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Title: Natural disturbance regimes as a guide for sustainable forest management in Europe

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ABSTRACT

In Europe, forest management has controlled forest dynamics to sustain commodity production over multiple centuries. Yet over-regulation for growth and yield diminishes resilience to environmental stress as well as threatens biodiversity, leading to increasing forest susceptibility to an array of disturbances. These trends have stimulated interest in alternative management systems, including natural dynamics silviculture (NDS). NDS aims to emulate natural disturbance dynamics at stand and landscape scales through silvicultural manipulations of forest structure and landscape patterns. We adapted a "Comparability Index" (CI) to assess convergence/divergence between natural disturbances and forest management effects. We extended the original CI concept based on disturbance size and frequency by adding the residual structure of canopy trees after a disturbance as a third dimension. We populated the model by compiling data on natural disturbance dynamics and management from 13 countries in Europe, covering four major forest types (i.e., spruce, beech, oak, and pine-dominated forests).

We found that natural disturbances are highly variable in size, frequency, and residual structure, but European forest management fails to encompass this complexity. Silviculture in Europe is skewed towards even-aged systems, used predominately (72.9% of management) across the countries assessed. The residual structure proved crucial in the comparison of natural disturbances and silvicultural systems. CI indicated the highest congruence between uneven-aged silvicultural systems and key natural disturbance attributes. Even so, uneven-aged practices emulated only a portion of the complexity associated with natural disturbance effects. The remaining silvicultural systems perform poorly in terms of retention as compared to tree survivorship after natural disturbances. We suggest that NDS can enrich Europe's portfolio of management systems, for example where wood production is not the primary objective. NDS is especially relevant to forests managed for habitat quality, risk reduction, and a variety of ecosystem services. We suggest a holistic approach integrating natural dynamics silviculture with more conventional practices.

Key words: clearcut, close-to-nature forestry, deadwood, emulation of natural dynamics, even-aged, forest management, natural disturbance, natural dynamics silviculture, residual structure, retention, severity, uneven-aged

1. INTRODUCTION

Growth, composition, structure, and age class distributions of the vast majority of European forests are tightly regulated under a variety of production driven, even-aged and continuous cover systems aimed at supplying industrial raw materials (Schelhaas et al. 2018, Puettman et al. 2008). However, maximizing growth and yield often diminishes resilience to environmental stressors (Farrell et al. 2000, Thomson et al. 2009, Sommerfeld et al. 2021) leading to increasing susceptibility to an array of human and natural disturbances (Cardinale et al. 2012). It may also lead to declines in many elements of biodiversity (Hobson and Schieck 1999, Brunet et al. 2010, Drapeau et al. 2016), like species dependent on forest cover continuity, deadwood, and large trees. Examples of such species include bryophytes, lichens, fungi, and saproxylic beetles (Müller et al. 2007, Paillet et al. 2010, Brunet et al. 2010, Roth et al. 2019). Moreover, forest operations decreased the share of old European forests (Vilén et al. 2012, Sabatini et al. 2018) and modified their natural structure, composition, and dynamics for centuries, reducing their overall naturalness in several parts of Europe (Wallenius et al. 2010a, Brumelis et al. 2011). Forest scientists in many regions around the world have therefore proposed innovative ways of managing forests both for a greater variety of services and biodiversity, and for enhanced resilience and adaptive capacity to global change (Bengtsson et al. 2000, Gustafsson et al. 2012; Mori and Kitagawa 2014, Fahey et al. 2018, Kuuluvainen et al. 2021). For example, there is growing interest in the development of forest management techniques designed to approximate the structural and compositional dynamics of "natural" (or less human-influenced) ecosystems (Angelstam 1998, Keeton 2007, Kuuluvainen and Grenfell 2012, Puettmann et al. 2015). Here we use the term "natural dynamics silviculture" to refer to these approaches, recognizing this as part of a larger trend towards "ecological silviculture" as described by Franklin et al. (2018) and others (e.g. Palik and D'Amato 2017, Keeton et al. 2018). In Europe, there has long been interest in ecological or multi-functional forest management approaches (Bengtsson et al. 2000, Diaci et al. 2006, Wolfslehner and Seidl 2010, Kraus and Krumm 2013, Brang et al. 2014, Pretzsch et al. 2017). Natural dynamics silviculture has the objective of emulating natural disturbance dynamics to better approximate the environmental conditions in which these organisms have evolved (Angelstam 1996, Aplet and Keeton 1999, Bengtsson et al. 2000, Franklin et al. 2007, Keeton 2007). In some cases, ecosystem services, such as carbon storage and hydrologic regulation (Ford and Keeton 2017), or wildlife habitat and improved risk management (Huuskonen et al. 2021) may be a co-benefit. A further goal is to enhance resilience to global change (through adaptive capacity) by providing a broader array of plant functional traits and functional complexity in managed forests (Messier et al. 2013, Thom et al. 2019, 2020). This is in contrast to the narrow range of traits and functional diversity representation offered by intensive forest management practices, such as short rotation, even-aged forestry, which simplify and homogenize forest stands and landscapes (Fahey et al. 2018). Natural dynamics silviculture is not intended to fully mimic natural disturbances; rather it is an approach advocated for its utility in building complexity of habitat conditions, seral community diversity, and ecosystem service provisioning into managed forests (North and Keeton 2008; Angelstam 1996), recognizing that there can be tradeoffs among multiple objectives (see, for example, Sabatini et al. 2019). Besides economic and logistic reasons, a major barrier to implementing natural dynamics silviculture has been the lack of comprehensive understanding of the ranges of variability (whether historic, contemporary, or future) in natural disturbance regimes, including frequencies, spatial attributes, and severities (Kulakowski et al. 2017). Moreover, the distribution, composition, and dynamics of European forest landscapes have been fundamentally altered by millennia of human influence (Kaplan et al. 2009, Keeton et al. 2013, Pretzsch et al. 2017, Angelstam et al. 2021). Consequently, finding reference forests in which to observe baseline disturbance dynamics is needed, but also highly challenging, since only small fragments of primary or old-growth forests remain in most places (Szwagrzyk and Gazda 2007, Mikoláš et al. 2019). The proportion of remnant old-growth (primary) forests is only 0.7% of the forest cover in Europe (without Russia), with montane beech forests overrepresented relative to other forest types (Sabatini et al. 2018). However, in recent decades great progress has been made in describing the disturbance regimes of European forests, by applying long-term observational data (e.g. Thom et al. 2013, Nagel et al. 2017a), statistical (Seidl et al. 2014), and dendrochronological data analysis (Nagel et al. 2014, Čada et al. 2020), literature review (Kuuluvainen and Aakala 2011, Thom and Seidl 2016, Kulakowski et al. 2017), conceptual approach (White and Jentsch 2001, Kulakowski et al. 2017), as well as analysis of remote sensing data (Senf and Seidl 2020). Our study advances the science by comparing such literature derived data on disturbance dynamics with a comprehensive database on forest management effects across 13 countries. The analysis encompasses four of the major European forest categories, including those dominated by Norway spruce (*Picea abies (L.) H. Karst.*), Scots pine (*Pinus sylvestris L.*), European beech, (*Fagus sylvatica L.*), and oak (*Quercus robur Pall., Q. petrea (Matt.) Liebl., Q. pubescens Brot., Q. cerris L.*). Without the Mediterranean forest types, oak forests include mesophytic and thermophilous deciduous oak dominated forests (EEA 2006, pp. 28).

1.1 Comparing natural disturbance dynamics to forest management

A consistent comparative framework is needed to analyze how ecologically important attributes of forests managed using conventional systems may differ from those associated with natural disturbances regimes, such as the structural and stand development dynamics of primary and long-time unmanaged forests. We explore this potential by assembling data on pan-European forest disturbances and management effects. We use those data to adapt for Europe the "Comparability Index" (CI) first proposed by Seymour et al. (2002) in North America and later modified by North and Keeton (2008). The CI plots the relative frequencies and sizes of dominant disturbance types – such as gap forming, intermediate and high severity events – against the frequencies and scales of regeneration harvesting methods, such as clearcutting or selection systems. Using the current version of the index, silviculturists can determine how to adjust harvesting regimes to better approximate natural disturbance dynamics in terms of spatial scale and frequency.

In this study we expand the CI framework by adding a third dimension that characterizes the residual structure of forest stands (see, for example, Turner et al. 1998). The third axis represents percent survival (post natural disturbance) or retention (post-harvesting) of canopy trees, and is thus comparable to the inverse of disturbance severity. This results in a 3-

dimensional framework showing ranges of variability both for natural disturbance dynamics and forest management systems, based on the shared parameters of spatial extent, frequency, and residual structure. A similar framework was employed for boreal forests in Canada (Bergeron et al. 2002). With this innovation, the framework now provides a comprehensive basis for assessing the congruence between forest management and natural disturbances in both temperate and boreal European forest ecosystems.

1.2 Understanding variability in disturbance regimes

We synthesized research on disturbance dynamics obtained from both a survey of expert knowledge on the forest management of 13 European countries and a literature review on the natural disturbance regime of European forests. For example, relevant research has utilized (i) stand level structural observations of remnant old-growth stands (Korpel 1995, Standovár and Kenderes 2003, Schütz et al. 2016, Jaloviar et al. 2017, Aakala 2018), (ii) dendrochronological studies (Splechtna et al. 2005, Svoboda et al. 2012, Nagel et al. 2014, Čada et al. 2020), and (iii) historical and remote sensing studies (Aszalós et al. 2012, Nagel et al. 2017a, Senf and Seidl 2018). There are many studies in the first group (i), describing composition and structure or short-term dynamics in old-growth forests, based on repeated measurements, but these have yielded only limited information on long-term and landscape scale dynamics. Dendrochronological studies (ii) have longer (e.g. multiple centuries) time-frames, but explore primarily stand-level processes; while the third group (iii) includes areas with forests under strong human influences. Therefore, in our study, we relied on expert knowledge to synthesize and triangulate data from multiple types of natural disturbance studies and for all four of the major forest categories.

There are multiple sources of spatial variability in European disturbance processes (Senf and Seidl 2018, 2020), differing among categories and biomes (Thom and Seidl 2016). For instance, historically, fire played a greater role in boreal forests as compared to European temperate systems. It was typically infrequent and high severity in Norway spruce stands, and frequent but of low to mixed severity in Scots pine stands (Angelstam 1998, Niklasson and Granström 2000, Aakala 2018). However, in all types, residual live trees, both dispersed and aggregated in patches, typically persisted post-fire (Berglund and Kuuluvainen 2021). Wind disturbances are also a dominant structuring process across all European forests, though varying greatly in intensity and frequency, for example exhibiting periods when high intensity wind storms are of greater prevalence (Zielonka et al. 2009; Svoboda et al. 2012, Čada et al. 2016). Recent research on the role of intermediate severity disturbances suggests a much broader range of variability in the resulting stand age class structure and tree demography than previously recognized for European forests (Nagel et al. 2014, Svoboda et al. 2014, Trotsiuk et al. 2014, Janda et al. 2017). For example, in central Europe multi-aged (i.e. multi-cohort) stands originating from partial disturbances and subsequent pulse tree recruitment are common in some primary conifer forests (Mikoláš et al. 2017).

Thus, contrary to dominant even-aged management practices, natural dynamics silviculture aims to manage for a range of structures, including multi-aged or multi-cohort forest structures (O'Hara 1998). These are more analogous to the stand structures created by periodic partial mortality events and associated pulses of tree recruitment (Meigs et al. 2017). Large, infrequent disturbances are also a component of European natural disturbance regimes, but are more challenging to accommodate as a management objective (Turner et al. 1998). The comparative framework we propose synthesizes the current knowledge of these ranges of variability, presenting a basis for consistent comparisons against forest management.

In this paper, we explore the central research question; namely, what is the congruence between the silvicultural systems and natural disturbances in Europe? The study addresses several related objectives. These include understanding how congruence/divergence relationships are influenced by adding residual structure as a third axis to the Comparability Index and how does management differ from the natural disturbance regimes for different forest categories. Finally, we discuss how management approaches could be modified, where desirable, to more closely emulate natural disturbances.

We hypothesize that contemporary forest management in Europe exhibits very low congruence with past and present natural disturbances. We also hypothesize that by adding the third axis (residual structure), the divergence between natural disturbances and silvicultural systems will increase, and that this divergence will vary by biome and by forest category.

2. METHODS

2.1 Scope of the Study

The geographical scope of this study spans the boreal and temperate forest regions of Europe. We excluded the Mediterranean zone because of the greater variability and fragmentation of the region's extant forests and fundamental differences in forest history and contemporary management. We addressed four broad forest categories, dominated by four focal species; namely Norway spruce, Scots pine, European beech and main European oak species (*Quercus robur, Q. petrea, Q. pubescens, Q. cerris*). The classification criterion for this typing required that the dominant tree species exceeded 50% of the mixture ratio. Where a tree species other than the four focal species was dominant, or where (e.g. in mixed species stands) no single species exceeded 50% of the mixture ratio, forests were assigned to the "other" category. The four focal forest categories encompass the most common forest types in the boreal and temperate zones of Europe (comp. EEA 2006, pp. 28, forest type categories 1-8), and represent different ranges along the disturbance continuum. Our study compared human and natural disturbances both in aggregate for all studied forests continent-wide, and individually within each of the four focal forest category, quantitatively for the former and qualitatively for the latter.

2.2 Compiling the dataset

2.2.1 National forest management data

To assess European forest management practices, we selected 13 target countries, representing boreal and temperate ecoregions in Europe (Fig 1), and asked forest experts of each country to complete a standardized questionnaire (Appendix S1). The questionnaire (Q) addressed four groups of questions which concerned: 1) silvicultural systems used in a given country; 2) the ratio and land area under different silvicultural systems as well as forests with no management or managed primarily for non-timber objectives ("non-timber and unmanaged" henceforward); 3) the area and proportion of the four forest categories and their typical management methods; and 4) harvest size, rotation period, and residual structure (live tree retention) for these silvicultural systems.

Our classification of silvicultural systems encompasses four main categories of forest management (Table 1): A) even-aged forest management methods, such as uniform shelterwood and uniform clearcutting systems; B) uneven-aged (continuous cover) and multi-aged forest management methods, represented by a variety of selection and irregular shelterwood systems (see Raymond et al. 2009); C) regular coppice and coppice with standards; and D) no management or management primarily for non-timber objectives (i.e. EU MCPFE categories 1.1, 1.2, 1.3, see Parviainen and Frank 2006).

The survey excluded "other wooded lands" (see definition in FAO 2000) and non-productive forests (defined as annual increment < 1 m^3/ha/yr). Short-rotation systems with final felling at stand ages of 40 years or less, usually intensively managed plantations, are considered as forests in some of the investigated countries (France, Slovakia, Hungary, Latvia), but not so in others (Austria, Italy), where they are instead classified as agroforestry, and thus were excluded from the analysis. For consistency, we harmonized the silvicultural terminology across country-specific data. The area and area proportion of the four forest categories dominated by the selected four tree species, and their typical management methods were also assessed by the questionnaire. Forests not covered by these four categories were assigned to an "other" category.

The intervention sizes for the different silvicultural systems were defined as the area of the final harvest in the case of shelterwood-, clearcutting-, and coppice systems (Cat. A1, A2, C1, C2, see Table 1 for categories). Intervention size in the case of uneven-aged systems (Cat. B) was defined as the size of the canopy openings created by the intervention of the single-tree-, group- or multicohort selection system. This was necessary to compare forestry practices with their natural analogues.

Harvest frequency was based on rotation period in the case of even-aged (Cat. A) and coppice forest management systems (Cat. C), and with entry cycles for uneven-aged systems (Cat. B).

Residual structure (i.e. survivorship or retention) was defined as the percentage of living woody biomass volume (m^3) post-harvest compared to the pre-harvest volume left on a 1 ha site after the final cutting operation for even-aged management systems (clearcutting system, shelterwood system), or after the regular entry period (uneven-aged forestry). Intermediate treatments, such as thinnings, were not considered in the determination of harvest frequency and residual structure. Multiple data sources were used by the national experts to complete the questionnaire. Sources included national forest inventories, national silvicultural guidelines, ministry reports, data archived by national research institutes, scientific papers, state forest service statistics, original datasets maintained by survey participants, and expert opinion (see Appendix S2).

2.2.2 Natural disturbance attributes of European forests

Our analysis was based on variables describing the spatial extent, frequency, and residual structure (inverse of severity) of natural disturbance events in Europe. We compiled data from, (i) long-term studies of primary and old-growth forests (see Sabatini et al. 2018 for definitions), (ii) dendrochronological studies, and (iii) other studies defining the ranges of variability in disturbance dynamics for the four forest categories (Appendix S3, Table 2). To define the attributes of natural disturbances at landscape scale, the experts used information from studies investigating many of the largest and most intact old-growth forests remaining in Europe, including Perućica forest reserve in Bosnia-Hercegovina (Nagel et al. 2014), primary forests in northern Finland (Aakala 2018), unmanaged boreal forests in Fennoskandinavia including Russian Karelia (Kuuluvainen and Aakala 2011), old-growth forests of the Carpathians (Čada et al. 2020, Frankovič et al. 2021), the Parangalitsa Reserve in Bulgaria (Panayotov et al. 2011), and forest reserves in the European Russia (Aakala et al. 2011, Ryzhkova et al. 2020).
Based on the classification of Kuuluvainen and Aakala (2011), we grouped natural disturbance types into four categories; 1) high-severity disturbances, like major windstorms or forest fires, 2) intermediate severity disturbances that result in a partial removal of canopy, like microbursts, ice

storms, and moderate bark beetle outbreaks, 3) low severity disturbances that result in spatially diffuse mortality, like low severity fires, windstorms, ice storms, mild bark beetle outbreaks and 4) low severity disturbances that result in aggregated tree mortality, such as "gap dynamics" driven by tree mortality at fine scales of small groups of trees or a single large tree (< 200 m^2). Finally, ranges for size, frequency, and severity parameters were attributed to these categories on the basis of the literature review (Appendix S3). This compilation of the European disturbance literature was then used to estimate the dimensions of the four disturbance types.

2.3 Data Analysis

We compared boreal and temperate natural forest disturbances in Europe with the silvicultural systems applied in the 13 target countries. First, we calculated ratios and areas by forest biome (temperate and boreal) and by forest category for the silvicultural systems presented in Table 1 from the raw database of national data (Data S1: [Forest Management Database] in Aszalós 2021). Three countries represented the boreal zone: Sweden, Finland, and Latvia. Though Latvia belongs to the transitional hemiboreal zone (Ahti et al. 1968), it was classified as a boreal country in this study on the basis of forest type and management similarities.

Second, we designed a 3D figure for visualization purposes, and populated it with the data obtained from our forest management survey and natural disturbance literature review. The figure's three axes compare the three variables disturbance size, frequency, and residual structure. For each silvicultural system, we obtained country-level averages of the given silvicultural system. Then, we visualized the volume (within the 3D figure) of natural disturbance types and silvicultural systems by drawing ellipsoids with the outer bounds concurring with the data ranges. To facilitate the derivation and interpretation of the CI, we used the same approach to populate three 2D figures presenting size and frequency, size and residual structure, and frequency and residual structure (*sensu* Seymour et al. 2002). The 3D and 2D figures were visualized in R (R Core Team 2020) using the rgl (Murdoch 2020) and the car packages (Fox et al. 2012), respectively (Data S2: [R_Code.r], [management_data.cvs] in Aszalós 2021).

We obtained the Comparability Line (CL) by fitting a linear regression through the centroids of the four natural disturbance types. Subsequently, we derived the relative distance (i.e., the CI) of each disturbance attribute for each silvicultural system comparing the centroids of silvicultural systems with the CL. For example, a CI of 0.2 indicates a 20% similarity between a silvicultural system attribute and a natural disturbance attribute (e.g., harvest and disturbance size). In total, this approach resulted in six comparisons: size relative to frequency, size relative to residual structure, frequency relative to size, frequency relative to residual structure, residual structure relative to size, and residual structure relative to frequency. The average through all six comparability indices constitutes the overall difference of a silvicultural system from the natural disturbance regime.

3. RESULTS

3.1 Silvicultural systems used in European forests and in the four focal forest categories

The total forest cover of the 13 target countries without the Mediterranean forests and short-rotation systems is approximately 109 million hectares (1 hectare area is equal to 10.000 m^2), see Fig. 2. According to the national forest management data we examined (Data S1: [Forest Management Database] in Aszalós 2021), the forested area of the three boreal countries

(Sweden, Finland and Latvia) accounts for 44% of this total, and the 10 temperate countries encompass the remaining 56%.

Our results show that use of silvicultural systems in Europe is skewed disproportionately towards even-aged systems. Even-aged silvicultural systems (Cat. A, see Table 1 for categories) dominate (72.9%) across all the target countries (Fig. 2). More than half of the investigated forests are managed by uniform clearcutting systems (51.9%, Cat. A2), and approximately 21% by uniform shelterwood systems (Cat. A1). Uneven-aged systems, by comparison, are employed to a far lesser degree. In our dataset 9.7% of forests are managed using uneven-aged systems (Cat. B), whereas coppice systems (Cat. C) are applied to 9.1% of forests. Only 8.3% of the forest included within the scope of our study is unmanaged or managed primarily for non-timber objectives (Cat. D), such as management for biodiversity (Fig. 2, Appendix S4).

There is a marked difference between boreal and temperate countries (Fig 2, Appendix S5). Clearcutting systems (Cat. A2) are employed across 86.7% of forests in the boreal zone, which are predominantly coniferous. For the three boreal countries included in our dataset (Finland, Latvia, and Sweden), all other management methods represent minor components. Uneven-aged management is applied on only 4.2% of forests, whereas 8.7% belong to the non-timber and unmanaged category in the boreal zone. In contrast, in the temperate zone shelterwood (Cat. A1), uneven-aged (Cat. B), and coppice systems (Cat. C) are applied over larger proportions of the forest area, i.e. 37.4%, 14.1%, and 16.4% of all forests, respectively (Fig. 2, Appendix S4). Within the temperate biome, however, dominant silvicultural systems vary by country. For example, coppice and uneven-aged systems are more prevalent in France and Italy; shelterwood systems are more common in Slovakia and Romania. Finally, in Czech Republic, Germany, Poland, Austria, and Hungary, clearcutting and/or uniform shelterwood systems are more widely represented. The majority of Slovenian forests are managed by irregular shelterwood systems (Appendix S5).

In Norway spruce and Scots pine dominated forests, the primary management system is even-aged with clearcutting system, applied to 68.9% and 78.1% of the area of all 13 countries respectively (Table 2). Less than one fifth of these two focal forest categories is managed by uniform shelterwood systems across all of the 13 target countries. In temperate Norway spruce dominated stands, even-aged methods have the highest representation (75.3%), but uneven-aged methods, such as single-tree and group selection, are also common (24.7%) (Table 2). The majority of European beech and oak dominated forests are managed with uniform shelterwood systems (67.7% and 48.9% respectively), indicating that natural regeneration (advanced regeneration) and subsequent release through overstory removal are the typical silvicultural techniques applied to these forest categories. Beech dominated forests have a fairly high ratio of uneven-aged management for all the 13 counties in the temperate forest countries, nearly 20% of beech forests in our dataset are managed with selection methods on both scales. One-third of temperate oak dominated forests are managed with a variety of coppice systems (Table 2, Appendix S6).

3.2 Characteristics of natural disturbances in European forests

The literature review revealed that disturbance sizes, frequencies and severities in European temperate and boreal forests are highly variable across space and time (Table 3). Small, aggregated canopy openings, where gap size usually does not exceed 200 m^2 (Mountford 2001, Kuuluvainen and Aakala 2011) are common throughout the region, typically removing less than 20% of the canopy (Nagel et al. 2014, Hobi et al. 2015). Individual low severity diffuse disturbances affect larger spatial extents, such as the low severity fires typical in boreal Scots pine forests and low severity ice storms in temperate Europe (Angelstam and Kuuluvainen 2004, Kenderes et al. 2007, Kuuluvainen and Aakala 2011). In such events, the total area of scattered canopy openings, tree mortality, and tree damage for an event may range from 200 m^2 to 100 ha even if locally the proportion of canopy disturbed remains low. Rotation periods for low severity, diffuse disturbances can be relatively short, often ranging between 10-100 years (Sannikov and Goldammer 1996). Intermediate severity wind and ice storms, having rotation periods of approximately 100-500 years (Nagel et al. 2014, 2017a), generate a diverse mosaic with 25-75% canopy loss (Nagel et al. 2014, Čada et al. 2020) suggesting a very broad range of variability. Disturbance patches resulting from intermediate severity disturbances are irregularly structured (i.e. often having variable residual tree survivorship densities and patterns) and range in size from 200 m^2 up to 100 ha (Kuuluvainen and Aakala 2011, Kameniar et al. 2021, Frankovič et al. 2021). High severity events are rare, returning at intervals usually of more than 300-500 years (Aakala 2018, Nagel et al. 2014). However, severe disturbances in mountain ecosystems, like in the conifer forests of the Carpathians, can have rotation periods as short as 174 years (Čada et al. 2016). The size of such disturbance areas varies widely, ranging from 1 to 1000 ha (Kuuluvainen and Aakala 2011).

3.3 Congruence of silvicultural systems with natural disturbances

Silvicultural systems differed clearly from natural disturbances with regard to the evaluated attributes; size, frequency, and residual structure (Table 4, Table 5, Fig. 3, Fig. 4 Fig. 5). With an average CI of 0.07 (7% congruence), clearcutting and uniform shelterwood systems had the lowest congruence with natural disturbances, followed by coppice systems (on average 13 %).

Uneven-aged systems were most similar to natural disturbances (on average 53 %) among all silvicultural systems investigated.

Altogether, silvicultural systems occupied a much smaller portion of the 3D attribute space than natural disturbances, indicating a much lower variability (Fig. 3). High and intermediate severity disturbances had a particularly high volume, followed by diffuse low severity disturbance. Only the volume of aggregated low severity disturbances occupied a 3D space similarly small as each individual silvicultural system.

Ellipsoids – representing the attribute space occupied by a given disturbance type or silvicultural system relative to the three axes – for clearcutting and uniform shelterwood systems had large overlapping zones (Fig 3, Fig. 4 a,b,c). The mean harvest sizes of these systems (2.8, 3.7 ha respectively, Table 4, Fig. 5) were intermediate between the mean size of low severity aggregated and diffuse natural disturbances, however their rotation periods were shorter (100 years).

The 2D plots added more detail to the relationship between natural disturbance and silvicultural systems (Fig. 4). The size-frequency plot (Fig. 4 a) showed an overlap of the ellipsoids of uneven-aged systems and low severity aggregated disturbance, indicating that uneven-aged systems are partly within the range of low severity aggregated disturbance. Coppice systems, and, to some degree even-aged silviculture systems, overlapped with low severity diffuse disturbance (Fig. 4 A). We found the highest congruence between uneven-aged forestry and natural disturbance for size relative to frequency, and frequency relative to size with CIs of 0.5 and 0.79 (i.e., 50% and 79%, respectively, see Table 5). Congruence values of other silvicultural systems ranged from 0.1 to 0.4 with natural disturbance. Lowest CI values (i.e., the largest divergence) were detected for frequency relative to residual structure and size relative to residual structure (Table 5, Fig 4 b, c). In particular, CI values for even-aged and coppice systems were only 0.01 or smaller. Further, these silvicultural systems diverged strongly from natural disturbance comparing residual structure relative to size and residual structure relative to frequency (Fig 4 b, c) with CIs of 0.03 and 0.06, respectively. In contrast, with CIs of 0.7-0.8 uneven-aged systems were considerably more similar to natural disturbances in the same pairwise comparisons.

The even-aged management systems overlapped with coppice systems in terms of size relative to residual structure. Ellipsoids of uneven-aged systems were detached from the three other silvicultural systems on each plot, but were often close to, or overlapping with, low severity aggregated natural disturbances (Fig. 3, Fig. 4 A, B, C).

4. DISCUSSION

4.1 Significance of the residual structure axis

Based on our findings, the majority of European forests are managed outside the range of their respective natural disturbance regimes, showing low congruence with past and present natural disturbances. For more than two centuries, European foresters have controlled tree mortality processes, growth and yield, and stand health based on a well-developed science. In this school of thought, management was focused on excluding natural disturbances and producing predictable outcomes. Acknowledging this tradition, we propose that there is an opportunity to expand Europe's portfolio of management options to diversify habitats, seral patch mosaics, and service provisioning. While previous studies have described natural disturbance regimes according to their size, frequency, and severity ranges (Turner et al. 1998, Bergeron et al 2002), this study is among the first to populate this framework with field-based data for forest management and literature derived data for natural disturbances. The expanded framework employed in our study defines the critical third axis, residual structure, expressed as the proportion residual canopy structure (i.e. tree survivorship) left on a site following harvest or disturbance. Adding this third axis to the forest disturbance conceptual model significantly improved the basis for comparison and proved critical in understanding incongruences with forest management. Silvicultural systems in Europe typically retain very low densities of diverse biological legacies, such as residual live, dead, and downed trees, either dispersed or aggregated (Paillet et al. 2015, Vítková et al. 2018). This is generally true for the selection systems as well – deadwood and old, large living trees are removed (Keren and Diaci 2018). Our model incorporated only residual living trees – but even this resulted in high divergence from natural dynamics.

The Comparability Index (CI) was initially proposed by Seymour et al. (2002) as a useful benchmark for what they and others (e.g. Franklin et al. 2007) termed "natural disturbance-based silviculture". Using the CI, Seymour et al. (2002) postulated that a *Picea* spp. plantation managed on harvest rotations of 50 years and using 20-ha clearcuts would be outside the range of variability for natural disturbances. And thus, in scenarios such as this one, cumulative ecological impacts over multiple rotations and at landscape scales are unlikely to be analogous to natural disturbance effects. Our findings show that forest management effects in Europe partly overlap with the range of variability of low intensity diffuse disturbances on the frequency-size attribute space. However, relative to residual structure (the third axis) there is a large divergence, as low intensity diffuse disturbances usually result in only 10-25% mortality of the tree canopy. North and Keeton (2008) modified Seymour et al.'s (2002) model by adding a hypothesized intermediate disturbance regime and suggested a third evaluation criterion, which is the amount or density of "biological legacies". Our study has applied and further developed the CI index – populated with data spanning the full range of natural disturbances in Europe, including intermediate disturbances. We calculated the overall congruence of silvicultural systems and natural disturbances relative to all three attribute dimensions, using the CL through the European forest disturbance regimes as reference line. Using the expanded index, forest managers can determine the congruence/divergence of a given harvesting regime relative to natural disturbance dynamics.

4.2 Uneven-aged silvicultural systems are the closest to Comparability Line of natural disturbances

The vast majority of the 109 million ha of temperate and boreal forests included in this study are managed under even-aged systems, having only 7% congruence with natural disturbances on average. Uneven-aged systems had the highest CI values, with 53% similarity to natural disturbances, but this silvicultural system constitutes only approximately 10% of all human management of the investigated forest land. Looking at the big picture the 3-dimensional ellipsoid for uneven-aged forest systems occupied an attribute space close to the ellipsoids for natural disturbances, whereas the three other silvicultural systems were located well outside the range of natural disturbances. Clearcutting and uniform shelterwood systems had the lowest CI in almost all comparisons, coppice systems were intermediate, and uneven-aged systems had the highest CI values in all paired comparisons. Using only axes for size and frequency, and disregarding structural complexity, the similarity of even-aged and coppice systems with natural disturbances was markedly higher. Management systems using 50-100 years rotations and few hectare harvest blocks have overlapping size and frequency attributes as compared to low severity diffuse and intermediate severity disturbances. However, these natural disturbances always have much higher residual structure (25-90%) than management systems leaving only a few residual trees. On the other hand, high severity disturbances can exhibit low residual structure (0-25% canopy survivorship) similar to even-aged and coppice systems. Still, the frequency of high severity natural disturbances is smaller by one order of magnitude than that of the rotation of silvicultural practices. Consequently, both size and frequency attributes for clearcutting, shelterwood, and coppice systems exhibited large departure with the residual structure axis included, with CI values dropping to only 0.01 or less congruence with natural disturbances.

This analysis clearly shows that Europe's natural disturbances have great complexity and variability across the multiple dimensions of spatial extent, frequency, and severity leading to variation in structural complexity. By contrast, management in most European forests perpetuates a landscape-scale condition incorporating little of this diversity (Angelstam 1996). Although uneven-aged forestry showed the highest congruence with natural disturbances on the basis of the three observed attributes, it does not emulate or fully encompass the great complexity of all natural disturbance effects. For example, where a disturbance regime of a forest type is characterized by intermediate and/or high severity disturbances, multi-cohort and/or variable retention systems would more closely emulate disturbance effects (Meigs and Keeton 2018; Kameniar et al. 2021), than uneven-aged systems using single tree or group selection methods. Other important features of forests with natural dynamics are also often missing in intensively managed uneven-aged forest stands – such as biological legacies or irregular structure within silvicultural gaps, presence of large, older trees, and diverse types, sizes and decay-stages of deadwood, both standing and downed (Keren and Diaci 2018).

4.3 Congruence of natural disturbance and management of the four focal forest categories

Interest in natural dynamics silviculture has taken root in many regions globally as foresters seek management alternatives that better integrate biodiversity and non-timber objectives. Similarly, in Europe the merits of intensive forest management, such as high yield, even-aged forestry practices, have been the subject of debate (Bollmann and Braunisch 2013; Schulze et al. 2014). Points of contention include tradeoffs among economic efficiency, hydrologic regulation, abiotic disturbance risks, susceptibility to insects and pathogens, carbon uptake and storage, and habitat provisioning (Mikoláš et al. 2014, Burrascano et al. 2016). In this context, comparison with natural disturbance analogues is particularly informative, for instance in developing forest management approaches that integrate competing objectives (Franklin et al. 2018; Schall et al. 2020). Knoke et al. (2020) showed that continuous cover forest management also can be an effective strategy for meeting economic objectives, for example if risk-avoidance is an important strategic consideration.

We found that even-aged management with clearcut regeneration harvesting is the most prevalent system in the boreal zone of Europe, yet resulted in very low congruence with natural dynamics. Primary or unmanaged boreal Norway spruce forests are dominated by finely-scaled, low severity aggregated gap openings, together with less frequent intermediate severity disturbance events (Caron et al. 2009, Aakala et al. 2009, Szewczyk et al. 2011, Aakala et al. 2011, Khakimulina et al. 2016). Boreal Scots pine stands also experience mixed-severity fire disturbances, leaving irregular age-class structures and high amounts of deadwood in variably distributed spatial patterns (Niklasson and Granström 2000, Wallenius et al. 2010b, Aakala 2018, Ryzhkova et al. 2020). Natural disturbance effects contrast starkly with the clear-felling regime most commonly practiced in boreal pine and spruce dominated forest types. Clear-felling results in mosaics of 2-10 hectare stands that are predominately even-aged at the patch scale, harvested on 60-90 year rotations, and have extremely low volumes and densities of post-harvest residual structure (i.e. biological legacies) (Angelstam and Manton 2021).

The temperate zone of Europe has a more diverse portfolio of harvest regimes, and consequently the congruence with natural disturbances greatly varies among both countries and forest types. Forests dominated by Scots pine, of which more than half are in Poland, are predominantly managed by clearcutting systems. Regional studies from the Carpathians, Rila Mountains (Bulgaria), and Bohemia (Czech Republic) suggest that mixed-severity disturbance regimes with wide variation of low to high disturbance severities historically operated in temperate mountain spruce forests (Panayotov et al. 2011, Szewczyk et al. 2011, Svoboda et al. 2014, Trotsiuk et al. 2014, Čada et al. 2016, Janda et al. 2017, Frankovič et al. 2021). We showed that this variability is not emulated by contemporary forest management. Nevertheless, in this study, almost 25% of temperate Norway spruce dominated stands are managed by uneven-aged systems, which suggests that the management of this forest category has the largest congruence with natural disturbances among the four forest categories we evaluated. On the other hand, Norway spruce has been planted widely outside its natural distribution in temperate Europe (Spiecker 2003, Caudullo et al. 2016). These stands are highly susceptible to windthrow and bark beetle outbreaks, which are significantly amplified by climate change. Foresters have responded by salvaging or "sanitary cutting" thousands of hectares of beetle or wind disturbed forests in recent decades (Schelhaas et al. 2003, Thom et al. 2013, Seidl et al. 2014, Hlásny et al. 2019), although this is not always profitable (Knoke et al. 2021).

Beech dominated forests are usually managed with uniform shelterwood systems, but on 20% uneven-aged silviculture is applied, thus emulating more closely the pattern created by the low severity aggregated disturbances (gap dynamics) associated with naturally dynamic beech forests (Emborg et al. 2000, Standovár and Kenderes 2003, Piovesan et al. 2005, Kral et al. 2014, Frankovič et al. 2021). However, intermediate and mixed severity disturbances are also common in beech-dominated forests (Splechtna et al. 2005, Nagel et al. 2014, 2017a; Frankovič et al. 2021), and these are not well emulated by contemporary harvesting systems in Europe. Natural dynamics of oak forests in Europe are difficult to separate from anthropogenic influences, as the latter have shaped the oak-zone landscapes since pre-historic times (Vera 2000, Bobiec et al. 2018, 2019).

Lacking robust natural reference stands and landscapes, researchers have only a limited understanding of natural regeneration and stand dynamics in European oak forests (Kohler et al. 2020). Light demanding oak species (*Quercus pubescens, Q. robur, Q. petrea*) require open habitats resulting from poor site productivity or strong human/natural disturbances that enhance natural regeneration ("oakspace", see Bobiec et al. 2018, 2019). In contrast to their natural regeneration strategy, much of the contemporary oak management employs closed coppice and high forest (originated from seed or planted seedlings) systems which have very low congruence with natural dynamics for this forest type.

4.4 Natural dynamics silviculture

The comparative framework and index presented in this paper are intended as a tool to encourage development of multifunctional landscapes by applying "natural dynamics silviculture", complemented by a variety of retention forestry approaches (see, for example, Mori and

Kitagawa 2014; Puettmann et al. 2015, Gustafsson et al. 2020). Interest in ecologically-oriented forest management has increased dramatically in recent decades both in North America and in Europe (Angelstam 1998, Bengtsson et al. 2000, Kuuluvainen 2002, Franklin et al. 2002, Lindenmayer et al. 2006, Bauhus et al. 2009, Krumm et al. 2020; Čada et al. 2020, Kuuluvainen et al. 2021), but there are key differences. In North America, ecological forest management increasingly looks to baselines provided by primary (i.e. never cleared by humans) forests, comparing forest dynamics driven by natural disturbances (e.g. wind, fire, insects, floods) with the impacts of different forest harvesting approaches (Franklin et al. 2002, Keeton 2007, Fahey et al. 2018, Keeton et al. 2018, Thom and Keeton 2019). In Europe interest in ecological forestry is also high (e.g. Bauhus et al. 2009, Pretzsch et al. 2017), but the common European approaches, variably termed "close-to-nature," "Plenterwald", or "Pro Silva" are quite different, being primarily modifications of conventional selection systems (Johann 2006, Brang et al. 2014). They are used for either conversion cutting in spruce plantations – promoting replacement by native mixed species or deciduous forest types – or as uneven-aged management (e.g. the "Plenterwald" and "Dauerwald" systems) in European beech and Silver fir-European beech forests, and other temperate deciduous or mixed species forest types. Close-to-nature silviculture, as commonly practiced, only partially replicates natural disturbance effects (Diaci 2006, Schütz et al. 2016) by providing a mosaic of structurally variable patches as well as tree age class diversity at the aggregate or stand scale. However, it rarely maintains irregular age-class structure or retention trees within patches and often neglects the dead wood (both standing and downed) component of structural complexity, despite its inevitable importance in biodiversity maintenance (Gossner et al. 2013, Larrieu et al. 2014, Roth et al. 2019). In parts of Central Europe deliberate efforts have been made to emulate consequences of natural processes observed in old-growth stands (Kraus and Krumm 2013, Schütz et al. 2016, Roth et al. 2019), such as retention of downed woody debris, habitat trees and other structures (Johann 2006). For example, research in old-growth forest reserves has supported the development of flexible irregular shelterwood system in Slovenia, by defining unique combinations of forest sites, stands, and social environments (see Diaci 2006, Boncina 2011). In the boreal forests, experimental work has been initiated to assess the feasibility and benefits of natural dynamics silviculture, including explicit dead wood goals (Koivula et al. 2014).The potential to incorporate a broader range of dynamics and structures – including old and habitat or "veteran" trees, standing deadwood, and downed trees, based on research on natural disturbance effects – is true both for European even-aged and continuous cover forest management (Pommerening and Murphy 2004, Kern et al. 2017, Nagel et al. 2017b).

Simplification and homogenization of European forests, for example through the widespread planting of mono-specific *Picea abies* plantations across formerly diverse landscapes and on former beech and other tree sites and through the coppicing system in the Mediterranean forests, is a well-documented phenomenon (Angelstam 1998, Björse and Bradshaw 1998, Tērauds et al. 2011, Keeton et al. 2013). This practice, implemented over centuries, has contributed to the high susceptibility of some European forests to spruce bark beetle (*Ips typographus*) outbreaks (Hlásny et al. 2021) as well as forest dieback associated with fungal pathogens, such as root rots (e.g. *Armillaria* sp., *Heterobasidion parviporum*, *H. annosum*, see Peri et al. 1990, Arhipova et al. 2011). Also as a result of homogenization and bias toward mature cohorts, European forests may be more vulnerable to increased disturbance intensity and frequency associated with climate change (Långström et al 2009, Seidl et al. 2014), leading to interest in management to restore greater heterogeneity in forest composition at landscape scales (Angelstam and Kuuluvainen

2004). Improved understanding of baseline disturbance dynamics – from both studies of reference stands as well as dendrochronological reconstructions – could guide this endeavor (Bauhus et al. 2009, Paillet et al. 2010; Čada et al 2020).

4.5 Limitation and perspectives of the study

Human presence and influence on forest ecosystems has been continuous since the last ice age, and became decisive from the Neolithic period onwards (i.e. -6000 y) in Europe (Angelstam et al. 2021). Hence the structure, composition, and natural dynamics of European forests have been fundamentally altered across millennia (Kaplan et al. 2009). This particularly concerns certain forest types, like oak dominated forests at lower elevations. Other forest types survived in a limited number of primary forest stands and landscapes, often in places with low accessibility (Sabatini et al. 2018). These remnants provided only limited capacity to reconstruct historical ranges of variability, particularly for landscape-scale processes. Consequently, reconstructing or inferring baseline disturbance dynamics is fraught with uncertainty, though dendrochronological approaches (Aakala et al. 2011, Svoboda et al. 2012, Nagel et al. 2014, Schurman et al. 2018, Čada et al. 2020; Frankovič et al. 2021) and retrospective modeling are proving increasingly robust. The CI presented here must be applied within this context, acknowledging human influences on our estimation of natural disturbance regime characteristics.

Disturbance regimes are changing rapidly (White and Jentsch 2001, Turner 2010). Recent studies indicate a significant increase in disturbance rates across Europe's natural and managed forests (Schelhaas et al., 2003, Seidl et al. 2014). However, it remains unknown how they will change exactly in the future and how they will be affected by climate change. The strong yet complex linkage between natural and human processes are already shaping the forested landscapes of

Europe (Senf and Seidl 2020), making the separation of human and natural dynamics very challenging.

Further research could strengthen the CI by incorporating information (by forest type and local content) on the amount and quality of deadwood, density of large trees, density and diversity of tree-related microhabitats on habitat trees, intensity of the given management method, proportion of admixing species, and use of natural or artificial regeneration. For example, while uneven-aged systems had the highest CI values on the basis of the three observed attributes, addition of dead wood and large tree attributes, specifically, might lower these values, as retention of these structure is not commonly practiced in Europe.

This framework must acknowledge the alteration of disturbance regimes caused by centuries of human influence as well as shifting boundary conditions associated with climate change (Seidl et al. 2014, Kulakowski et al. 2017, Thom et al. 2017, Senf and Seidl 2020). It must also consider the broad range of forest management approaches and harvesting intensities in Europe, varying by region, forest type, ownership and subsidy programs, local conditions and accessibility, importance of non-timber services, and other factors (Schelhaas et al. 2018). Application of portfolios of diversified forest management approaches need to be considered across tree, stand, and landscape scales, and be adapted to differing forest ownerships (Lazdinis et al. 2019, Angelstam et al. 2020). Consideration of these factors can help forest practitioners to down-scale and operationalize the comparability framework we propose.

4.6. Management implications

We present this conceptual model to help inform forest management practices designed to more closely emulate natural disturbance effects, and in so doing provide a broader range of ecosystem goods, services, and habitats compared to conventional practices (Mönkkönen et al. 2014, Eyvindson et al. 2018, Huuskonen et al. 2021). The CL and CI, which helps to compare natural and human disturbances, highlights the importance of understanding the three main attributes of disturbances: size, frequency, and severity. These must be considered jointly, both for understanding natural disturbance baselines and for developing and testing ecologically-based, sustainable forest management practices in Europe. With downscaling to incorporate information on more proximate disturbance effects and habitat relationships (e.g. key elements of stand structure and patch configuration emulated through retention forestry), the CI provides a useful tool for planning and assessing biodiversity outcomes in managed forests, complementing other approaches (see, for example, Thom and Keeton 2020, Mikoláš et al. 2021).

Natural disturbances create a much broader range of variability for all three attributes as compared to human disturbances. Forest practitioners could approximate the Comparability Line at any point of the continuum represented by the ranges of variability for the three attributes. However, to apply the entire range of disturbance processes to a landscape heavily altered by millennia of land-use history will be challenging. For example, intermediate and mixed-severity disturbances play a formative structuring role in many European forest types (Svoboda et al. 2014, Trotsiuk et al. 2014, Khakimulina et al. 2016, Nagel et al. 2017a, Aakala 2018, Čada et al. 2020). The emulation of intermediate and mixed-severity disturbances, with broad range of age classes and high level of biological legacy will require a fundamental change in forest practices. Advances in multi-cohort and retention silvicultural practices in North America, shifting away from even-aged management and derived from efforts to emulate natural disturbance regimes, may prove informative in this regard (Harvey et al. 2002, North and Keeton 2008, Long 2009). The forestry community's perceptions of the role of natural disturbances are also vital (Nagel et al. 2017b). Foresters will need to feel comfortable emulating certain aspects of natural disturbance effects, such as deliberately creating (or retaining following natural disturbances) variability in residual structure, both live and dead, without defaulting always to sanitary cutting (Diaci et al. 2017). In the case of coarse-scaled interventions (larger than 10 ha), the rarely used irregular shelterwood method and retention forestry systems would have much higher similarity to intermediate severity disturbances. Irregular shelterwood systems keep relatively high residual structures after the interventions, but their use is extremely low in European silviculture as a proportion (< 3%) of overall management based on our data (Data S1: [Forest Management Database] in Aszalós 2021). Instead of changing the predominant even-aged management regime to just one type of silviculture, we and others recommend broader diversification of management regimes (Schall et al. 2018, Nolet et al. 2018), adapted to both ecological and social systems (Angelstam et al. 2020). A combination of uneven-aged selection and irregular shelterwood systems with even-aged clearcutting and uniform shelterwood system – with high level of remaining biological legacies – could promote landscape-scale diversity of seral stages, stand structures and biodiversity (see Mönkkönen et al. 2014, Schall et al. 2018).

Natural dynamics silviculture must incorporate deadwood management and tree retention (including large and habitat trees) to decrease the divergence from natural disturbances by increasing the amount and type of biological legacies (Larrieu et al. 2014, Krumm et al. 2020). Compared to naturally dynamic forests the amount of deadwood is low in European forests (Guby and Dobbertin 1996, Lombardi et al. 2008, Bölöni et al. 2017, Vítková et al. 2018, Puletti et al. 2019). According to the national reported values, total deadwood ranges between 2.3 and 28 m^3/ha (Forest Europe, 2020), and the mean for the EU countries is 16 m^3/ha (Puletti et al. 2019), much lower than the recommended threshold values (see Müller and Bütler 2010).

However, effective deadwood management should not only increase the amount and size, but also manipulate the position, arrangement, and decay stages of retained trees (Vítková et al. 2018), since deadwood diversity is pivotal for many taxa (see e.g. Ódor et al. 2006, Fritz et al. 2008, Gossner et al. 2013, Bouget et al. 2013). As climate change intensifies bark beetle outbreaks, deadwood management, tree retention, and disturbance-based forestry should be harmonized with bark beetle management strategies in forests most susceptible to bark beetles (Hlásny et al. 2019, Hlásny et al. 2021).

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Table 1. Classification and the definition of the silvicultural systems

Category	Silvicultural system	Definition
A	Even-aged silvicultural systems	Even-aged management
A1	Even-aged forest management with uniform shelterwood system	Regeneration is usually natural. Interventions are intermediate thinnings and subsequent cuttings. New seedlings are established before the mature trees are fully removed. Final cut after a certain target diameter or age has been reached. The size of the final cut is usually between 0.5 ha and 10 ha.
A2	Uniform clearcutting system (rotation time is > 40 years)	Regeneration is usually artificial (planted). Interventions are intermediate thinnings. Clearcut after a certain target diameter or age has been reached. The size of the clearcut is usually between 0.5 ha and 10 ha.
B	Uneven-aged silvicultural systems (continuous cover forestry)	Selection cutting based usually on target diameter distribution. Predominantly trees of large dimensions are cut
B1	Single tree selection	Scattered individual trees of multiple age classes are harvested
B2	Group selection	Small to medium sized openings created by the removal of several adjacent trees, gap size is typically under 0.3 ha
B3	Multi-cohort (irregular shelterwood) system	Multi-aged forestry, permanent retention with ≥10% basal area
C1	Coppice systems	Woodlands regenerated asexually from stump sprouts on harvested crop trees
C2	Coppice with standards systems	Two distinct elements: a lower storey treated as coppice; and an upper storey of scattered older tree individuals (standards) treated as high forest
D	Non-timber and unmanaged forests	No forest management, or management primarily for non-timber objectives, such as protection forest (against erosion, avalanche, etc.), conservation-oriented management, management for biodiversity, non-productive forests, forests with no defined rotation time, abandoned forests, set-asides.

Table 2. Forested area or proportion by forest categories (as represented by dominant species) and silvicultural system.

Forested area or silvicultural system	Norway spruce	Scots pine	European beech	Oak species	Combined totals
Forested area (hectares)					
Area	**24 994 098**	**33 494 125**	**8 615 899**	**11 003 675**	**78 107 797**
Boreal	15 083 066	23 539 760	151 800	9 355	38 783 981
Temperate	9 911 032	9 954 365	8 464 099	10 994 320	39 323 816
Percent					
A1 Shelterwood	**19.1**	**17.1**	**67.7**	**44.5**	**27.2**
Boreal	2.1	12.3	0.0	100.0	8.3
Temperate	45.1	28.5	68.9	44.4	45.8
A2 Clearcutting	**68.9**	**78.1**	**5.3**	**13.7**	**58.1**
Boreal	94.4	83.8	96.0	0.0	88.0
Temperate	30.2	64.6	3.7	13.7	28.6
B Uneven-aged	**11.9**	**4.3**	**19.9**	**5.6**	**8.6**
Boreal	3.5	3.9	4.0	0.0	3.7
Temperate	24.7	5.3	20.2	5.6	13.5
C Coppice	**0.0**	**0.5**	**7.0**	**36.3**	**6.1**
Boreal	0	0	0	0	0
Temperate	0	1.6	7.2	36.3	12.1

Table 3. Size, frequency, and residual structure data by natural disturbance category. Size means the area affected by a single disturbance event, frequency the interval between such disturbance events in years, while residual structure the percentage of residual living woody biomass volume related to 1 ha area.

Disturbance type	**Size (m^2)**	**Frequency (years)**	**Residual structure (%)**	**References**
High severity	$10^4 – 10^7$	150-1000	0-25	Kuuluvainen and Aakala 2011, Aakala 2018, Nagel et al. 2014
Intermediate severity	$200-10^6$	100-500	25 -75	Nagel et al. 2014, 2017a Kuuluvainen and Aakala 2011, Čada et al. 2020, Frankovic at al 2021
Low severity, diffuse effects	$200-10^6$	10-100	75-90	Angelstam and Kuuluvainen 2004, Kenderes et al. 2007, Kuuluvainen and Aakala 2011, Thom et al. 2013
Low severity, aggregated effects	20-200	1-10	80-85	Khakimulina et al. 2016, Mountford 2001, Kuuluvainen and Aakala 2011, Hobi et al. 2015

Table 4. Average size, frequency, and residual structure for silvicultural systems and natural disturbances of European forests.

System or disturbance	Size (ha)	Frequency (years)	Residual structure (%)
Silvicultural system			
A1 Uniform shelterwood systems	3.7	104.0	1.6
A2 Clearcutting systems	2.8	91.4	1.9
B Uneven-aged systems	0.1	8.4	78.7
C Coppice systems	3.2	48.0	1.7
Natural disturbance			
High severity	500.5	575.0	12.5
Intermediate severity	50.0	300.0	52.5
Low severity, diffuse effects	50.0	55.0	82.5
Low severity, aggregated effects	0.01	5.5	82.5

Table 5. Comparability Index (CI) values, representing the congruence between silvicultural systems and natural disturbances. As shown in Fig. 4, each attribute (size, frequency, and residual structure) was assessed relative to another attribute to derive the CI values, measuring the distance from the centroids to the Comparability Line (CL). The final row of the table presents the average CI across all pairwise comparisons.

CI	**A1 Shelterwood**	**A2 Clearcutting**	**B Uneven-aged**	**C Coppice**
Size relative to frequency	0.11	0.11	0.50	0.26
Size relative to residual structure	<0.01	<0.01	0.11	<0.01
Frequency relative to size	0.20	0.20	0.79	0.40
Frequency relative to residual structure	0.01	0.01	0.26	<0.01
Residual structure relative to size	0.03	0.04	0.70	0.03
Residual structure relative to frequency	0.06	0.06	0.80	0.05
Average	0.07	0.07	0.53	0.13

Figure captions

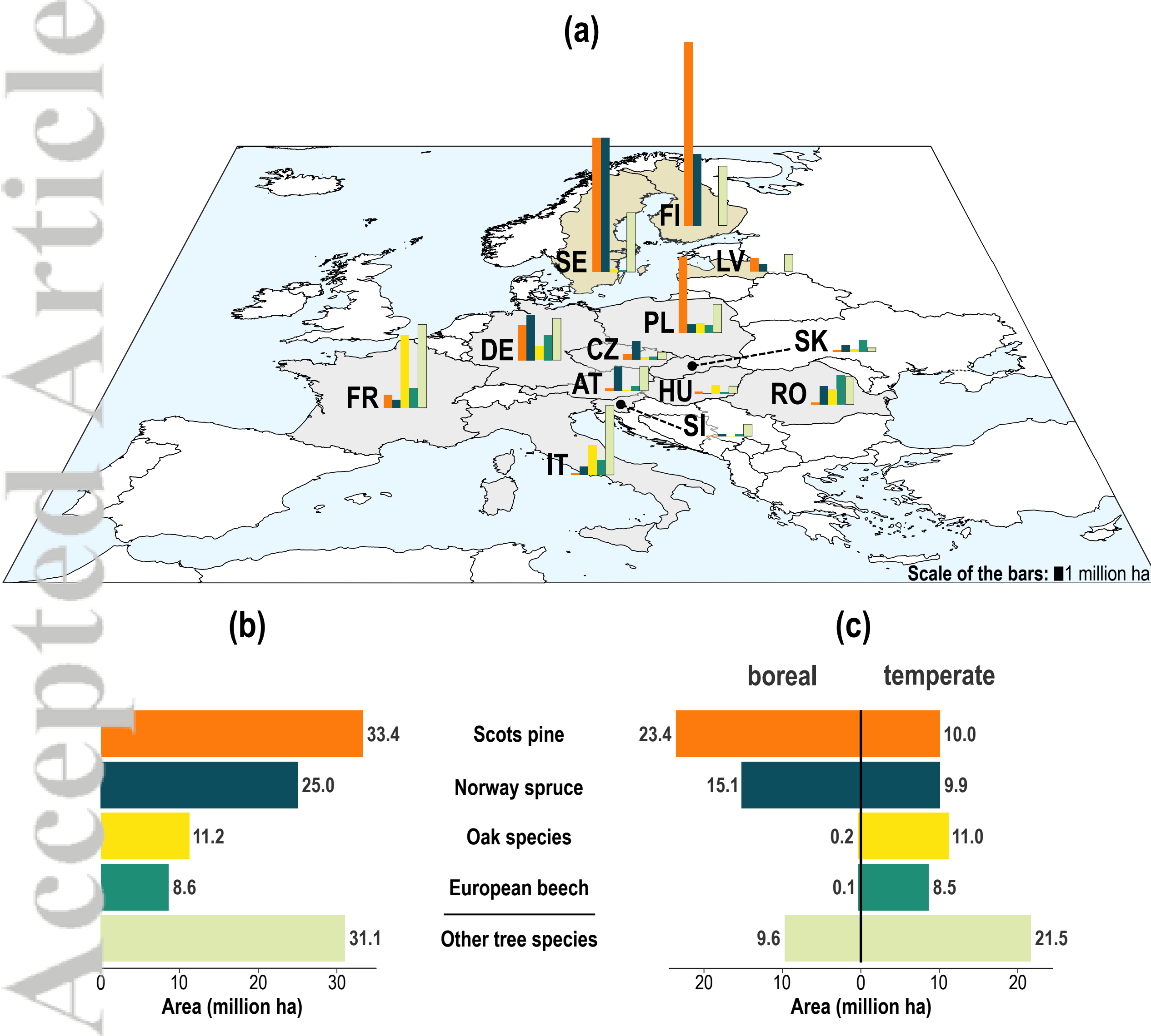
Figure 1. Area and proportion of the forest categories (as represented by dominant species) within the scope of this study in total (b), by country (a) and by biome (c).

Figure 2. Proportion of silvicultural systems used in the observed regions of Europe.

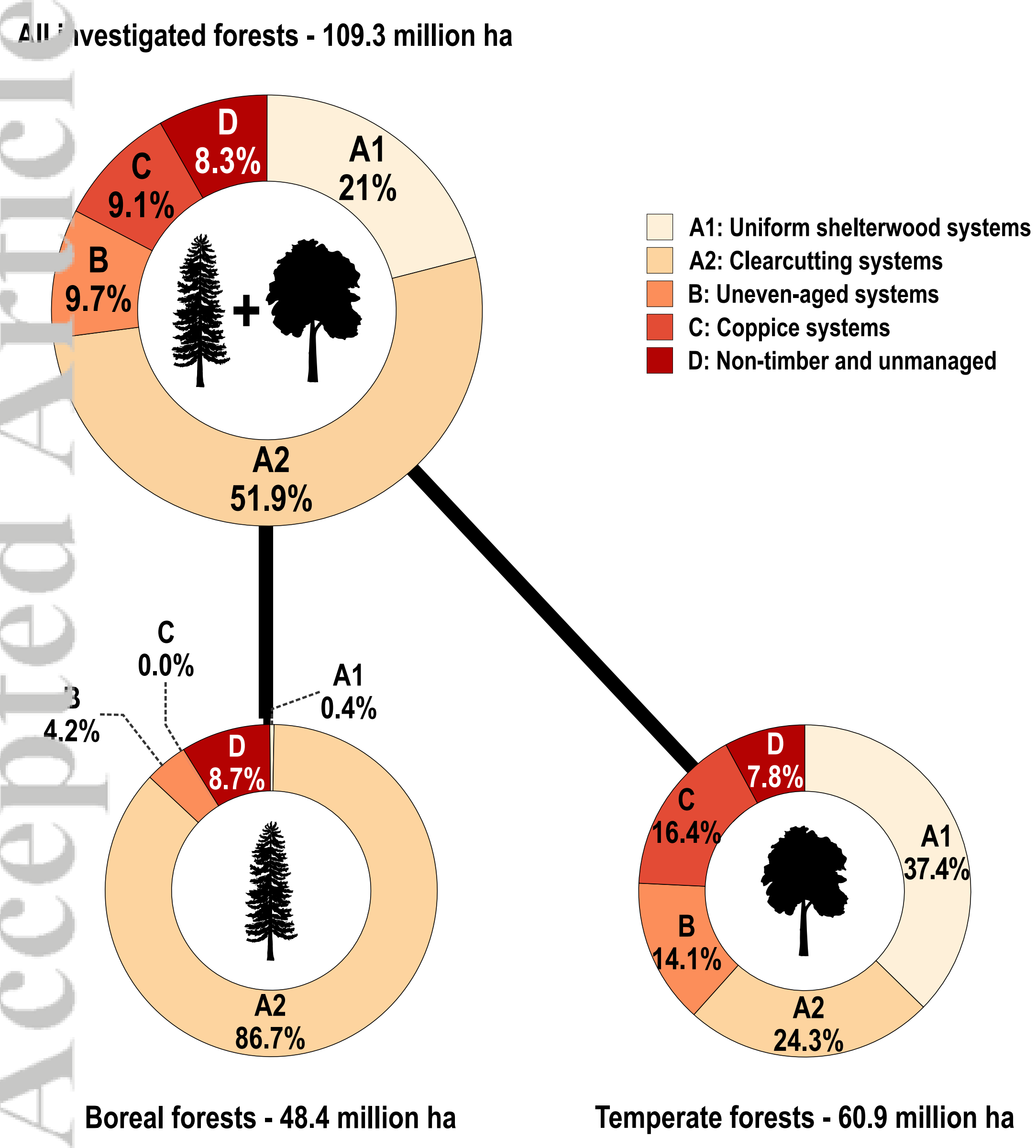
Figure 3. Three dimensional figure displaying size, frequency, and residual structure attributes of silvicultural systems and natural disturbances in European boreal and temperate forests. Axes were log+1 transformed.

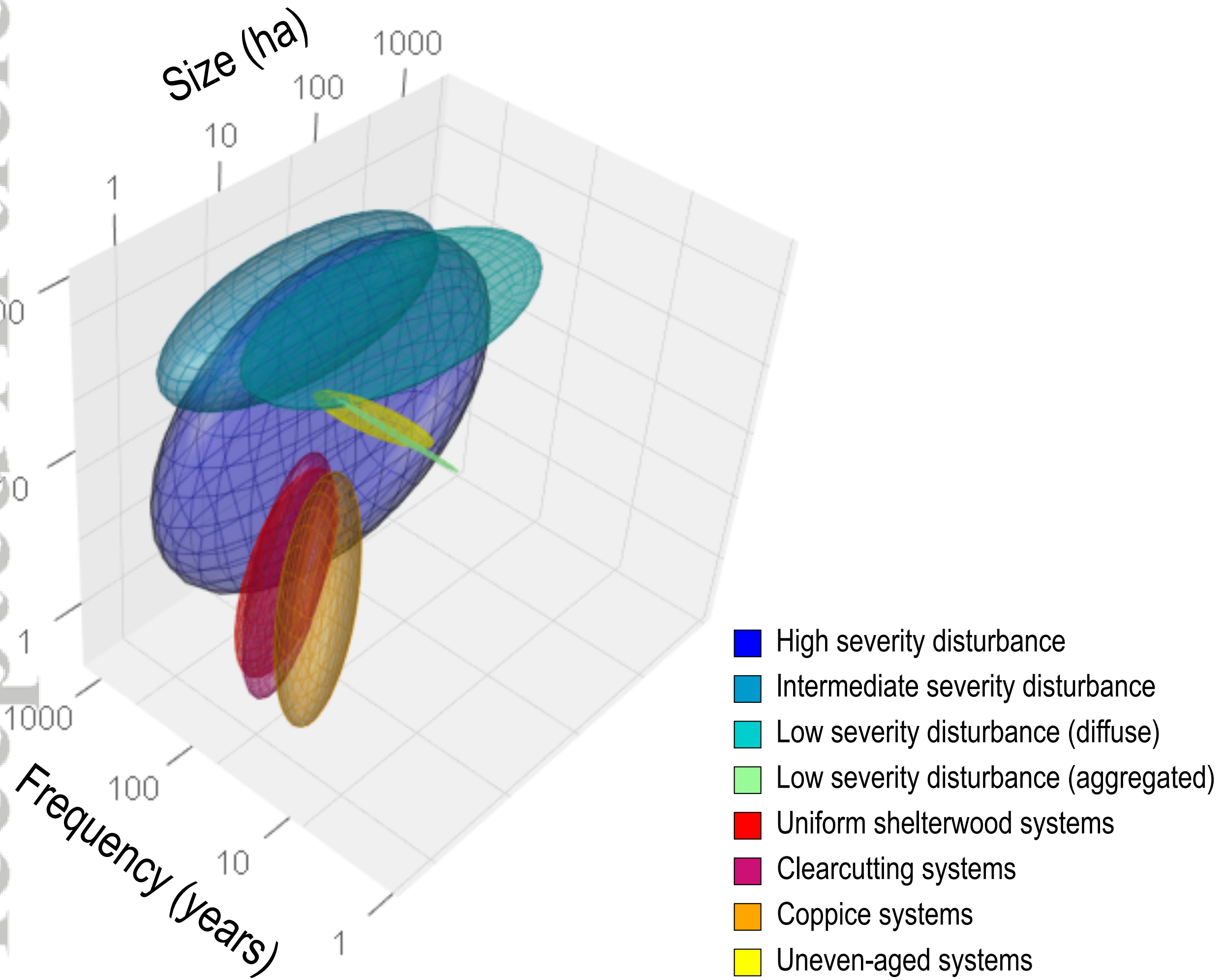
Figure 4. Size, frequency, and residual structure attributes for natural disturbances and silvicultural systems in Europe. Shown are: (a) size and frequency; (b) frequency and residual structure; and (c) size and residual structure comparisons. Dots indicate the centroids of natural disturbance types and silvicultural systems. The Comparability Line (CL) is based on the centroids of all the natural disturbance types assessed. Axes were log+1 transformed.

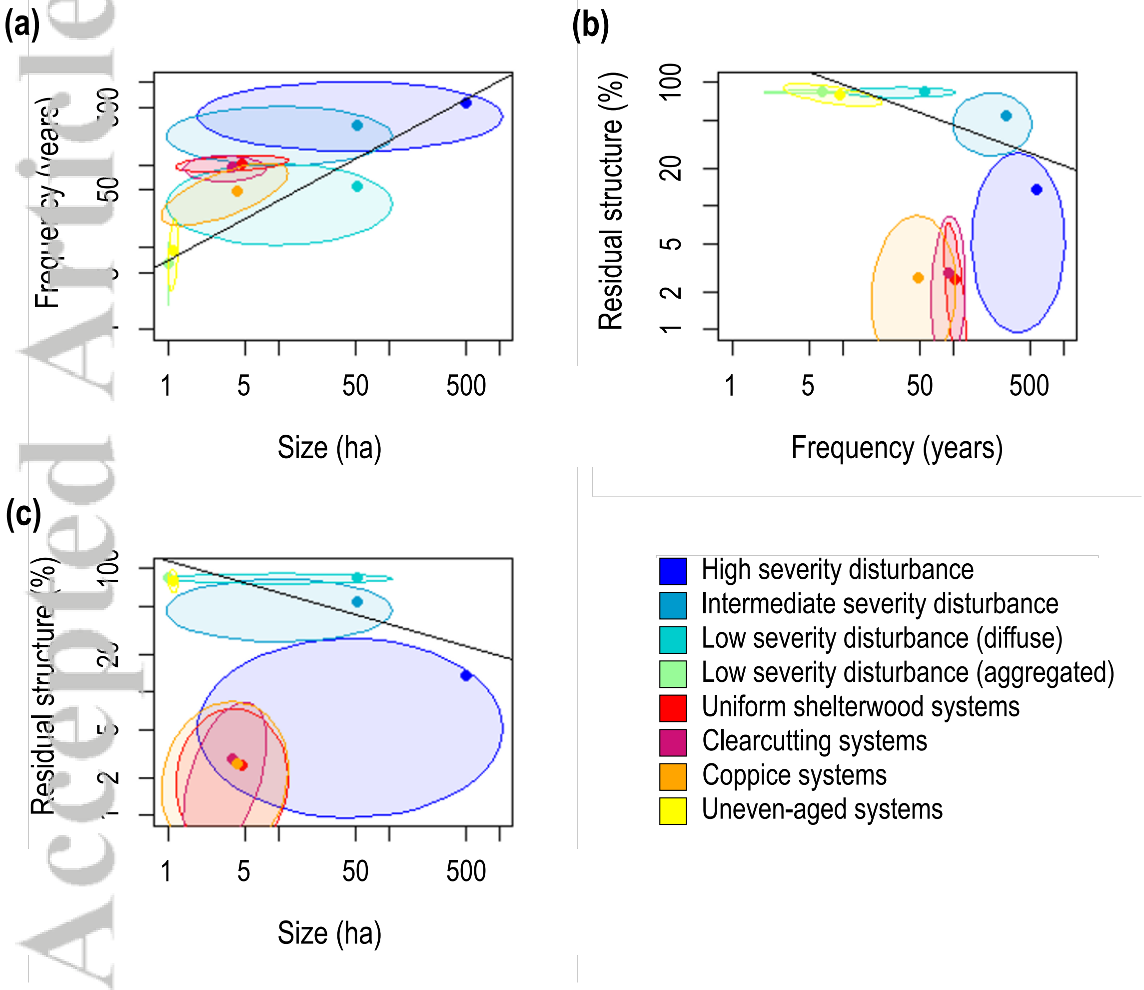
Figure 5. Boxplots of (a) size, (b) frequency and (c) residual structure of silvicultural systems in Europe. A1 = Shelterwood systems, A2 = Clearcut systems, B = Uneven-aged systems, C = Coppice systems. Dots indicate the national averages of the given attribute. Intervention size is the area of the final harvest in case of A1, A2 and C, and defined as the size of the canopy gaps created by the intervention in case of B. Harvest frequency is the rotation period in the case of A1, A2 and C and entry cycles for B. Residual structure is defined as the percentage of living woody biomass volume (m^3) post-harvest compared to the pre-harvest volume left on a 1 ha site.

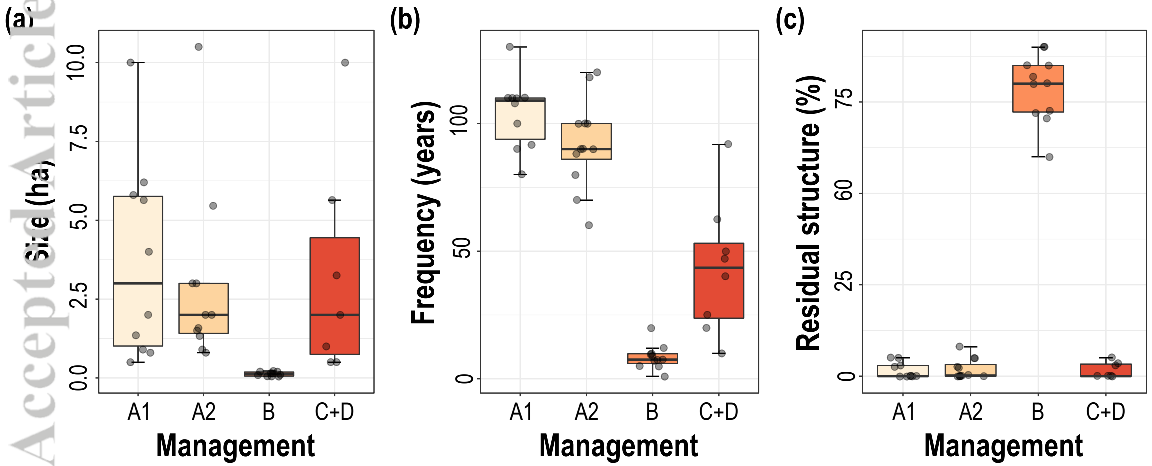


(a)
FI
SE
LV
PL
DE
CZ
SK
FR
AT
HU
RO
SI
IT
Scale of the bars: 1 million ha
(b)
33.4
25.0
11.2
8.6
31.1
0
10
20
30
Area (million ha)
Scots pine
Norway spruce
Oak species
European beech
Other tree species
(c)
boreal
temperate
23.4
10.0
15.1
9.9
0.2
11.0
0.1
8.5
9.6
21.5
20
10
0
10
20
Area (million ha)


All investigated forests - 109.3 million ha
A1
21%
A2
51.9%
B
9.7%
C
9.1%
D
8.3%
A1: Uniform shelterwood systems
A2: Clearcutting systems
B: Uneven-aged systems
C: Coppice systems
D: Non-timber and unmanaged
C
0.0%
B
4.2%
A1
0.4%
D
8.7%
A2
86.7%
Boreal forests - 48.4 million ha
D
7.8%
C
16.4%
A1
37.4%
B
14.1%
A2
24.3%
Temperate forests - 60.9 million ha


Size (ha)
1
10
100
1000
Residual structure (%)
1
10
100
Frequency (years)
1
10
100
1000
High severity disturbance
Intermediate severity disturbance
Low severity disturbance (diffuse)
Low severity disturbance (aggregated)
Uniform shelterwood systems
Clearcutting systems
Coppice systems
Uneven-aged systems


(a)
Frequency (years)
50
1
5
50
500
Size (ha)
(b)
Residual structure (%)
100
20
5
2
1
1
5
50
500
Frequency (years)
(c)
Residual structure (%)
1
5
50
500
Size (ha)
High severity disturbance
Intermediate severity disturbance
Low severity disturbance (diffuse)
Low severity disturbance (aggregated)
Uniform shelterwood systems
Clearcutting systems
Coppice systems
Uneven-aged systems


(a)
Size (ha)
0.0
2.5
5.0
7.5
10.0
A1
A2
B
C+D
Management
(b)
Frequency (years)
0
50
100
A1
A2
B
C+D
Management
(c)
Residual structure (%)
0
25
60
75
A1
A2
B
C+D
Management