidence Rate Ratios***	***CI***	*p*
(Intercept)	58036.42 ***	23542.65 – 143054.76	**<0.001**
Martonne	0.98 ***	0.97 – 0.99	**0.004**
Admixture broad	0.00 ***	0.00 – 0.02	**0.001**
Martonne x Admixture broad	1.18 ***	1.07 – 1.29	**0.001**
Zero-Inflated Model			
(Intercept)	0.17 ***	0.05 – 0.62	**0.007**
Martonne	1.00	0.98 – 1.02	0.867
Random Effects			
σ^2	0.88		
τ_{00} Localization	0.00		
$N_{\text{Localization}}$	4		
Observations	93		
Marginal R^2	0.197		

* *p<0.1;* ** *p<0.05;* *** *p<0.01.*

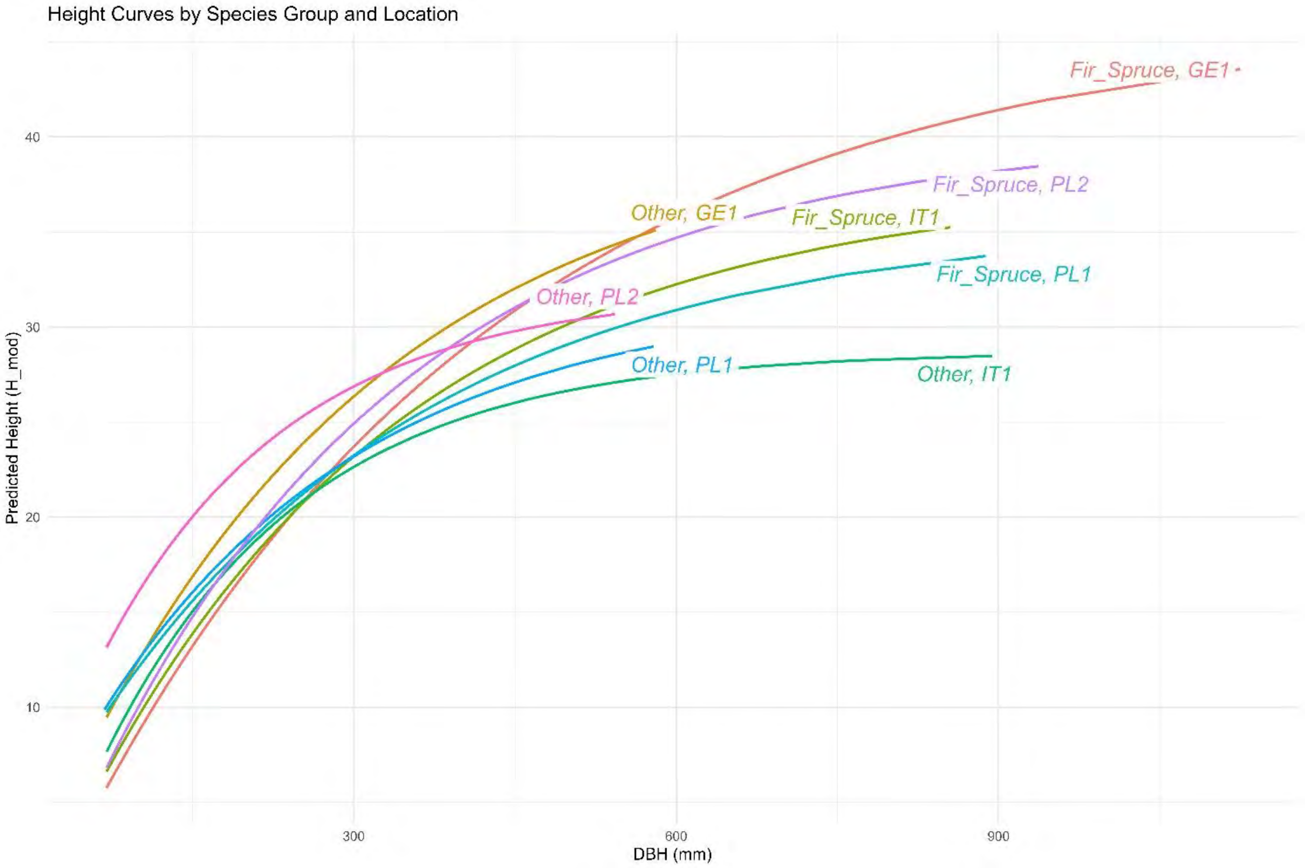

Figure S1. Height curves for selected species groups across four sites.

Figure S2. Even-aged, monospecific stand (left) and uneven-aged, mixed stand (right).

Warsaw, 02.06.2025

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Kolisnyk, B., Wellstein, C., Czacharowski, M., Drozdowski, S., & Bielak, K. (2024). Contrasting Regeneration Patterns in Abies alba-Dominated Stands: Insights from Structurally Diverse Mountain Forests across Europe. Forests, 15, Article 7. https://doi.org/10.3390/f15071182

my individual contribution constitutes the major part of the work presented in this publication, including the conceptualization and design of the study, development of the methodology, performance of the analysis, drafting of the original manuscript, and the review and editing of the final version.

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my individual contribution involved data collection, study conceptualization, and contribution to the review and editing of the manuscript.

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my individual contributions included securing research funding, data collection, as well as reviewing and editing of the manuscript.

Kamil Bielak

Article 3: <u>Kolisnyk, B.</u>, Czacharowski, M., Bingham, L., Wellstein, C., Uhl, E., Drozdowski, S., & Bielak, K. (2025). Tree size diversity can enhance the drought resilience of *Abies alba* Mill. in the European mountain forests. Forest Ecology and Management, 589, 1–14. https://doi.org/10.1016/j.foreco.2025.122765

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Tree size diversity can enhance the drought resilience of *Abies alba* Mill. in the European mountain forests

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ABSTRACT

The increasing frequency and severity of extreme events, such as drought, are expected to disturb forest ecosystems worldwide. Stand structure, including tree size diversity, may play a crucial role in how forests respond to these changes. This study examines the effect of tree size diversity on the drought resilience of silver fir (*Abies alba* Mill.) using data from 138 circular plots in even- and uneven-aged mountain stands across Germany, Italy, and Poland. Increment cores from nearly 600 trees were evaluated to calculate complementary resilience indices. Generalized linear mixed-effect models were fitted to assess how tree size diversity affects individual tree growth response to drought stress under varying environmental conditions, mediated by admixture of broadleaf species, stand density, and individual tree size. We found that tree size diversity improves the growth response of silver fir to drought stress, expressed by higher resistance and stress-driven deviation (SDD) indices, in more water-limited sites. However, this benefit diminishes or becomes slightly negative with increasing climate humidity. Similarly, smaller trees demonstrated higher resistance and SDD, although these effects also weakened with more favorable water conditions. The admixture of broadleaf species and stand density did not mediate the impact of tree size diversity on growth resilience. Our results are in line with the stress-gradient hypothesis. Ecophysiological adaptations to prevailing conditions can lead to different competition regimes (symmetric and asymmetric), causing variations in the impact of stand structure on drought resilience. Since tree size diversity is crucial in water-limited environments, it can be considered a strategic forest management tool for adapting silver fir-dominated forests to anticipated global changes.

1. Introduction

Ensuring balanced forest management that meets timber demand, preserves ecosystem functions, and maintains a high level of stability in the face of global change is one of the main challenges in European forestry today. It is crucial to understand how current silvicultural systems and resulting stand structures might influence ecological processes and how to use those systems as tools to sustain ecosystem services provisioning.

Forest management systems have been traditionally classified into two types: even-aged and uneven-aged, also referred to as multi-aged (O'Hara, 2014; Pommerening et al., 2024). Even-aged silviculture, which has been extensively used in Europe for more than 200 years, entails creating uniform, single-layered stands through large canopy openings (>0.5 ha), often followed by artificial regeneration and intermediate thinning from below (Kuuluvainen et al., 2012; Nyland, 2016) or crop tree thinning (Abetz, 1974; Schädelin, 1942). In contrast, uneven-aged management promotes structurally diverse forests with multiple age classes and layers (O'Hara, 2014), utilizing techniques like single-tree selection and small-group fellings to modify the forest canopy

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and increase stand spatial diversity (Kuuluvainen et al., 2012; Schütz, 2002). While system classification can be helpful for simplification, it should not constrain forest management outcomes (O'Hara, 2014). The approach to complex silviculture has evolved towards a spectrum of stand structural diversity and moving beyond the traditional dichotomy (Bradshaw, 1992; O'Hara, 2014).

Forest structural diversity encompasses the horizontal and vertical distribution of components within a stand and is a measure of spatial entropy (LaRue et al., 2023). From a practical standpoint, this diversity is typically quantified by assessing tree size diversity and distribution, most commonly the diameter at breast height (DBH) distribution. Pioneered by Liocourt's (1898) research, the 'reverse J′ DBH distribution pattern in uneven-aged forests indicates a steady-state distribution essential for long-term sustainable management (Lundqvist, 2017; Picard and Gasparotto, 2016).

The increasing frequency and intensity of drought stress have become pressing concerns, disrupting forested ecosystem stability (Brodribb et al., 2020). Drought stress leads to reduced growth rates and frequently results in the mortality of individual trees, groups of trees, or even the dieback of entire forest stands (Boczoń et al., 2018). Several theories address how ecosystem processes and properties may respond to various silvicultural systems and resulting structural diversity. Recent advances in understanding resilience emphasize the importance of risk dispersion and developing stable forest ecosystems to effectively navigate future uncertainties (Colfer and Kanninen, 2008). Resistance and resilience to drought stress can be improved through species mixing by promoting asynchronous resource acquisition and stress responses (Pretzsch et al., 2013) or through reducing competition by regulating stand density (total basal area) through thinning operations (Giuggiola et al., 2013; Misson et al., 2003). However, while the evidence that tree species diversity and stand density impact forest ecosystem functioning is growing (Giuggiola et al., 2013; Grossiord, 2020; Jankowski et al., 2024; Pretzsch et al., 2013), the specific effects of tree size diversity are only now being explored (Dănescu et al., 2016; Gazol and Camarero, 2016; LaRue et al., 2023). Similarly to species mixing (Pretzsch, 2014), tree size diversity may lead to changes in growing space allocation via vertical and horizontal spatial clustering, below- and aboveground niche partitioning, and complementarity between trees of different sizes (Ali, 2019; Forrester, 2019; LaRue et al., 2023). Regional peculiarities moderate tree size diversity impact and strongly vary across biomes, forest types, and species, instigating inconsistent results among existing studies (Forrester, 2019). Comprehensive research on the most ecologically and economically important tree species with a design to specifically cover this gap is required.

This study focuses on *Abies alba* Mill., commonly known as silver fir, one of the most abundant coniferous species in the European mountain forests (Desplanque et al., 1999). Silver fir is able to tolerate high temperatures and withstand the unfavorable effects of drought stress better compared to other species occupying a similar ecological niche, such as the Norway spruce (Vitali et al., 2017; Zang et al., 2014), suggesting that it has substantial potential to expand its share within forested areas under projected global warming scenarios (Vitasse et al., 2019). Recent paleoecological studies also indicate the broad presence of silver fir in the past across territories characterized by significantly warmer climates (Tinner et al., 2013). Despite this, extreme drought events (such as the summer drought in 2018 in Central Europe) may lead to the reduction of the stability of the silver fir-dominated forests (Gbur et al., 2025; Schuldt et al., 2020).

Silver fir has excellent plasticity and adaptability to light regimes due to its life strategy, particularly its exceptional epinastic control. In conditions of light scarcity, silver fir favors an "umbrella-shaped" or excurrent crown shape, which, combined with its needles' functional adaptability, enables it to withstand long-term suppression and lack of light (Brzeziecki and Kienast, 1994; Dobrowolska, 2008; Dobrowolska et al., 2017; O'Hara, 2014; Tucker et al., 1987). Silver fir also forms forest stands of varying structures, making it an excellent candidate for uneven-aged and mixed forest management. Therefore, silver fir is a suitable model tree species to advance our understanding of the relationship between tree size diversity, shaped by different silvicultural systems, and drought resilience (Manetti and Cutini, 2006; Mazza et al., 2014). While some studies have linked silvicultural systems and structural diversity to silver fir growth stability and resilience, findings remain inconsistent (Dănescu et al., 2018).

Therefore, we explore how tree size diversity affects the growth resilience of individual silver fir trees in different forest stand structures under drought stress. We aim to determine whether there is a general relationship between tree size diversity and growth resilience to drought stress and if climatic conditions, other forest stand characteristics (including admixture and stand total basal area), or individual tree size mediate this relationship.

To address the research objective, we tested the following hypotheses (Fig. 1):

H1: Tree size diversity improves the growth resilience of silver fir trees to drought stress.

H2: The effects of tree size diversity on drought resilience vary across climatic gradients.

H3: The effects of tree size diversity on drought resilience are mediated by the admixture of broadleaf tree species and stand total basal area.

H4: Smaller silver fir individuals have higher growth resilience to drought stress.

2. Materials and methods

2.1. Study sites and data acquisition

We established 138 circular plots, each spanning 0.05 ha, across four sites in Germany, Italy, and Poland (Fig. 2, Table 1) in comparable eutrophic site conditions according to the Polish national site classification (Kliczkowska, 2004). This distribution covers a substantial portion of the natural range of silver fir. The selected sites represent a range of climatic conditions: from marginal populations with water scarcity in the Holy Cross Mountains (PL1), optimal conditions in the Low Beskid Mountains (PL2) and South Tyrol, Italy (IT1) to water-rich sites in the Bavarian Alps, Germany (GE1). This gradient provides a suitable basis for evaluating the effects of tree size diversity on silver fir growth resilience under varying growth-limiting factors. Further details on the study sites are available in Kolisnyk et al. (2024a).

At each site, 34–36 circular plots were established to capture two gradients: the first gradient is tree size diversity, from simple even-aged stands through two-aged and more irregular stand structures to structurally complex, uneven-aged forest stands (Fig. 3, vertical axis). The second gradient is the admixture of broadleaf tree species (Fig. 3, horizontal axis), primarily European beech (*Fagus sylvatica* L.). This approach ensures that the plots comprehensively represent a range of compositional and structural variations across the sites.

Tree positions were recorded in a three-dimensional local coordinate system. Species identity, diameter at breast height (DBH), and any information about tree damage were recorded for all trees with a DBH of 7 cm or larger. Heights were measured for selected trees from different social strata to facilitate the subsequent reconstruction of the heights of the remaining trees.

The management of silver fir-dominated stands across the study sites has transitioned from clear-cutting to shelterwood and selection systems in recent decades. In PL1 and PL2, low-intensity, high-frequency single-tree selection dominates, while in DE1, foresters employ high-intensity, low-frequency interventions targeting the upper layer. IT1, due to the challenging terrain, has the lowest intervention frequency and intensity. Study plots include pre-mature (40–80 years) and mature (100–140 years) even-aged stands. Uneven-aged and transition stands comprise multiple generations, from 15-year-old understory trees to some overstory individuals exceeding 150 years. PL1, PL2, and DE1 are state-

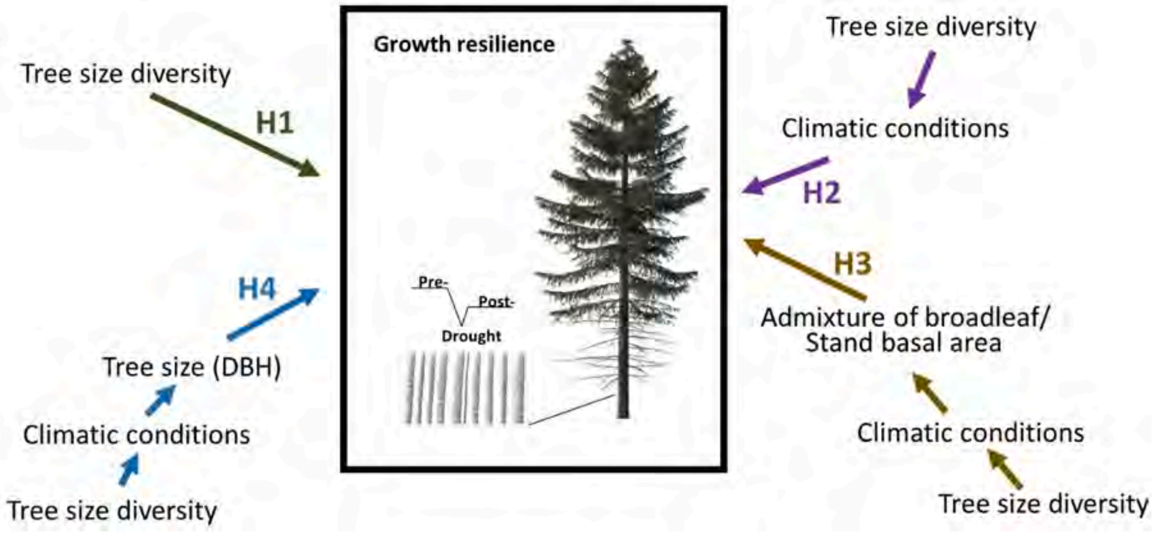
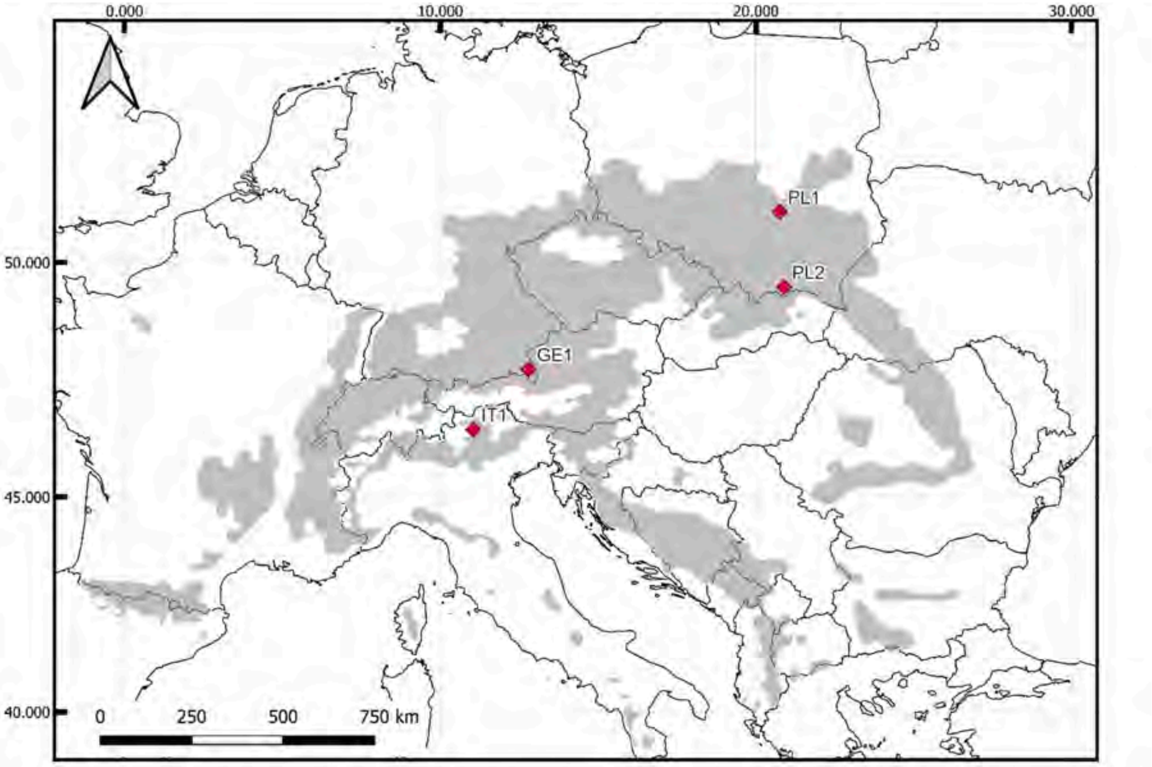


Fig. 1. Schematic representation of formulated hypothesis (H1-H4).



source: European Forest Genetic Resources Programme (EUFORGEN, source: https://www.euforgen.org/species).

Fig. 2. The location of study sites (red rhombi) and distribution of *Abies alba* Mill. in Europe (grey shaded area), source: European Forest Genetic Resources Programme (EUFORGEN, source: https://www.euforgen.org/species).

managed, while IT1 has mixed ownership.

Increment cores, taken from around 600 healthy silver fir trees, were used for the analysis. Increment cores were collected from one direction perpendicular to the slope of the hill to avoid reaction wood. In even-aged stands, 3–4 silver fir trees closest to the plot center were cored. In uneven-aged and transition stands, 4–6 cores were taken from trees of different strata. The increment cores were stored in wooden plates for transportation, air-dried, glued to wooden plates, polished in two steps (first using 120-grit sandpaper, then 800-grit sandpaper on the belt sanding table), and scanned at fine resolutions (ranging depending on ring visibility from 1200 to 2400 dpi). Tree ring width (TRW) was measured and cross-dated using CooRecorder and CDendro software (Maxwell and Larsson, 2021) with an accuracy of 0.01 mm. The tree ring width series length varies across sites. In PL1, chronologies range from 24 to 141 years, averaging 75 years. In PL2, they span 25–158 years, with a 70-year average. IT1 ranges from 24 to 239 years (average 95), while DE1 spans 23–169 years (average 106).

For IT1 and GE1, daily data from the ensembled version of the E-OBS temperature and precipitation data sets (Cornes et al., 2018) with a resolution of 0.1 degrees were used. For PL1 and PL2, due to the

Table 1
The general characteristics of the study sites.

Site	Elevation	Average annual temp. (C)	Sum of annual precipitation (mm)	Total basal area (m^2 ha^{-1})	Admixture of broadleaf species (%)
Tissens-Laurein, Italy *(IT1)*	1050–1750 (1320)	3.1– 8.8 (6.8)	642–1336 (894)	29.8 – 90.5 (53.4)	0 – 34.3 (13.9)
Inzel, Germany *(GE1)*	820 – 1140 (920)	6.2 – 8.5 (7.6)	1471–2081 (1805)	40.7 – 70.1 (54.4)	0 – 35.7 (11.5)
Zagnansk, Poland *(PL1)*	320–400 (350)	6.7–9.1 (8.1)	608 – 1003 (749)	21.1 – 46.9 (34.1)	0 – 36.5 (13.0)
Nawojowa, Poland *(PL2)*	580 – 820 (650)	5.9–8.4 (7.0)	731 – 1522 (989)	31.0 – 62.9 (45.4)	0 – 58.8 (15.3)

Note: Values on the left indicate the minimum across plots for the selected years, on the right the maximum, and in parentheses the mean. For IT1 and GE1, climatic data refer to 2001–2020; for PL1 and PL2, 2001–2019.

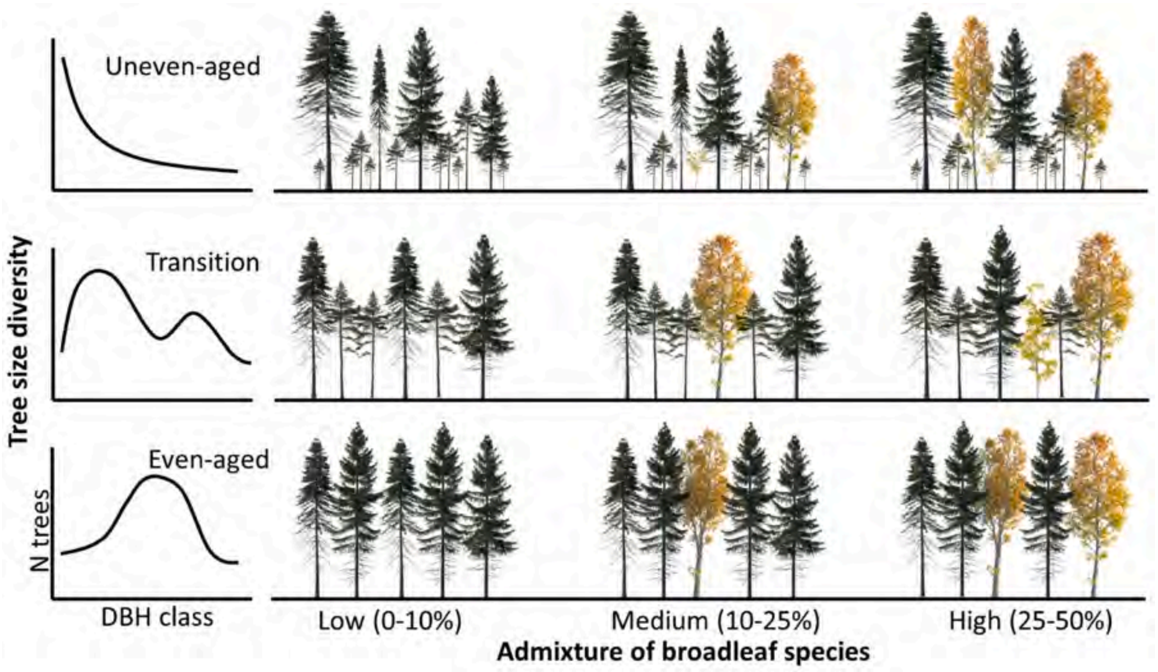


Fig. 3. Plot selection matrix illustrating tree size diversity (vertical axis) and the admixture of broadleaf tree species (horizontal axis). This design guided plot selection in the field to ensure that plots at each site represent a range of compositional and structural gradients. The DBH distribution represents the theoretical diameter at breast height distribution for each stand structural type.

tendency of E-OBS data to underestimate precipitation in eastern Europe, specifically central Poland, data from the gridded 2 km G2DC-PL+ dataset (Piniewski et al., 2021) were used.

2.2. Data processing

2.2.1. Drought identification and long-term climatic conditions

To assess the impact of drought on ecosystem functioning, it is essential to identify drought events objectively (Schwarz et al., 2020; Slette et al., 2019; Van Loon et al., 2016). Given the ability of trees to adapt phenologically and genetically to changing environmental conditions (Bussotti et al., 2015; Csilléry et al., 2020), this study examines how temporal variations in relative water availability influence growth resilience. Thus, we focus on meteorological drought, defined as a prolonged period of below-average precipitation that disrupts the water balance, leading to reduced soil moisture and increased evapotranspiration deficits (Andrews et al., 2020; Sadiqi et al., 2022; Schwarz et al., 2020; Van Loon et al., 2016). We calculated the Standardized Precipitation-Evapotranspiration Index (SPEI) using “SPEI” R package version 1.8.1 (Beguería and Vicente-Serrano, 2023) for selected time windows (Supplementary 1). Years were identified as drought stress years when at least two of the three selected SPEI variations had values below −1.5 (Supplementary Table 1). This approach is advantageous considering the wide climatic gradient in this study. For example, the highest precipitation in PL1 over the last 20 years is much lower than the lowest in GE1. The identified years must be termed dry, relative drought years, or drought stress rather than drought years. The study covers the period 2001–2020 for DE1 and IT1 and 2001–2019 for PL1 and PL2, based on the availability of climatic data. Besides, stand management within the plots is well-documented for this timeframe. Including earlier years could introduce bias, as stand structure is the subject of constant change.

To characterize climate humidity in absolute terms and quantify long-term climatic conditions across study sites, we used a singular metric, namely the Forest Aridity Index (FAI) developed by Führer et al., (2011) (Eq. 1).

$$FAI = 100 \quad \times \frac{T_{VII-VIII}}{P_{V-VII} + P_{VII-VIII}} \tag{1}$$

where $T_{VII-VIII}$is the mean temperature in July and August, P_{V-VII} and $P_{VII-VIII}$ are the precipitation sums from May to July and July to August, respectively. The FAI is based on observations of critical growth periods and was initially designed for the Hungarian climate and broadleaf tree species. Nonetheless, the fundamental principle—that the period from May to August is crucial for growth—also applies to silver fir at our study sites.

2.2.2. Cross-dating and dendrochronological assessment of tree ring width series

To assess the reliability of the recorded TRW, ten series at each site were selected from dominant trees with clearly visible rings and a high correlation coefficient ($\geq$0.7) with the rest of the selected trees, both overall and in 20-year segments. The TRW series were averaged to create a reference curve (master chronology) using CDendro software (Maxwell and Larsson, 2021). Additionally, pointer years were identified using the pointRes R package version 2.0.2 (Maaten-Theunissen et al., 2023). Overstory trees were chosen for these purposes as climatic conditions primarily influence their growth patterns, and they are less affected by competition compared to their counterparts in lower biosocial positions (Wang et al., 2023). The remaining increment cores were then tested against the reference curve, accepting the TRW series with a correlation coefficient of $\geq$ 0.5. Series below this threshold underwent visual inspection and were included if pointer years matched growth trends of inspected TRW throughout the core length. Trees with shifts in pointer years indicating missing or false rings were excluded. TRW series were detrended using the spline function of the dplR R package (Bunn, 2022) with an adaptive smoothing spline rigidity of 0.7 times the series length and a wavelength cutoff of 0.5.

2.2.3. Calculation of the tree growth response to the drought stress

We used the framework of *complementary resilience indices* proposed by Lloret et al. (2011) to analyze the growth *resilience (Rs)* (Schwarz et al., 2020), defined as the ability of tree growth to return to pre-disturbance levels after experiencing a disturbance event (Eq. 2). According to this framework, growth resilience comprises two components: growth *resistance (Rt)* and *recovery (Rc)*. Resistance refers to the ability to withstand unfavorable growing conditions (Eq. 3), while recovery refers to the ability to increase the growth rate after the disturbance compared to the growth during the stress year (Eq. 4).

$$Rs = \frac{\sum_{j=1}^{m} TRWI_{post,j} \times \frac{1}{m}}{\sum_{i=1}^{n} TRWI_{pre,i} \times \frac{1}{n}} \tag{2}$$

$$Rt = \frac{TRWI_{dist}}{\sum_{i=1}^{n} TRWI_{pre,i} \times \frac{1}{n}} \tag{3}$$

$$Rc = \frac{\sum_{j=1}^{m} TRWI_{post,j} \times \frac{1}{m}}{TRWI_{dist}} \tag{4}$$

where $TRWI_{dist}$ is growth during the disturbance (drought), $TRWI_{pre,i}$ and $TRWI_{post,j}$ growth in the i-th year pre- and j-th year post-disturbance correspondingly, n is the number of years pre-disturbance, m – number of years post-disturbance.

Even though the indices defined by Lloret et al. (2011) are considered the standard for analyzing drought stress growth reactions, they have notable limitations. The primary issue is that the recovery index mirrored the resistance index when trees were able to recover rapidly and fully after a drought (Schwarz et al., 2020); thus, the recovery index was not calculated in this research. Besides, Lloret complementary indices may provide an incomplete or misleading depiction of lagged drought responses or prolonged recovery times (Schwarz et al., 2020; Thurm et al., 2016). To address these issues, we calculated the total growth reaction (TGR) during the drought stress and recovery period compared to the pre-drought growth level (Eq. 5).

$$TGR = \sum_{j=1}^{m} \left(\frac{\sum_{i=1}^{n} TRWI_{pre,i}}{n} - TRWI_{post,j} \right) + \frac{\sum_{i=1}^{n} TRWI_{pre,i}}{n} - TRWI_{dist} \tag{5}$$

The final piece of the puzzle missing in the literature is understanding how drought-induced growth reduction compares to natural growth variability before drought stress. To address this, we introduce the *stress-driven deviation index* (SDD), a normalized metric based on the z-score formula (Eq. 6). The SDD quantifies how growth during a disturbance year deviates from pre-disturbance variability by scaling this difference against total absolute deviations and multiplying by the number of pre-disturbance years. A negative and positive SDD indicates growth reduction and increase, respectively, higher than the pre-disturbance average variability.

$$SDD = n \times \frac{TRWI_{dist} - \frac{1}{n} \times \sum_{i=1}^{n} TRWI_{pre,i}}{\sum_{i=1}^{n} \left| TRWI_{pre,i} - \frac{1}{n} \times \sum_{i=1}^{n} TRWI_{pre,i} \right|} \tag{6}$$

A reference period of four years was chosen for both pre- and post-disturbance. This duration was selected because most trees were capable of recovering their pre-drought growth within a year, and four years is the minimum period required to capture growth variability. Additionally, a four-year period avoids overlap with other extreme events that could affect the analysis.

2.2.4. Assessing of tree size diversity and admixture of broadleaf tree species

The Shannon diversity index (ShD) was used to describe the continuous tree size diversity based on 4-meter height classes (Kolisnyk et al., 2024a) (Eq. 7; Fig. 4). The basal area (BA) of all trees with a DBH bigger or equal to 7 cm and within each defined height class was summed to represent the class share. For instance, in the (4,8] class, the BA of all trees taller than 4 m but equal to or shorter than 8 m was summed and used as the proportion of trees in that class.

$$ShD = -\sum_{i=1}^{N} p_i \times \ln(p_i) \tag{7}$$

where N is the number of defined height classes, and p_i is the proportion of trees by BA in the i-th class.

The ShD and TBA values were normalized to a 0–1 scale at each site (ShD_{Norm} and TBA_{Norm}) to facilitate comparison across different sites using Eq. 8.

$$E_{Norm,k} = \frac{E_{k,s} - E_{\min,s}}{E_{\max,s} - E_{\min,s}} \tag{8}$$

where $E_{k,s}$ is the stand characteristic of interest (ShD and TBA) on the plot k, site s, $E_{\min,s}$ and $E_{\max,s}$ are the minimum and maximum values of the characteristic at the site s, correspondingly.

The share of broadleaf tree species within each plot was determined by calculating the proportion of the total basal area represented by broadleaf species (Eq. 9).

$$Admix = \frac{BA_{broadleaf}}{BA_{all}} \tag{9}$$

Where $BA_{broadleaf}$ is the sum of the basal area of broadleaf trees, and BA_{all} is the total stand basal area. For trees not directly measured, heights were reconstructed using the Meyer height-DBH function (Meyer, 1940) (Supplementary Figure 1).

2.3. Statistical analysis

2.3.1. Modelling approach

The approach of sequential generalized linear mixed-effect models (GLMMs) was selected to address the increasing complexity of the four formulated hypotheses. By gradually introducing a more complex system of variables, we ensured that the primary effects were depicted before introducing additional ones. A random slope model (Eq. 10) was used to answer the first hypothesis to understand if there is a general trend between forest resilience parameters and tree size diversity across all sites. This approach accounts for potential differences in the

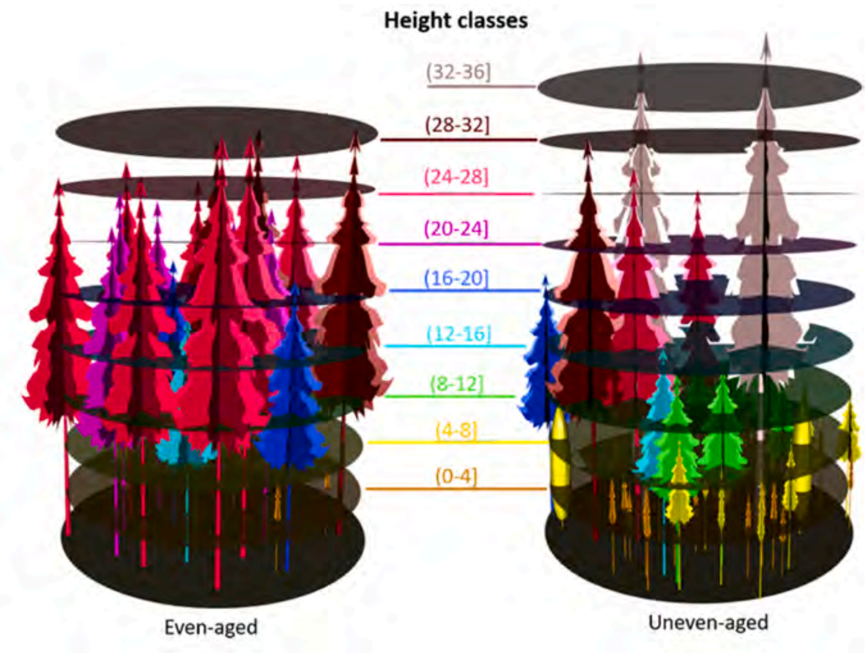


Fig. 4. Visual representation of tree distribution within the height classes used to calculate the ShD index. Two selected plots from the GE1 are shown, representing even-aged and uneven-aged stand structures. Trees are colored based on their height classes. In the even-aged plot, most trees are in the same or adjacent height classes, though certain level of vertical profile diversification is present due to the shade-tolerant nature of silver fir. In contrast, the uneven-aged stand shows a more random distribution of trees throughout the vertical profile.

relationship between explanatory and response variables at each site, thus avoiding within-site deviations from observed values and preventing over- or under-estimation of the explanatory variable's impact without the need to understand underlying cross-site differences.

$$y_{jk} = \beta_0 + \beta_1 ShD_{Norm,jk} + u_{0j} + u_{1j} ShD_{Norm,jk} + u_{2k(j)} + \epsilon_{jk} \quad (10)$$

Where y_j are the response variables (Rt, Rs, TGR, SDD). β_0 is the model intercept, and β_n are the fixed parameters and their interaction coefficients. ShD_{Norm} stands for the normalized Shannon tree size diversity index, and Rt for resistance. u_{0j} is the random intercept and u_{1j} is the random slope for site j, and $u_{2k(j)}$ is the random intercept for the given tree k nested in the site j.

For hypothesis II, we expanded our analysis to include the site-specific climatic conditions (FAI) as fixed slopes (Eq. 11).

$$y_{jk} = \beta_0 + \beta_1 ShD_{Norm,jk} + \beta_2 FAI_{jk} + \beta_3 \left(ShD_{Norm,jk} \times FAI_{jk}\right) + u_{0j} + u_{2k(j)} + \epsilon_{jk} \quad (11)$$

Hypothesis. III aimed to determine whether broadleaf tree species' admixture or stand density mediate tree size diversity's impact on resilience components. The admixture of broadleaf tree species (Admix) and the normalized stand total basal area (TBA_{Norm}) were introduced into the models to test this (Eq. 12).

$$y_{jk} = \beta_0 + \beta_1 ShD_{Norm,jk} + \beta_2 FAI_{jk} + \beta_3 Admix_{jk} + \beta_4 \left(ShD_{Norm,jk} \times FAI_{jk} \times Admix_{jk}\right) + \beta_5 TBA_{Norm,jk} + \beta_6 \left(ShD_{Norm,jk} \times FAI_{jk} \times TBA_{Norm,jk}\right) + u_{0j} + u_{2k(j)} + \epsilon_{jk} \quad (12)$$

A top-down approach was selected to address hypothesis IV and determine whether the impact of tree size remains consistent over the tree size diversity gradient. As a first step, DBH was introduced as a parameter with interaction with ShD, using the most complex model structure for the given response variable as the base (Eq. 13). In the second step, backward stepwise regression was employed to determine if the best-fitting model includes or excludes the interaction of DBH with ShD_{Norm}. The significance of the parameter and the AIC were compared to select the best-fitting model.

$$y_{jk} = \beta_0 + \beta_1 ShD_{Norm,jk} + \beta_2 FAI_{jk} + \beta_3 DBH_{ijk} + \beta_4 \left(ShD_{Norm,jk} \times FAI_{jk} \times DBH_{ijk}\right) + u_{0j} + u_{2k(j)} + \epsilon_{jk} \quad (13)$$

2.3.2. Data transformation and GLMM family selection

Most of the existing literature uses untransformed, "raw" resilience component values for analysis of drought stress reaction (Dănescu et al., 2016; Gazol and Camarero, 2016; Lloret et al., 2011); however, in certain cases, this approach can be misleading. When assessing the impact of climatic drought on growth resilience components, the primary goal is determining whether trees have reacted to drought stress and, if so, the extent of their reaction. For instance, if Rt values exceed one, the tree has sustained growth under adverse conditions and even increased its growth rate. Values above one surpass a theoretical maximum and do not reflect growth resistance, defined as the tree's ability to maintain growth under deteriorated conditions, but rather other growth dynamics, such as enhanced growth due to improved photosynthesis with rising temperatures when water is not the main limiting factor. Similarly, as the Rs helps to understand whether a tree has returned to its pre-drought growth rate and, if not, the extent of the growth reduction, including values above one for both Rt and Rs can misrepresent phenomena beyond the scope of this study. To address this, the Rt and Rs values were capped at one (Fig. 5; Table 2) to retain critical information about the proportion of trees that did or did not react to the drought stress.

Furthermore, as positive SDD values indicate that growth during the disturbance year exceeds the pre-disturbance mean growth variability, SDD was limited to a maximum of value of zero. SDD values were then scaled using a min-max approach (Eq. 8, Table 2) to facilitate model convergence and ensure numerical stability crucial for proper optimization. Conversely, TGR values were constrained to a minimum of zero (Table 2), as values below zero show no cumulative growth reduction

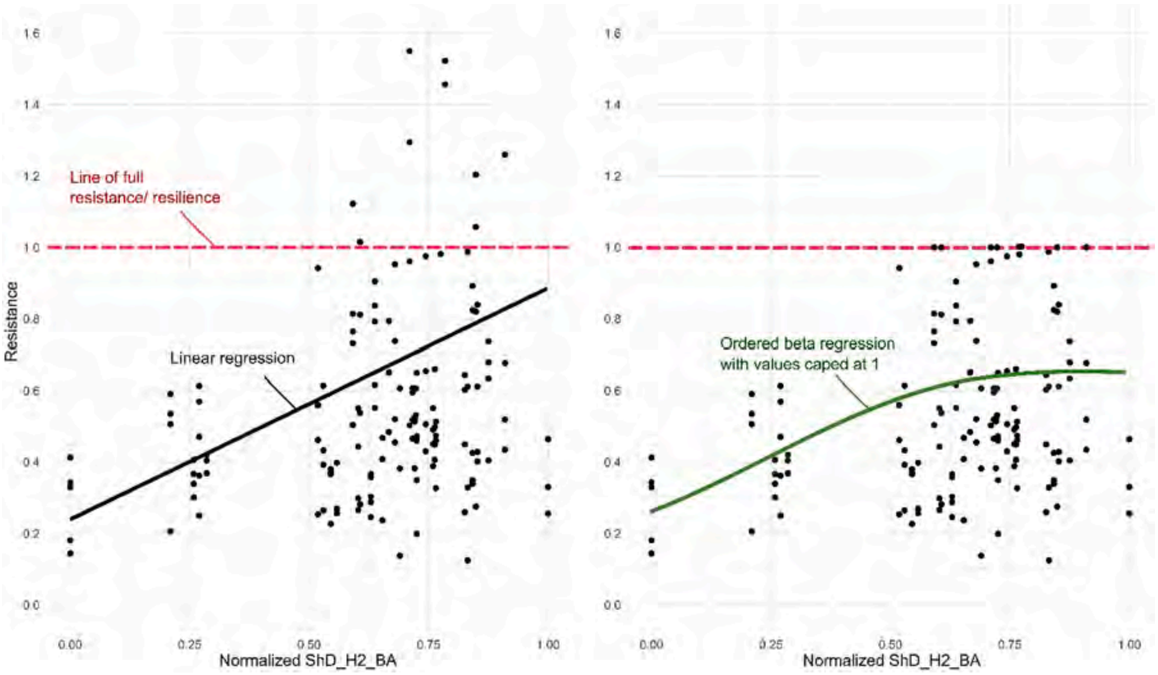


Fig. 5. Illustration of the impact of data transformation and model selection on predicted Rt values at site PL1 in 2006.

Table 2
Summary of model specifications and transformations for components of growth resilience.

Component of growth resilience	Theoretical range	Transformation applied and resulting range	GLMM distribution	Additional model parameters
Rt	(0,+∞)	Capped to maximum 1 (0, 1]	Ordered beta	
Rs	(0,+∞)	Capped to maximum 1 (0, 1]	Ordered beta	
TGR	(-∞,+∞)	Capped to minimum 0 (0, +∞]	Gaussian	Zero-inflation parameter
SDD	(-∞,+∞)	Capped to maximum 0, min-max transformation [0,1]	Ordered beta	

during and after the disturbance compared to the pre-drought period.

To address the bounded range of resistance, resilience, and transformed SDD values, we employed the ordered beta regression model developed by Kubinec (2023). This approach was preferred over the zero-one-inflated model for its simplicity and capacity to utilize all available data effectively. However, since TGR values do not have an upper limit, a zero-inflated model was used for the analysis. All models were fitted using the glmmTMB package in R, version 1.1.9 (Brooks et al., 2024), with optimization performed via the Broyden-Fletcher-Goldfarb-Shanno (BFGS) algorithm (Brooks et al., 2017).

3. Results

3.1. Selected drought years

The current year growth rate of silver fir is mostly correlated with growing conditions from May to July across all study sites. In GE1 and IT1, the growth rate of silver fir is strongly linked with SPEI_2_July, SPEI_2_June, and SPEI_3_July (Supplementary Table 1). However, in PL2, an even slightly higher correlation than SPEI_2_July and SPEI_3_July was observed with SPEI_5_September, indicating a relatively longer active growth period at this site. In contrast, in PL1, in addition to SPEI_2_July and SPEI_1_June, SPEI_6_July was also correlated with growth, thus signifying that water accumulated during the spring can be crucial for tree growth at this site. Based on the selected SPEI variations, the following years had an SPEI value of −1.5 or lower for at least two of these SPEI variations and were thus identified as drought years: 2003 and 2008 for GE1, 2018 for IT1, 2006 for PL1, and 2015 for PL2 (Supplementary Figure 2).

3.2. Response to the drought stress

We found no consistent impact of ShD_{Norm} on the growth resilience components (Rt, Rs, SDD, TGR) across sites (Eq. 10). The lack of a general trend indicates that tree size diversity alone does not uniformly affect growth resilience components across all sites. However, when the site-specific effect of water availability, expressed through the FAI, is introduced in the model (Eq. 11), tree size diversity significantly impacts Rt and SDD (Fig. 6; Table 3), but not Rs and TGR. The intercept for Rt and SDD increases with FAI (Fig. 6), indicating that, on average, as climate aridity increases, trees reduce their growth rate during drought more than in relatively humid climates compared to their average pre-disturbance growth rate and variability. Moreover, the slope of the relationship between individual tree Rt or SDD and the stand ShD_{Norm} depends on the value of the FAI. For a relatively high FAI, which represents the water-limited site PL1, Rt, and SDD show a marked increase with increasing ShD_{Norm}. Conversely, as the FAI decreases, this relationship flattens and can even show downtrends, as observed at the FAI levels of the highly water-rich site GE1 (Fig. 6).

When TBA_{Norm} and Admix are sequentially introduced in the GLMM with an interaction with ShD_{Norm} (Eq. 12), they do not yield significance in any model describing resilience components. Thus, the admixture of broadleaf tree species and stand density does not mediate the impact of tree size diversity on the growth resilience components.

Similarly, the impact of DBH is not significant, when gradually incorporated into the model with an interaction term for tree size diversity. However, when DBH is added only with an interaction with the

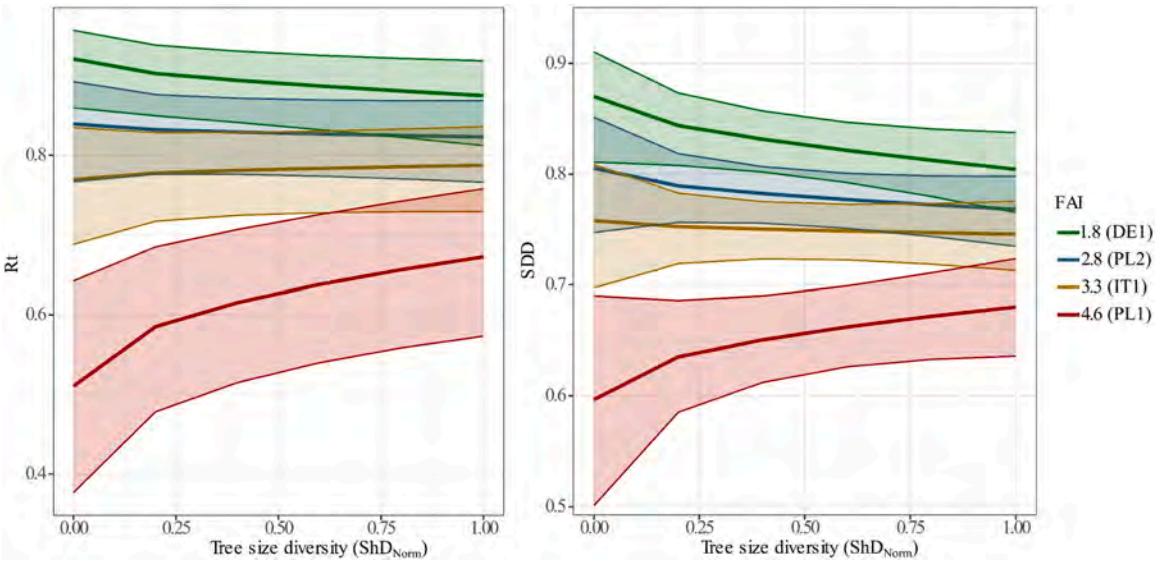


Fig. 6. Predictions of the growth resistance (Rt) and stress-driven deviation (SDD) indices (thick lines) based on normalized tree size diversity (ShD$_{\text{Norm}}$) and levels of the Forest Aridity Index (FAI) representing our study sites (different colors). The 95 % confidence intervals are enclosed in the shaded areas between the thin lines.

Table 3
GLMM summary on the influence of ShD$_{\text{Norm}}$ mediated by FAI on the growth resilience components (Rt and SDD).

	Rt	**SDD**				
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	53.10	15.87 – 188.45	< 0.001	28.67	10.53 – 72.90	< 0.001
FAI	0.40	0.24 – 0.65	< 0.001	0.50	0.41 – 0.70	< 0.001
ShD$_{\text{Norm}}$ [sqrt]	0.21	0.06 – 0.69	0.011	0.27	0.09 – 0.77	0.033
FAI × ShD$_{\text{Norm}}$ [sqrt]	1.75	1.22 – 2.37	0.002	1.53	1.09 – 1.94	0.021
Random Effects						
σ^2	0.03	0.05				
τ_{00}	0.11 $_{\text{ID2:Location}}$	< 0.01 $_{\text{ID2:Location}}$				
	0.17 $_{\text{Location}}$	0.02 $_{\text{Location}}$				
ICC	0.90	0.31				
N	485 $_{\text{ID2}}$	483 $_{\text{ID2}}$				
	4 $_{\text{Location}}$	4 $_{\text{Location}}$				
Observations	592	590				
Marginal R^2	0.496	0.696				

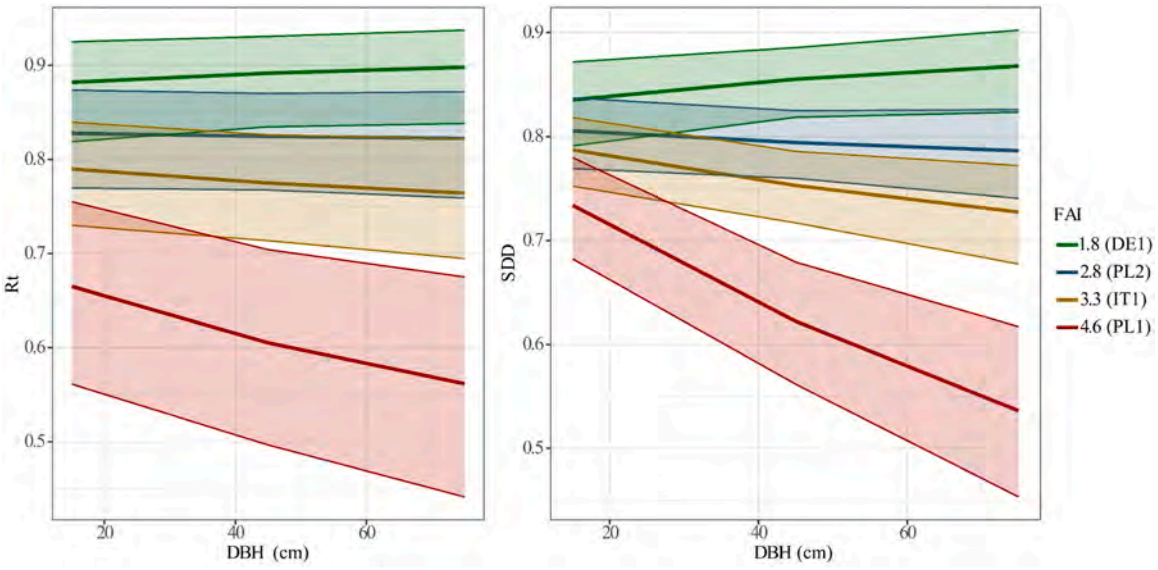


Fig. 7. Predictions of the growth resistance (Rt) and stress-driven deviation (SDD) indices (thick lines) based on the DBH in cm and levels of the Forest Aridity Index (FAI) representing our study sites (different colors). The 95 % confidence intervals are enclosed in the shaded areas between the thin lines.

FAI (without tree size diversity), it becomes significant for Rt and SDD, but not for Rs and TGR. With a relatively high FAI representing the water-limited site PL1, Rt and SDD show a marked decrease with increasing DBH. Conversely, as the FAI decreases, this relationship flattens and can even show uptrends, as observed at the FAI levels of the water-rich site GE1 (Fig. 7; Table 4).

4. Discussion

4.1. Positive or neutral: exploring niche complementarity and mediating role of growth limiting factors

The growth of trees can be modulated by the structural organization of canopy and root systems, reduced within stand layer density and individual tree competition, as well as the general increase in resource acquisition efficiency and availability caused by the tree size diversification (Binkley et al., 2013; Bolte et al., 2010, 2013; Vanhellemont et al., 2018; Ali, 2019; Forrester, 2019), especially during resource scarcity (Chu et al., 2009; Jucker et al., 2016). Intensive management required to maintain the uneven-aged structure (O'Hara, 2014) modify intra- and inter-specific levels of competition, and increase resource availability for individual trees during extreme events (Forrester, 2019). As a result, structurally diverse stands are believed to have higher growth resistance and resilience to adverse climatic influences (Gazol and Camarero, 2016). Most of existing studies report positive or neutral impacts of uneven-aged silviculture or resulting tree size diversification on silver fir's growth resilience and stability.

Manetti and Cutini (2006) conducted research on forest structures' impact on the individual tree growth performance in the Apennines, Italy, and found that even-aged stands had more pointer years, suggesting lower resilience, while multilayered, uneven-aged forests exhibited more stable radial growth. Podlaski (2021) corroborated this by noting more homogeneous growth in silver fir individuals from uneven-aged stands. In earlier work, Podlaski (2018) found that diversifying tree sizes in forest patches enhances the resistance and resilience of silver fir-dominated forests against disturbances, such as high atmospheric SO_2 concentrations, by facilitating rapid recovery and stable growth post-depression. Cavlovic et al. (2015) theorized that reactive management and high mortality rates due to high SO_2 levels in the late 20th century resulted in the current forest structure and prevalence of younger fir generations in the Dinaric region. Čater and Levanič (2013) also found more stable radial growth in silver fir under a single-tree selection management system compared to group selection, particularly during the general growth depression between 1960 and 1990.

Table 4
GLMM summary on the influence of DBH on the growth resilience components Rt, SDD.

	Rt			**SDD**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	22.72	3.48 – 148.49	0.001	6.43	1.45 – 28.56	0.014
FAI	0.56	0.32 – 0.98	0.043	0.93	0.59 – 1.45	0.736
DBH [sqrt]	1.16	1.00 – 1.34	0.046	1.31	1.12 – 1.52	0.001
ShD_{Norm} [sqrt]	0.22	0.07 – 0.71	0.012	0.29	0.09 – 0.95	0.041
FAI × DBH [sqrt]	0.94	0.90 – 0.98	0.008	0.90	0.85 – 0.94	< 0.001
FAI × ShD_{Norm} [sqrt]	1.73	1.22 – 2.44	0.002	1.48	1.03 – 2.11	0.032
Random Effects						
σ^2	0.03			0.05		
τ_{00}	$0.10_{\text{ID2:Location}}$ 0.19_{Location}			$< 0.01_{\text{ID2:Location}}$ 0.04_{Location}		
ICC	0.90			0.46		
N	485_{ID2}			483_{ID2}		
Observations	592			590		
Marginal R^2	0.485			0.688		

In contrast to the previous studies, Dănescu et al. (2018) and Gazol and Camarero (2016) designed the research specifically to examine silver fir's growth resilience across the gradient of stand structures. Gazol and Camarero (2016) reported only minor impacts of tree size diversity on radial growth stability when examining silver fir responses to drought stress across a structural diversity gradient in the Central Spanish Pyrenees. Similarly, Dănescu et al. (2018) found no significant effects of tree size heterogeneity on the growth stability, resistance, and resilience of silver fir to summer drought stress in Germany.

However, the aforementioned studies are primarily based on single sites or sites with similar growing conditions, which limits broader interpretation. Addressing this gap, our findings demonstrate that the influence of tree size diversity on the drought resilience components of silver fir growth is contingent upon climatic conditions (Fig. 6). The impact of the tree size diversity on the growth resilience components is positive in places with limited water while flattening and becoming slightly negative with increasing water availability. This reconciles the divergent results within the existing literature and underscores the necessity of considering the ecological traits of a given species across a broader environmental context. Our findings are in line with the stress-gradient hypothesis that facilitation in plant communities is more frequent under strong abiotic stress relative to more favorable growing conditions (Bertness and Callaway, 1994; Maestre et al., 2009) and expand this notion to encompass tree size diversification

In more light-limited systems (where the amount and spatiotemporal distribution of plant-available below-ground resources like water or nutrients are sufficient to sustain growth during the whole vegetative season, such as GE1), stand growth tends to be size-asymmetric. Conversely, in systems where belowground resources are scarce (such as PL1), growth tends to become size-symmetric or inverse asymmetric (Pretzsch and Biber, 2010). Dominant trees may profit more, in terms of the growth rate from tree size diversification, in light-limited sites due to the improvement in prevailing resource limitations (Pretzsch and Biber, 2010). Tree size diversity allows for aboveground clustering and creates additional space (Godlee et al., 2021), enabling dominant trees to suppress the growth of younger generations by seizing a disproportionate amount of light, resulting in asymmetric growth patterns (Metsaranta and Lieffers, 2010; Yi et al., 2022). Thus, dominant trees with extended growth not limited by nutrient or water availability can theoretically use the maximum growing season and compensate for the loss in the number of "large" growth contributors compared to even-aged patches, resulting in strong positive growth dominance. However, this strategy does not improve water availability or water use efficiency; thus, the relative growth of individual trees may deteriorate more in structurally diverse stands during drought years as water becomes the growth-limiting factor.

Water-limited systems exhibit the contrasting dynamics. Belowground resource scarcity contributes to symmetric or inverse asymmetric growth types as these resources are rapidly diffused and difficult for larger individuals to monopolize (Pretzsch and Biber, 2010). Thus, the abundance of younger generations and dominant trees with symmetrically higher growth rates may not bridge the productivity gap, and diversification of tree sizes may create negative growth dominance. This adaptational functional distribution between trees of different sizes maximizes the effects of tree size heterogeneity and resulting below-ground stratification. Reduced competition for water allows for sustained relative growth during extreme water scarcity events (Dănescu et al., 2016; Forrester, 2019). Thus, tree size heterogeneity and resulting belowground stratification in water-limited ecosystems positively influence the relative growth resilience of forest stands to drought stress (Figs. 6, 8).

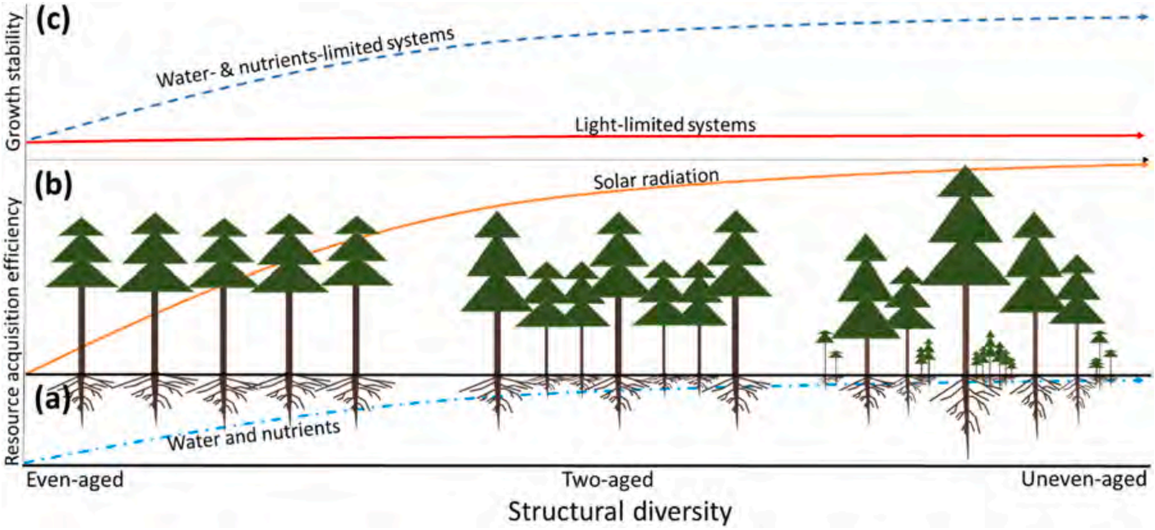


Fig. 8. Schematic representation of a hypothetical resource acquisition strategy along a structural gradient. In systems with scarce belowground resources, water and nutrient use efficiency (a) and growth stability (c) increases with structural diversity. Similarly, in "light-limited" systems, solar radiation use efficiency increases (b); however, growth stability remains intact (c).

4.2. Lack of mediation effects of admixture and stand density on the growth resilience

While tree size diversity can enhance spatial resource-use stratification, species diversity and mixing are thought to reduce overall competition for scarce resources through both spatial and temporal stratification (Forrester, 2014; Loreau and Hector, 2001). The underlying principle involves interspecific complementarity, including competitive reduction (where intraspecific competition is stronger than interspecific competition) and facilitation (where one species supports the functioning of another) (Bottero et al., 2021; Forrester, 2014; Gillerot et al., 2021; Loreau and Hector, 2001). Although mixing broadleaf species is crucial for supporting silver fir survival in early developmental stages, due to soil acidification in monodominant stands (Becker and Drapier, 1984; Kolisnyk et al., 2024b), it does not significantly aid in growth facilitation through temporal competitive reduction.

Beech, an anisohydric species (Leuschner, 2020; Pretzsch et al., 2013), maintains open stomata and high photosynthetic rates during stress events longer than silver fir, which closes its stomata earlier during droughts to reduce the risk of cavitation (Jones and Sutherland, 1991). While this strategy allows beech to continue accessing water longer into a drought by risking morphological changes (Jones and Sutherland, 1991; Pretzsch et al., 2013), it does not alter silver fir's response to stress. Hence, although there is temporal stratification between these species, it does not result in a complementarity that benefits fir and does not mediate the impact of the tree size diversification.

Additionally, spatial clustering resulting from mixing tree species, which is frequently suggested to improved drought resistance (del Río et al., 2017; Hilmers et al., 2019; Jones and Sutherland, 1991), inherently leads to increased tree size diversity. For instance, Ray et al. (2023) noted that species diversity in controlled even-aged stands leads to increased structural complexity. This intrinsic connection between species mixture and tree size diversity also explains the absence of a mediation effect of broadleaf species admixture on the relationship between tree size diversity and growth resilience components in our modeling approach. Thus, even though integrating broadleaf species is essential for stable ecosystem functioning in silver-fir-dominated forests, such as regeneration (Paluch and Jastrzębski, 2013), it has neutral effects on the growth resilience of silver fir to drought stress.

Surprisingly, the TBA similarly neither modulated nor complemented the model's estimation of the impact of tree size diversity on growth resilience components. Stand density is considered a primary driver of resource competition (Mina et al., 2018; Power et al., 2019; Vallet and Pérot, 2011), significantly influencing tree growth (Steckel et al., 2020). It is commonly believed that reducing TBA can accelerate tree growth (Steckel et al., 2020) and reduce growth sensitivity to short-term fluctuations in environmental conditions (Giuggiola et al., 2013). This reduction can also help moderate the effects of drought-induced stress by increasing the resource availability per individual (Steckel et al., 2020). Factors contributing to this include reduced water transpiration through the larger leaf area (Boncina et al., 2007; Bréda et al., 1995) and the development of root systems reaching deeper soil profiles (Aussenac and Granier, 1988), which may increase water availability and water use efficiency under reduced competition (Steckel et al., 2020). However, multiple studies have also shown the opposing effects of lower stand densities and report decreased plant-available water due to increased evapotranspiration losses from higher wind speeds and penetration of solar radiation in recently thinned stands (Aussenac, 2000; Brooks and Mitchell, 2011; Steckel et al., 2020). These opposing mechanisms might counterbalance each other and are likely rooted in several confounding factors (Steckel et al., 2020).

4.3. Impact of the tree size

Tree growth and reactions to unfavorable growing conditions are metabolically influenced by tree size (Niinemets, 2010). Our findings show that smaller trees have higher resistance (Rt and SDD) under stronger water limitations, such as at sites like PL1 (Fig. 7). As water availability increases, this trend changes, resulting in a flattened relationship or even a slight increase in Rt and SDD with increasing DBH.

These findings align with previous studies on silver fir and other shade-tolerant European tree species. Smaller individuals are typically less efficient in light usage (Gspaltl et al., 2013; Zeller and Pretzsch, 2019) or resource utilization in general (Assman, 1961; Assmann, 1970; Zeller and Pretzsch, 2019). While younger, smaller trees have smaller volume increments, they are believed to be more resistant and resilient to external influences in terms of relative growth change (Cavlovic et al., 2015; Lebourgeois et al., 2014; Pretzsch et al., 2018), as in absolute terms the growth of smaller individuals is already metabolically limited (Assman, 1961). For instance, silver fir and beech individuals with larger diameters can have a higher sensitivity to drought stress during active growth (Mérian and Lebourgeois, 2011), as their demand for water supply is elevated due to increased exposure to radiation and high temperatures due to their biosocial position (Bréda et al., 2006; Mérian and Lebourgeois, 2011). Under cold and wet climates, conifers respond similarly among size-diameter classes (Meyer and Bräker, 2001). This phenomenon can be attributed to the lower biosocial position of smaller individuals of shade-tolerant species, such as fir, and the resulting benefits of micro-climatic variations, including buffered temperature variations under the canopy, reduced thermal stress, and transpiration during summer (Aussenac, 2000; Mérian and Lebourgeois, 2011; Pretzsch et al., 2018).

The slight positive slope for the impact of increasing DBH in water-rich sites can, counterintuitively but similarly to the effects of the tree size diversity on the growth resilience components, be explained by size-asymmetric growth (Pretzsch et al., 2018). Dominant trees seize a disproportionate amount of resources in light-limited systems (Pretzsch and Biber, 2010), and we believe that this behavior can be sustained during water scarcity events. The phenological adaptations of the trees that are normally not limited by water availability, including developed crown structures and fine roots, but most importantly, needle functional adaptability does not disappear with drought stress. The levels of stomatal conductance of silver fir needles are the results of ecophysiological adaptations to climatic conditions (Peguero-Pina et al., 2007; Robakowski et al., 2003). Thus, larger trees may sustain the level of their functioning, acting more like anisohydric species than those in arid sites. While this strategy seems effective in the comparatively low severity of drought stress analyzed in water-rich sites, it increases the risk of cavitation during severe droughts.

We also found that the tree size diversity did not modify the impact of individual tree size on the growth resilience components. Nevertheless, it remains uncertain whether differences in tree responses to stressors can be attributed solely to size-related physiological characteristics (Anderson-Teixeira et al., 2022; Coomes and Allen, 2007) or if the trees' biosocial positions played a crucial role (Pretzsch et al., 2018). Despite including even-aged stands of various ages at each site, we solely focused on pre-mature (40–80 years old) or mature even-aged stands (100–140 years old). Thus, data for the smallest suppressed trees were obtained from individuals growing beneath the canopy, which do not represent all the possible tree size-biosocial position combinations.

4.4. *Components of forest resilience*

Some components of forest resilience did not exhibit any connection with the stand characteristics we examined, while others did. This does not imply a contradiction among the components or diminish their utility. In contrast, as Lloret et al., (2011) described, these components serve as complementary indices, each highlighting distinct aspects of growth resilience. For example, neither the Rs nor the TGR was affected by any stand characteristic, mainly because silver fir typically responds to the growing conditions of the current year (Michelot et al., 2012), and post-drought years usually provided favorable conditions, enabling most trees to restore their growth to pre-disturbance levels.

The introduction of the SDD supplements the analysis by addressing aspects of growth resilience that were previously overlooked. However, this approach also presents limitations. Much like the resistance, resilience, and recovery indices proposed by Lloret et al. (2011), carefully selecting the pre-drought period is essential to ensure that it is long enough to capture variability but does not include the impact of other extreme events, such as droughts or early frosts.

5. Conclusions

Under more extreme climate scenarios, conditions may rapidly become increasingly arid in some parts of the natural range of silver fir (López-Tirado et al., 2024). This scenario presents a binary choice for sustained ecosystems and their management: gradually adapt or face abrupt replacement with more suitable species under emerging climate. The latter could result in the uncontrolled development of biotic disturbance agents and outbreaks (Pietrzykowski and Woś, 2021), undermining the core pillars of sustainable silviculture, including CO_2 storage in growing stock (Favero et al., 2021).

Silver fir demonstrates considerable plasticity and can align life strategy with prevailing growing conditions (Dobrowolska et al., 2017; Robakowski et al., 2003). We found that the impact of tree size diversity on the growth resilience of silver fir to drought stress is contingent upon the site's long-term climatic conditions and growth-limiting factors. On sites with water limitations, tree size diversity significantly improves resistance to drought stress. Conversely, increasing water availability makes this relationship less pronounced or even slightly negative. A similar pattern is observed regarding the impact of tree size: smaller trees exhibit a greater resistance to drought stress than their larger counterparts in water-limited sites, but as water availability increases, this trend flattens and reverses. Ecophysiological adaptations to prevailing growing conditions, which foster symmetric competition for resources in water-limited sites and more asymmetric competition with increased water availability, may partially explain the influence of tree size diversity and individual tree size on silver fir's response to drought stress. Notably, the admixture of broadleaf tree species and stand density did not modulate the effect of tree size diversity on growth resilience components.

Efforts to increase beta diversity and irregular structure by reducing the size of extensive clear-cutting, creating canopy openings for group selection systems, and enhancing species diversity are underway in European forests to mitigate growing risk. However, implementing uneven-aged forestry and increasing tree size diversity (and thus alpha diversity) is considered relatively challenging. Since tree size diversity is particularly crucial on more arid sites, it can be regarded as a strategic management tool to adapt silver fir-dominated forests to anticipated global change.

CRediT authorship contribution statement

Uhl Enno: Writing – original draft, Resources. **Wellstein Camilla:** Writing – original draft, Resources. **Bingham Logan:** Writing – review & editing, Writing – original draft. **Czacharowski Marcin:** Writing – original draft. **Bielak Kamil:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Drozdowski Stanisław:** Writing – original draft, Resources. **Kolisnyk Bohdan:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization.

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used OpenAI ChatGPT and Grammarly in order to improve the clarity and coherence of the manuscript. After using the tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122765.

Data availability

Data will be made available on request.

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Supplementary materials for the publication: "Tree size diversity can enhance the drought resilience of *Abies alba* Mill. in the European mountain forests".

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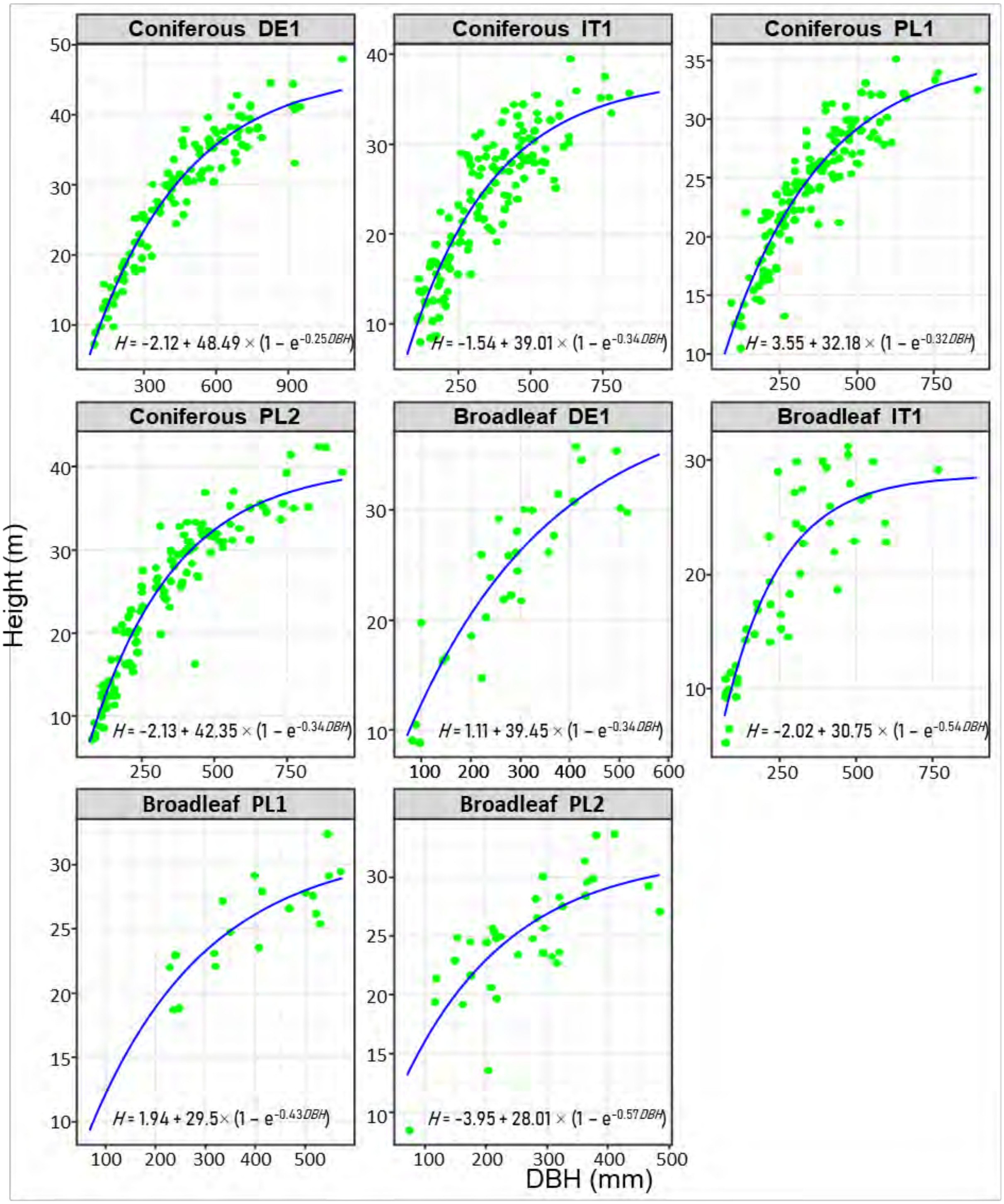
Supplementary 1. Using SPEI involves selecting fixed periods that vary widely in duration. Some studies use extended periods of up to 42 months (Sohn et al., 2016) or shorter intervals of a few months (Jankowski et al., 2024). The selection of these periods should be based on the ecological traits of the studied species and site-specific conditions, as they can yield vastly different results. Some tree species may not respond directly to climatic conditions during the current year but rely on mobilizing previously accumulated resources (Michelot et al., 2012). Additionally, certain species react more to spring droughts (Allard et al., 2008), while others are more affected by summer droughts in terms of radial growth or carbon deposition (Lebourgeois et al., 2013; Vitali et al., 2018). Silver fir, however, has a simple resource acquisition strategy and is highly dependent on conditions and resources available during the current growing season. This species typically begins growth comparatively late (commonly in May under Central European conditions) and exhibits a sharp increase in cumulative increment, with around 80% of the annual increment occurring by the end of July (under Central European conditions) (Knott, 2004; Lebourgeois, 2007). This makes silver fir highly sensitive to drought stress within a specific and relatively short time window. The rapid growth time window can be site-specific, and continuous dendrometer data would be highly beneficial for precise estimation of this period. However, such data are virtually nonexistent on a large scale and thus unavailable for this study. Instead, an alternative yet effective approach was adopted: various fixed periods of SPEI (ranging from 1 to 12 months) for all months (for example, SPEI_4_July is the SPEI for July and three previous months) were correlated to the master chronology per site (as described in the Tree Ring Series section) using the nonparametric Spearman correlation coefficient (de Winter et al., 2016). The top three SPEI durations per site exhibiting the highest correlation with growth trends were selected.

Supplementary Table 1. Correlation between silver fir growth and selected (most correlated) Standardized Precipitation-Evapotranspiration Index (SPEI) variables across four study sites

Location	SPEI (Length_Month)	Correlation
GE1	SPEI_2_July	0.424
GE1	SPEI_2_June	0.316
GE1	SPEI_3_July	0.287
GE1	SPEI_1_June	0.239
GE1	SPEI_4_July	0.187
IT1	SPEI_3_July	0.381
IT1	SPEI_2_June	0.350
IT1	SPEI_2_July	0.310
IT1	SPEI_3_June	0.289
IT1	SPEI_4_July	0.258
PL1	SPEI_2_July	0.501
PL1	SPEI_1_June	0.452
PL1	SPEI_6_July	0.438
PL1	SPEI_3_July	0.419
PL1	SPEI_3_August	0.379
PL2	SPEI_5_September	0.577
PL2	SPEI_2_July	0.568
PL2	SPEI_3_July	0.555
PL2	SPEI_1_July	0.540
PL2	SPEI_3_September	0.548

Supplementary Figure 1. Height reconstruction using the Meyer curve for different groups of tree species (coniferous and broadleaf) across four sites



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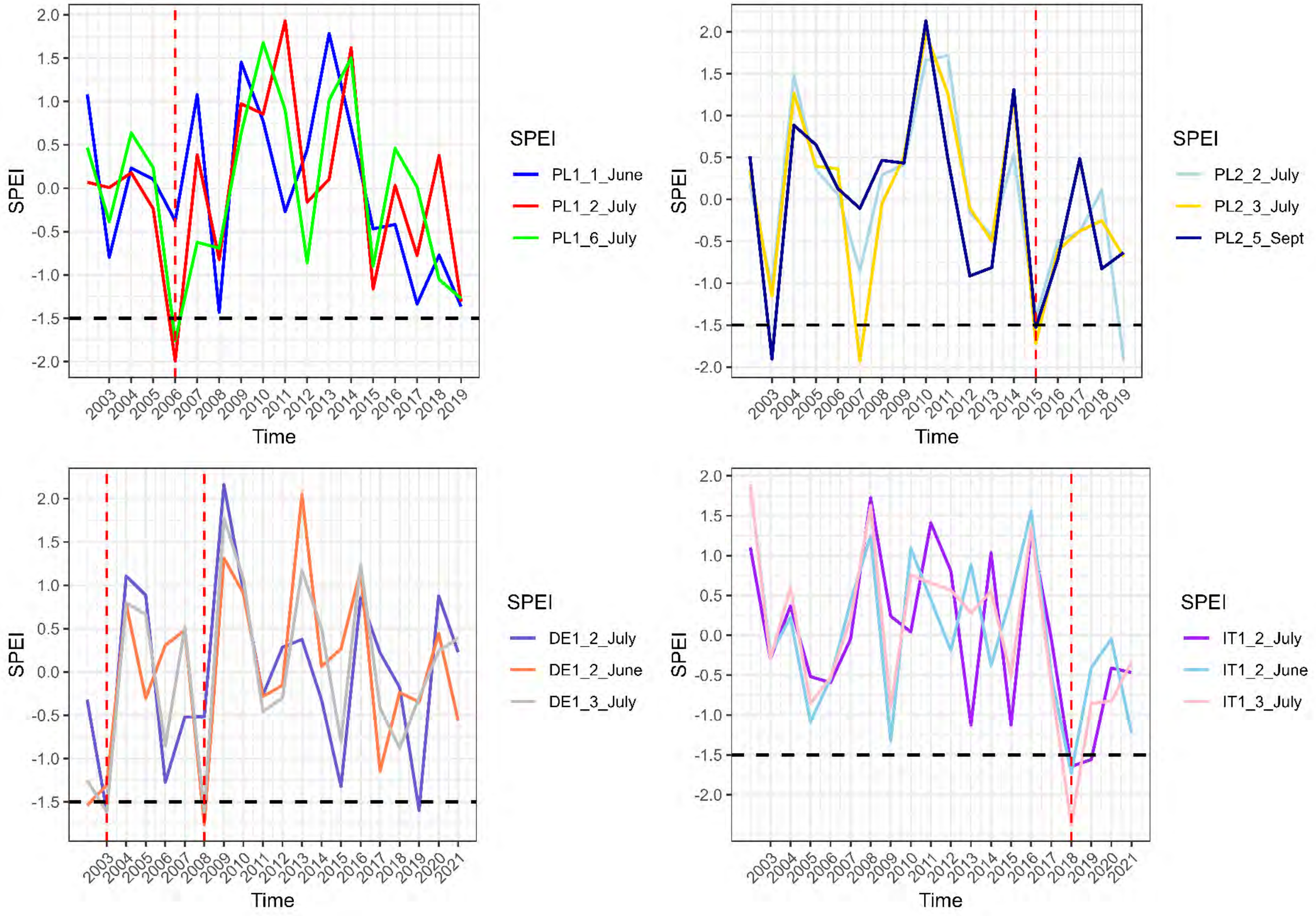
Supplementary Figure 2. Visualization of selected (most correlated) Standardized Precipitation-Evapotranspiration Index (SPEI) variables for four study sites



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my individual contribution constitutes the major part of the work presented in this publication, including the conceptualization and design of the study, development of the methodology, performance of the analysis, drafting of the original manuscript, and the review and editing of the final version.

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my individual contributions included securing research funding, conceptualisation of the study, data collection, as well as reviewing and editing of the manuscript.

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