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

Published version:

DOI:10.1002/eap.2596

(Article begins on next page)

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

list and order of authors:

Réka Aszalós,[1] Dominik Thom, Tuomas Aakala, Per Angelstam, Guntis Brumelis, László Gálhidy, Tomáš Hlásny, Bence Kovács, Thomas Knoke, Laurent Larieu, Renzo Motta, Jörg Müller, Péter Ódor, Dušan Rozenbergar, Yoan Paillet, Diana Silaghi, Tibor Standovár, Miroslav Svoboda, Jerzy Szwagrzyk, Philipp Toscani, William S. Keeton*

[1] Corresponding author

* Senior author

Authors in alphabetic order, and the data provided (only for inner use), FMD = forest management data, NDD = natural disturbance data:

Tuomas Aakala (Finland FMD, boreal spruce and Scots pine forests NDD), Per Angelstam (Sweden FMD), Réka Aszalós (oak forests NDD, data analysis, manuscript writing), Guntis Brumelis (Latvia FMD), László Gálhidy (Hungary FMD), Tomáš Hlásny (Slovakia FMD), William S. Keeton (study origin, USA FMD, manuscript writing), Thomas Knoke (Germany FMD), Bence Kovács (Figures), Laurent Larieu (France FMD), Renzo Motta (Italy FMD), Jörg Müller (Germany FMD), Péter Ódor (beech forests NDD), Dušan Rozenbergar (Slovenia FMD), Yoan Paillet (France FMD), Diana Silaghi (Romania FMD), Tibor Standovár, Miroslav Svoboda (Czech Republic FMD, mountain spruce forests NDD), Jerzy Szwagrzyk (Poland FMD), Dominik Thom (data analysis, manuscript writing), Philipp Toscani (Austria FMD)

ABSTRACT

In Europe, there has long been interest in natural dynamics silviculture, although the vast majority of forests remain tightly regulated under a variety of production-driven silvicultural systems. A major barrier has been incomplete understanding of the ranges of variability in disturbance regimes, including frequencies, spatial attributes, and severities. Addressing this constraint in European forest management, we adapted a “comparability index” that was first developed in the US to compare natural disturbances and forest management effects based on disturbance size and frequency. We extended the original concept by adding residual structure of canopy trees after disturbance (i.e. retention in case of forest management and the inverse of disturbance severity) as a third dimension. We populated the model by compiling published data on disturbance dynamics from 13 countries, covering four major forest types (i.e. spruce, beech, oak, and pine-dominated). Expert-derived data on harvesting effects by country and forest type for a variety of silvicultural systems were obtained through a questionnaire, with standardized estimation protocol, distributed to collaborators. The data for both natural and harvest disturbances were visualized in two- and three-dimensional plots indicating ranges for frequency, size, and severity. "Comparability Lines (CL)" were fit as the central tendency among all two-dimensional combinations of disturbance attributes while controlling for the third dimension. Congruence of common silvicultural systems with the CL was then calculated as a Comparability Index (CI). Specifically, we computed the CI as the relative distance between the centroids of each silvicultural system to the respective CL. Natural disturbances are highly variable in size, frequency, and severity, but European forest management does not reflect this complexity. The CI indicates the highest congruence between uneven-aged silvicultural systems and key natural disturbance attributes. Other silvicultural systems perform poorly in terms of retention as compared to tree survivorship after natural disturbances. Applying the CI to a variety of forest management contexts will help European silviculturists determine how to adjust harvesting regimes to better approximate the complexity of natural disturbance dynamics. This, in turn, may aid efforts to provide a broader array of ecosystem services and habitat conditions in managed forests.

1. INTRODUCTION

Forest scientists in many regions are exploring innovative ways of managing forests both for a greater variety of services and biodiversity than in the past and for enhanced resilience and adaptive capacity to global change (Gustafsson et al. 2012, 2019; Mori and Kitagawa 2014, Fahey et al. 2018). 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 (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. D'Amato et al. 2017, Keeton et al. 2018). In Europe, there has long been interest in ecological or multi-functional forest management approaches (Diaci et al. 2006, Wolfslehner and Seidl. 2010, Kraus and Krum 2013, Brang et al. 2014, Pretzsch et al. 2017). However, growth, composition, structure, and age class distributions of the vast majority of European forests remain tightly regulated under a variety of production driven, even-aged and continuous cover systems (Schelhaas et al. 2018). As Gustafsson et al. (2019) suggest, the former may be more common in boreal regions and the latter more dominant in temperate regions of Europe.

However, 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 disturbance regimes, including frequencies, spatial attributes, and severities (Kulakowski et al. 2017). Moreover, the distribution, composition, and dynamics of European forests have been fundamentally altered by centuries, even millennia, of human influence (Keeton et al 2013, Pretzsch et al. 2017). Consequently, finding reference forests in which to observe baseline disturbance dynamics is highly challenging, since only small fragments of primary or old forests remain in most places (Szwagrzyk and Gazda 2007, Mikoláš et al. 2019). The proportion of remnant old-growth (primary) forests is very low in Europe (0.7% of the forest cover); montane beech forests are 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 (e.g. Seidl et al. 2011, Kuuluvainen and Aakala 2011, Thom et al. 2013, Kulakowski et al. 2017, Thom and Seidl 2016; 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 types, including those dominated by European beech (*Fagus sylvatica*), spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and oak (*Quercus spp*.) respectively.

1.1 Comparing natural disturbance dynamics to forest management

Wider adoption of natural dynamics silviculture in Europe has, in the past, been limited by incomplete understanding of how forests managed using conventional systems differ – in terms of developmental pathways, diversity of seral structural conditions, and functional outcomes –

from the processes and dynamics occurring in primary and less human-influenced forests. A consistent comparative framework is needed. 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 (Schelhass et al. 2018).

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 severity, and stand replacing wind 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 scale and frequency.

In this study we expand the CI framework by adding a critical third dimension or axis (see, for example, Turner et al. 1998), namely residual structure, survival of canopy trees (i.e., the inverse of disturbance severity). This results in a 3-dimensional framework showing ranges of variability both for disturbance dynamics and forest management, 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 rigorous basis for assessing the congruence between forest management and natural disturbances in both temperate and boreal European forest ecosystems. With all three parameters represented, the framework will capture more completely the variation in both natural disturbance effects and silvicultural regimes. Furthermore, we hypothesize that contemporary European forest management is likely to exhibit very low congruence with past and present natural disturbance regimes. We predict that the divergence between natural disturbances and forest management will increase by adding a new axis (residual structure) to our comparative framework.

1.2 Understanding variability in disturbance regimes

How should management approaches be modified to more closely emulate natural disturbances? And furthermore, how does management differ from the ranges of variability in disturbance processes for different forest types? To answer these questions we synthesize 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 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, Aakala 2018, Schutz et al. 2018), (ii) dendrochronological studies (Splechtna 2005, Svoboda et al. 2012, Nagel et al. 2014, Čada et al. 2016), and (iii) historical and remote sensing studies (Nagel et al. 2017). There are many studies in the first group, 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 scaled dynamics. Dendrochronological studies have longer (e.g. multiple centuries) time-frames, but explore primarily stand level processes; while the third group 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 types.

There are multiple sources of spatial variability in European disturbance processes (Senf and Seidl 2018, 2020); these differ among forest types and between boreal and temperate forested biomes (Thom and Seidl 2016). For instance, fire plays a greater role in boreal forests as compared to European temperate systems but is typically infrequent and stand replacing in Norway spruce (Aakala et al. 2009, 2018), whereas fire more frequent and of low to mixed severity in Scots pine (Niklasson and Granström 2000, Aakala 2018). This contrast differs from wind disturbances, which are a dominant structuring process across all European forests, though varying greatly in intensity (e.g. gap forming, diffuse low severity, mixed severity, or stand replacing) and temporal dynamics, 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). And finally, recent research on the role of intermediate severity disturbances suggests a much broader range of variability in potential age class structures than previously recognized for European forests (Svoboda et al. 2014, Trotsiuk et al. 2014). Thus, rather than conceptualizing forest management as a choice between even or uneven-aged approaches, silviculturists are challenged to manage for a range of multi-aged or multi-cohort forest structures as well. These are more analogous to the stand structures created by periodic partial mortality events and associated pulses of tree recruitment (Meigs et al. 2017). The comparative framework we propose synthesizes the current knowledge of these ranges of variability, presenting a basis for consistent comparisons against forest management.

2. METHODS

2.1 A Scope of the Study

The 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. Within the scope of our study were four main forest types, dominated by four focal species respectively; Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), European beech (*Fagus sylvatica*) and European oak species (*Quercus robur*, *Q. petrea*, *Q. pubescens*, *Q. cerris*). These forest types are the most common ones in the boreal and temperate zones of Europe, and represent different points on the disturbance continuum. Our study compared human and natural disturbances both in aggregate for all forests continent-wide, and individually within each forest type, quantitatively for the former and qualitatively for the latter.

2.2 Compiling the dataset

2.2.1 National forest management data for 13 target countries

To assess European forest management practices, we selected 13 target countries, representing West-, Central-, and North-Europe (Fig 1), and asked forest experts of each country to complete a standardized questionnaire (Supplement Table 1). The questionnaire (Q) was designed to assess four groups of questions: 1) silvicultural systems used by 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 objective ("unmanaged" henceforward); 3) the area and ratio of forest types dominated by the four focal species and their typical management methods; and 4) harvest size, rotation period, and residual structure (live tree retention) for these silvicultural systems.

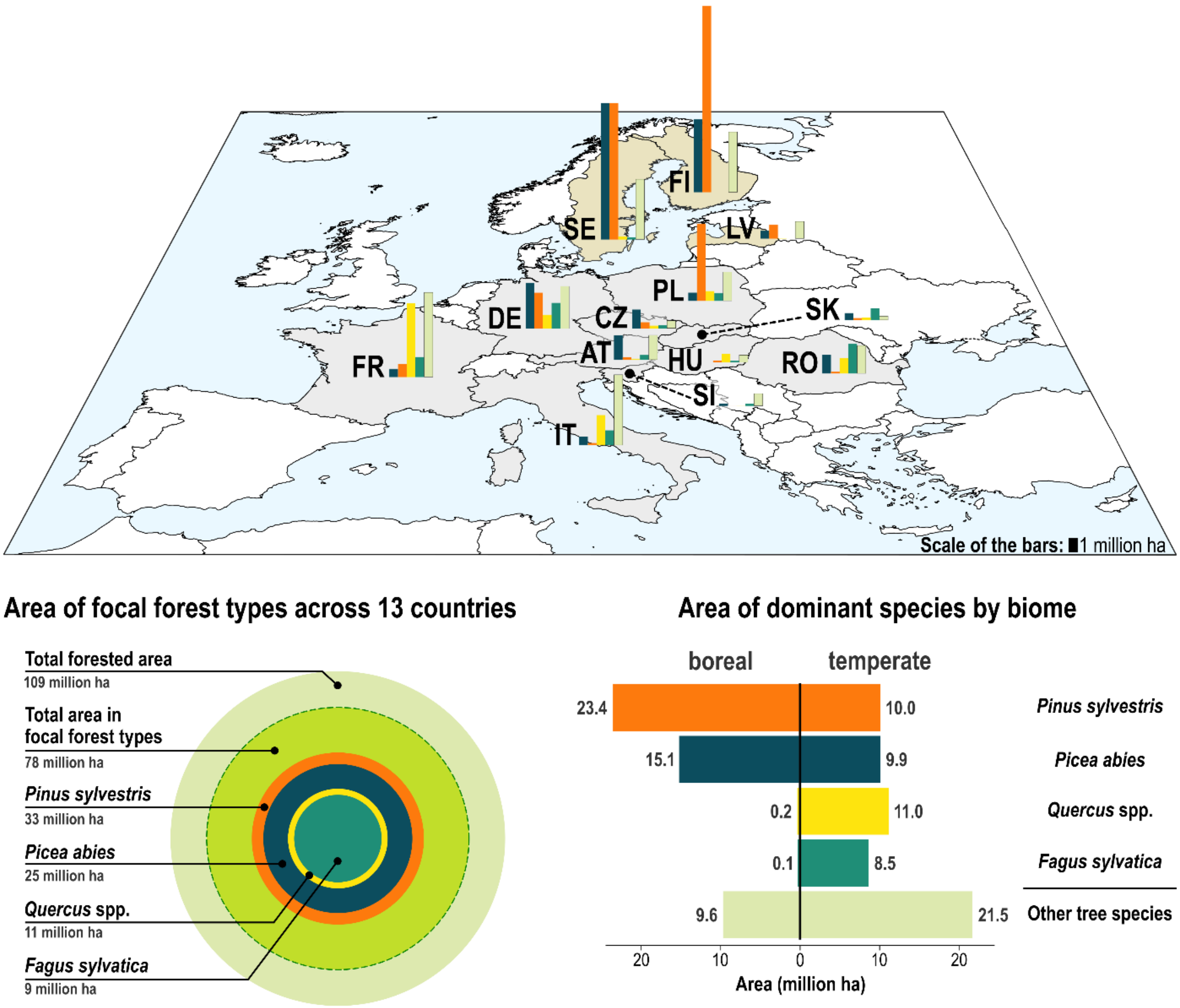


Fig. 1. Area and proportion of the four forest types within the scope of this study by country and region.

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 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 (EU MCPFE categories 1.1, 1.2, 1.3, see Frank & Parviainen 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). Mediterranean forests, like evergreen oak

(*Quercus ilex*) and Mediterranean pine (*Pinus* spp.) forests, were excluded in the cases of Italy and France, as the present study focuses on the temperate and boreal forests of Europe.

To produce a standardized database, we also excluded the short-rotation clearcutting systems (≤ 40 years). Short-rotation systems, usually intensively managed plantations, are considered as forest in some countries (France, Slovakia, Hungary, Latvia), but not so in others (Austria, Italy), where they are instead classified as agroforestry. For consistency, we harmonized the silvicultural terminology across country-specific data. The area and ratio of the forest types dominated by the four focal species and their typical management methods were also assessed by the questionnaire. Forests not covered by these four types 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-, clearcut-, and coppice systems (Cat. A1, A2, C1, C2). Intervention size in the case of uneven-aged systems (Cat. B) was defined as the size of the canopy gaps created by the intervention of the single-tree-, group- or multicohort selection. 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), or with entry cycles for uneven-aged systems (Cat. B). Residual structure (retention) was defined as the percentage of living woody biomass volume (m^3) compared to the pre-harvest volume left on a 1 ha site after the final cutting operation (clearcutting system, shelterwood system) or after the regular entry (uneven-aged forestry). Intermediate treatments, such as thinnings were not considered in the determination of harvest frequency and residual structure.

Multiple primary data sources were used by the national experts we surveyed in response to 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. Sources varied by country depending on data availability (see Supplement Table 2).

Table 1. Classification and the definition of the silvicultural systems

	Silvicultural system	**Definition**
A	Even-aged forest management	Even-aged management

A1	• even-aged forest management with uniform shelterwood system	Regeneration is usually natural. Intermediate thinnings and subsequent cuttings. New seedlings are established before the mature trees are fully removed. Removal cut after a certain target diameter or age has been reached.
A2	• uniform clearcutting system (rotation time is > 40 years)	Regeneration is usually artificial (planted) or sometimes natural. Thinnings. Clearcut after a certain target diameter or age has been reached.
B	Uneven-aged forest management (continuous cover forestry)	Selection cutting based usually on target diameter distribution
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
B3	• multi-cohort (irregular shelterwood) system	Multi-aged forestry, permanent retention with ≥10% basal area
C1	Coppice	Woodlands regenerated asexually from stump sprouts on harvested crop trees
C2	Coppice with standards	Two distinct elements: a lower storey treated as coppice; and an upper storey of standards treated as high forest
D	Unmanaged	No forest management, or management primarily for non-timber objectives, such as conservation-oriented management, management for biodiversity, non-productive forests, forests with extremely high rotation time, abandoned forests, set-asides, long-time not managed

2.2.2 Natural disturbance attributes of European forests

Our analysis was based on parameters describing the frequency, severity, and spatial extent of natural disturbances in Europe. For this part of the assessment, we compiled a literature review by collecting and extracting data from, (i) long-term studies of primary and old-growth forests (see Sabatini et al. 2018 for definitions), (ii) dendrochronological studies, and (iii) and other studies defining the ranges of variability in disturbance dynamics for the four forest types (Supplement Note 1). Then, the categories of the natural disturbance types of European boreal and temperate zones were defined by adapting the classification of Kuuluvainen and Aakala (2011). We grouped natural disturbance regimes into four categories; 1) high-severity, stand-replacing disturbances, like major windstorms or fire events, 2) intermediate severity disturbances driven by partial disturbances, like microbursts, ice storms, and bark beetle outbreaks, 3) low severity diffuse disturbances, like low severity fires, windstorms, ice storms, bark beetle outbreaks, 4) low severity, aggregated disturbances, such as “gap dynamics” driven by tree mortality at fine scales (< 200 m2). Finally, ranges for size, frequency, and severity parameters were attributed to these categories by expert consensus, on the basis of the literature review.

2.3 Data Analysis

The core of our analysis is to compare European natural forest disturbance regimes with common silvicultural systems in the target countries. To this end, we calculated (Figure 1) ratios and areas by forest biome (temperate and boreal) and forest type for the silvicultural systems presented in Table 1 from the raw database of national data (Supplement Table 3).

Next, we designed a 3D figure for visualization purposes, populated with the data obtained from our forest management survey and natural disturbance literature review. The 3D figure compares disturbance size, frequency, and residual structure simultaneously, with each parameter displayed along an independent axis. 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 using the rgl (Murdoch 2020) and car package (Fox et al. 2019), respectively.

We obtained the CI line 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 CI line. 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 and dominant tree species of European forests

Our results showed 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 (proportion of all studied forests: 72.9%) across all the target countries. More than half of the investigated forests are managed by uniform clearcutting systems (51.9%, Cat. A2), and approximately one-fifth by shelterwood systems (21%, Cat. A1). Uneven-aged systems, by comparison, are employed to a far lesser degree. In our dataset 9.7% 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 (Fig. 2, Supplement Table 4).

However, there is a marked difference between boreal and temperate countries (Supplement Fig. 1). Clearcutting systems (Cat. A2) are utilized across 85.9% of forests in the boreal zone, which are predominantly coniferous. For the three boreal countries included in our dataset, all other management methods represent minor components. Uneven-aged management is applied on only 4.2% of forests, whereas 8.7% are unmanaged. By comparison, in the temperate zone shelterwood (Cat. A1), uneven-aged (Cat. B), and coppice systems (Cat. C) have higher ratios, employed at 37.4%, 14.1%, and 16.4% of all forests, respectively (Fig 2, Supplement Table 4). 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. This compares to Czech Republic, Germany, Poland, Austria, and Hungary, where clearcutting and/or uniform shelterwood systems are more widely represented. The majority of Slovenian forests are managed by irregular shelterwood systems (Supplement Fig. 1).

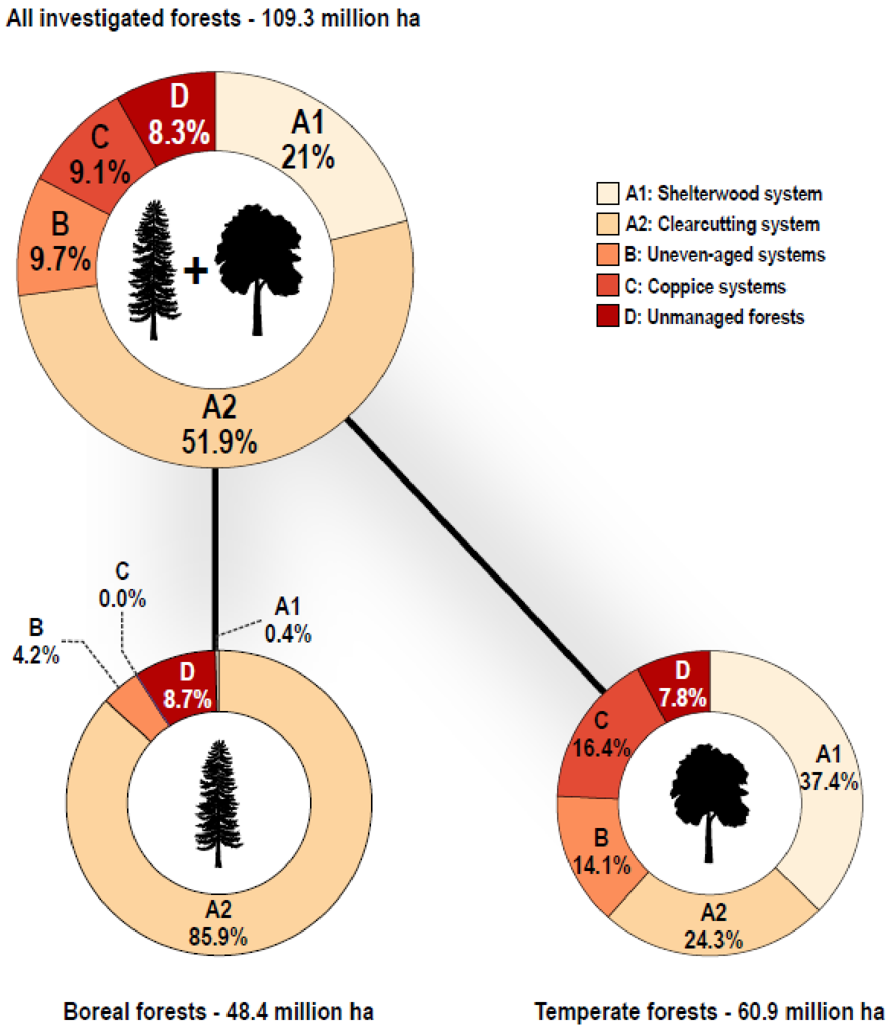


Fig. 2 Silvicultural systems used by target European countries.

3.2 Frequencies, spatial attributes, and severities of natural disturbances in European forests

The literature review (Supplement X) revealed that disturbance sizes, frequencies and severities in European temperate and boreal forests are highly variable across space and time (Table 2). Small, aggregated canopy openings, where gap size usually does not exceed 200 m^2 (Mountford et al. 2001, Kuuluvainen and Aakala 2011) most commonly are of low severity, with less than 20% of the canopy removed (Nagel et al. 2014, Hobi et al. 2013). Individual low severity, diffuse disturbance events affect larger spatial extents, as is the case, for example, with the low severity fires typical in boreal forests and low severity ice storms in temperate Europe. The total area of scattered canopy openings, tree mortality, and tree damage for an event may range from 200 m^2 to 100 ha. Return intervals for low severity, diffuse disturbances are relatively short, ranging between 10-100 years. Intermediate severity wind and ice storms, having return intervals of approximately 100-500 years (Nagel et al. 2014, 2017), 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 10 ha (Kuuluvainen and Aakala 2011, Kameniar et al. 2021). Stand-replacing, 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 up to thousands of hectares (Kuuluvainen and Aakala 2011).

Table 2. Size, frequency, and severity data by natural disturbance category

Disturbance type	**Size (m^2)**	**Frequency (years)**	**Severity (%)**	**Residual structure (%)**	**References**
High severity	10 000 – 10^7	150-1000	75-100	0-25	Kuuluvainen and Aakala 2011, Aakala 2018, Nagel et al. 2014
Intermediate severity	200-1 000 000	100-500	25 -75	25 -75	Nagel et al. 2014, 2017 Kuuluvainen and Aakala 2011, Čada et al. 2020
Low severity, diffuse effects	200-1 000 000	10-100	10-25	75-90	Thom et al. 2013.
Low severity, aggregated effects	20-200	1-10	15-20	80-85	Khakimulina et al. 2016, Mountford et al. 2001 Kuuluvainen and Aakala 2011, Hobi et al. 2013

3.3 Congruence of silvicultural systems with natural disturbances

We identified a low congruence of silvicultural systems with natural disturbance regimes, referring to the attributes size, frequency, and residual structure (Table 3, Table 4, Fig. 3, Fig. 4). With an average CI of 0.07 (7% congruence), clearcutting and 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 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 shelterwood systems had large overlapping zones (Fig 3, Fig 4 A, B, C). The mean harvest sizes of these systems (2.84, 3.72 ha respectively, Table 3) were intermediate between the mean size of low severity aggregated and diffuse natural disturbances, however their return intervals were higher (100 years). The even-aged management systems overlapped with coppice systems in the size to residual structure comparison. Ellipsoids of uneven-aged systems are 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).

The 2D plots add more detail to the relationship between natural disturbance and silvicultural systems (Fig. 4). The size-frequency plot shows an overlap of the ellipsoids of uneven-aged systems and low severity aggregated disturbance, indicating that uneven-aged systems are partly within the range 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 % congruency), respectively (Table 4). CI values of other silvicultural systems ranged from 0.1 to 0.4 (i.e., 10% to 40% congruence with natural disturbance). Lowest CI values (i.e., the largest divergence) were detected for size relative to residual structure and frequency relative to residual structure (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 and 0.8 uneven-aged systems were considerably more similar to natural disturbance in the same pairwise comparisons.

Table 3. Average size, frequency, and residual structure for silvicultural systems in the 13 countries we investigated and natural disturbance regimes of European forests.

Silvicultural system	**Size (ha)**	**Frequency (years)**	**Residual structure (%)**
A1 Shelterwood system	3.72	103.98	1.56
A2 Clearcutting system	2.84	91.42	1.89
B Uneven-aged system	0.12	8.36	78.70
C Coppice system	3.27	48.04	1.66
Natural disturbance			
High severity	500.50	575.00	12.50
Intermediate severity	50.01	300.00	52.50
Low severity, diffuse effects	50.01	55.00	82.50
Low severity, aggregated effects	0.01	5.50	82.50

Table 4. Comparability Index (CI) values, representing the congruence between silvicultural systems and natural disturbance regimes. 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 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

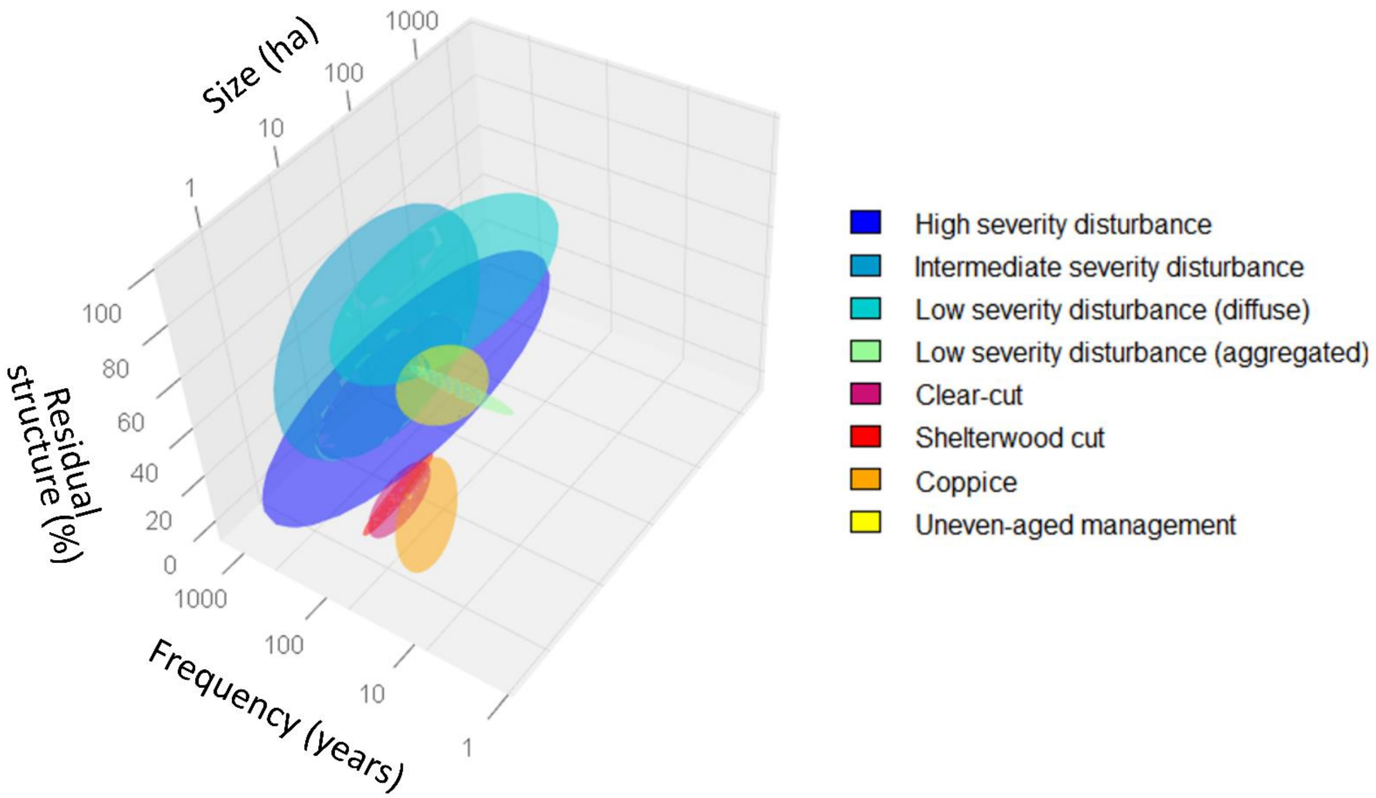


Fig 3. Three dimensional figure displaying size, frequency, and residual structure attributes of silvicultural systems and natural disturbance regimes in European boreal and temperate forests. Axes were log+1 transformed.

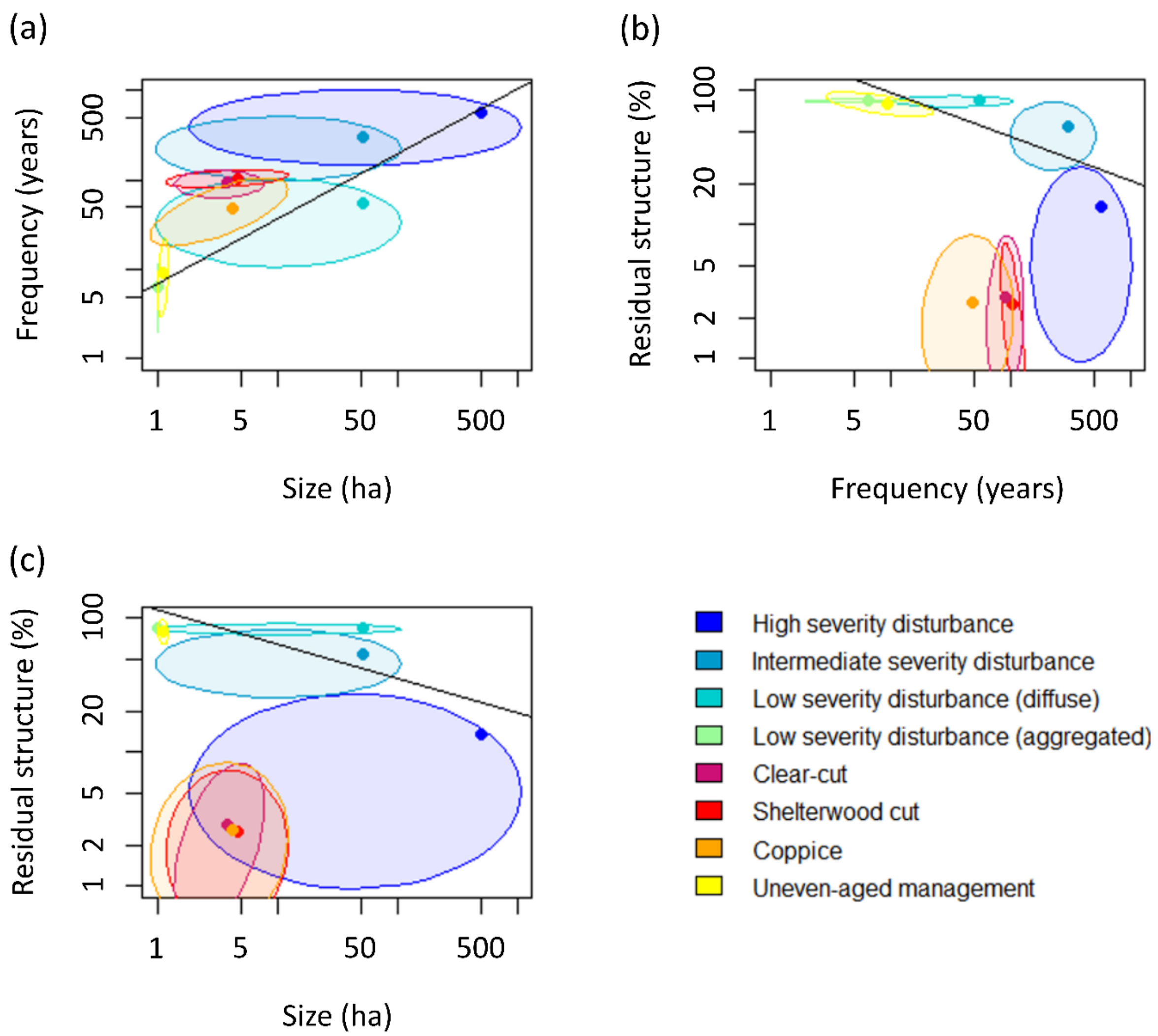


Fig 4. Size, frequency, and residual structure attributes for natural disturbance regimes and silvicultural systems in Europe. Shown are: (a) size and frequency; (b) frequency and residual structure; and (c) size and residual structure comparisons. Dots indicate the centroids of natural disturbance types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

3.4 Silvicultural systems applied to four of the most common European forest types

The total forest cover of the 13 target countries – without the Mediterranean forests and short-rotation systems – is approximately 109 M hectares (109 298 966 hectare) based on assessment. According to the national forest management data we examined (Supplement Table 3), 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%.

In Norway spruce and Scots pine forests, the primary management system is even-aged with clearcutting system, applied to 68.9% and 78.1% of the area respectively (Table 5). Less than one fifth of these two forest types is managed by shelterwood systems across all of the 13 target countries. However, in temperate Norway spruce stands, shelterwood cutting has the highest representation among silvicultural systems (45.1%), and uneven-aged methods, such as single-tree and group selection, are also common (24.7%) (Table 5). The majority of European beech and oak dominated forests are managed with 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 types. Beech dominated forests have a fairly high ratio of uneven-aged management on European scale and in the temperate 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 5, Supplement Fig. 2).

Table 5. Forested area or proportion by forest type (as represented by dominant species) and silvicultural system.

	Picea abies	***Pinus sylvestris***	***Fagus sylvatica***	***Quercus sp.***	**Combined totals**
			Hectares		
Area	**24 980 665**	**33 475 301**	**8 615 899**	**9 943 379**	**77 015 244**
Boreal	15 069 633	23 520 936	151 800	9 189	38 751 558
Temperate	9 911 032	9 954 365	8 464 099	9 934 190	38 263 686
			Percent		
A1 shelterwood	**19.1**	**17.1**	**67.7**	**48.9**	**27.5**
Boreal	2.1	12.3	0.0	100.0	8.3
Temperate	45.1	28.5	68.9	48.9	47.0
A2 clearcut	**68.9**	**78.1**	**5.3**	**15.1**	**58.9**
boreal	94.4	83.8	96.0	0.0	88.0
temperate	30.2	64.6	3.7	15.1	29.4
B uneven-aged	**11.9**	**4.3**	**19.9**	**3.5**	**8.4**
boreal	3.5	3.9	4.0	0.0	3.7
temperate	24.7	5.3	20.2	3.5	13.2
C coppice	**0.0**	**0.5**	**7.0**	**32.4**	**5.2**
boreal	0.0	0.0	0.0	0.0	0.0
temperate	0.0	1.6	7.2	32.5	10.4

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 natural disturbance regimes, showing low congruences with past and present natural disturbances. While previous studies have described natural disturbance regimes according to their size, frequency, and severity ranges (Turner et al. 1998, Bergeron et al 2010), ours is among the first to populate this framework with real data for both forest management and disturbances. The expanded framework employed in our study defines the critical third axis, severity, as percent residual canopy structure left on a site following management or disturbance. Adding this third axis to the forest disturbance conceptual model significantly improved the basis for comparison and proved critical in understanding incongruences. Silvicultural systems in Europe, excepting selection systems, typically retain very low densities of biological legacies, such as residual live, dead, and downed trees, either dispersed or aggregated. 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 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 regression line (CL) through the European forest disturbance regimes as reference line. Using the expanded index, forest managers can determine the divergence of a given harvesting regime from natural disturbance dynamics.

4.2 Uneven-aged silvicultural systems are most similar to natural disturbances

The vast majority of the 109 million ha of temperate and boreal forests included within the scope of 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. 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 shelterwood systems had the lowest CI in almost all comparisons, coppice systems was intermediate, and uneven-aged system had the highest CI values in all paired comparisons. Using only axes for size and frequency, and disregarding structural complexity, the similarity of silvicultural systems with natural disturbances was markedly higher. However, both size and frequency attributes for clearcut, 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 showed that Europe's natural disturbance regimes have great complexity and variability across the multiple dimensions of spatial extent, frequency, and severity. In contrast, forest management perpetuates a landscape-scale condition incorporating little of this diversity (Angelstam et al. 1998?). This mismatch has been noted in other regions of the world subject to intensive forest management practices as well (Bergeron et al 2010, Messier et al. 2013).

4.3 Congruence of natural disturbance and human management for Europe's four most dominant forest types

The relative merits of intensive forest management, such as high yield, even-aged forestry practices, has been the subject of debate in Europe as in any parts of the world (Bollan 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 (Mikolas 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). We found that even-aged management with clearcut regeneration harvesting is the most prevalent system in the boreal zone of Europe, and yet has results in very low (7%) 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, 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 a variability distributed spatial pattern (Niklasson and Granström 2000, Wallenius et al. 2010, Aakala 2018, Rhyzkova et al. 2020). Natural disturbance effects contrast starkly with the dominant forest management regimes of boreal pine and spruce dominated forest types; these create mosaics of 2-10 hectare stands that are predominately even-aged, harvested on 80-90 year rotations, and have extremely low volumes and densities of post-harvest residual structure (i.e. biological legacies).

The temperate zone of Europe has a more diverse portfolio of harvest regimes, and consequently the congruence with natural disturbances greatly varies between countries and forest types. Forests dominated by Scots pine (more than half are in Poland), like the boreal zone, 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, Svoboda et al. 2014, Trotsiuk et al. 2014, Čada et al. 2016, Janda et al. 2017). This variability is not emulated by contemporary forest management (Citations). And yet, almost 25% of temperate Norway spruce stands are managed by uneven-aged systems, having 53% similarity to natural processes, which suggests that the management of this forest type has the largest congruence with natural disturbances. On the other hand, Norway spruce has been planted widely outside its natural distribution in temperate Europe (Caudullo et al. 2016). These stands are highly susceptible to climate change and bark beetle outbreaks; 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). Beech dominated forests are usually managed with even-aged shelterwood systems, but on 20% uneven-aged silviculture is applied, emulating more closely the pattern created by the low severity aggregated disturbances (gap dynamics) associated with beech forests (Schuck et al. 1994, Emborg et al. 2000, Standovár and Kenderes 2003, Kral et al. 2014). However, intermediate and mixed severity disturbances are also common in beech-dominated forests (Splechtna et al. 2005, Nagel et al. 2014, 2017), and these are not well emulated by the present harvest system of Europe based on our results. Natural dynamics for 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). Lacking robust natural reference stands, researchers have only a limited understanding 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 of poor site productivity or strong human/natural disturbances that enhance natural regeneration ("oakspace" see Bobiec et al. 2018). In the contrast to their natural regeneration strategy, much of the contemporary oak management employs closed coppice and high forest 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 reference to help guide "natural dynamics silviculture," including retention forestry approaches (see, for example, Mori and Kitagawa 2014; Puettmann et al. 2015, Gustafsson et al. 2019). Natural dynamics silviculture has the objective of emulating natural disturbance dynamics to better provide the environmental conditions to which organisms are evolutionarily adapted (Aplet and Keeton 1999, Franklin et al. 2007, Keeton 2007). In some cases, provisioning of ecosystem services, such as carbon storage and hydrologic regulation, may be a co-benefit (Ford and Keeton 2018). 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 compared to the trait and functional diversity representation offered by more intensive management practices, such as short rotation, even-aged forestry, which tend to simplify and homogenize forest stands and landscapes (Fahey et al. 2018).

Interest in ecologically-oriented forest management has increased dramatically in recent decades both in North America and in Europe (Angelstam 1998, Kuuluvainen 2002, Lindenmayer et al.

2006, Franklin et al. 2007, Krumm et al. 2020). 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 2006, 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 primarily for either conversion cutting in spruce plantations – promoting replacement by endemic mixed species or deciduous forest types – or as uneven-aged management (e.g. the "Plenterwald" and "Dauerwald" systems) in European beech (*Fagus sylvatica*) and other temperate deciduous or mixed species forest types. Close-to-nature silviculture, as commonly practiced, only partially replicates natural disturbance effects (Diaci 2006, Schutz et al. 2016), because 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. It does provide a mosaic of structurally variable patches as well as tree age class diversity at the aggregate or stand scale. Moreover, in parts of Central Europe deliberate efforts have been made to incorporate natural processes observed in old-growth stands (Kraus and Krum 2013, Schutz et al. 2016), such as retention of downed woody debris and other structures (Johann 2006). For example, research of the old-growth forest reserves has constantly helped 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). The potential to incorporate a broader range of dynamics and structures, including old, dead, and downed trees, based on research on natural disturbance effects is true both for European even-aged and continuous cover forest management (Kern et al. 2016).

Simplification and homogenization of European forests, for example through the widespread planting of mono-specific *Picea abies* plantations across formerly diverse landscapes and on non-endemic sites, is a well-documented phenomenon (Angelstam 1998, Björse and Bradshaw 1998, 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 as well as forest dieback associated with fungal pathogens, such as root rots (e.g. *Armillaria sp.*; *Heterobasidion annosum*). Also as a result of homogenization, European forests may be more vulnerable to increased disturbance intensity and frequency associated with climate change (Seidl et al. 2014), leading to interest in management to restore greater heterogeneity in forest composition at landscape scales (Angelstam and Kuuluvainen 2004, Seidl et al. 2018). 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).

4.5 Management implications

We present this conceptual model to help inform silvicultural 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. The Comparability Line and Comparability Index, which helps to compares 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 while developing and testing ecologically-based, sustainable forest management practices in Europe.

Natural disturbances create much broader range of variability for all the 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. 2017, Aakala 2018, Čada et al. 2020). However, emulation of intermediate and mixed-severity disturbances, with broad range of age classes and high level of biological legacy needs will require a fundamental change in forest practices. Advances in multi-cohort and retention silvicultural practices in North America, derived from efforts to emulate natural disturbance regime, 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. 2017). Foresters will need to feel comfortable emulating certain aspects of natural disturbance effects, such as deliberating creating (or retaining following natural disturbances) variability in residual structure, both live and dead, without defaulting always to sanitary cutting (Diaci et al. 2017).

Natural dynamics silviculture must incorporate deadwood management and tree retention to decrease the divergence from natural disturbances by increasing the amount and type of biological legacies (Krumm et al. 2020). The net amount of deadwood is considerably low in European forests; according to the national reported values, the estimates at country level, for both standing and lying deadwood range between 5 and 15 m^3/ha for most countries (Europe, Forest, 2015). However, effective deadwood management not only increases the amount, but also considers/manipulates the size, position and arrangement, and decay stage of retained trees (Vítková et al. 2018). As climate change intensifies bark beetle outbreaks, deadwood management, tree retention, and disturbance-based forestry efforts should be harmonized with bark beetle management strategies in forests most susceptible for bark beetle (Hlásny et al. 2019).

4.6 Limitation of the study

Human presence and influence on forest ecosystems has been continuous since the last ice age in Europe. Hence the structure, composition, and natural dynamics of European forests have been fundamentally altered across millennia. This particularly concerns certain forest types, like oak dominated forests at lower elevations. Other forest types survived in small old-growth fragments, 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 (Svoboda et al. 2012, Nagel et al. 2014, Čada et al. 2020) and retrospective modeling (Citation) are proving increasingly robust. The Comparability Index presented here must be applied within this context, acknowledging human influences our estimation of natural disturbance regime characteristics.

Disturbance regimes are changing rapidly (Turner 2010). Recent studies indicate a significant increase in disturbance rates across Europe's natural and managed forests (Schelhaas et al., 2003, Seidl 2014). However, it remains unknown how they will change 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 Comparability Index by incorporating more detailed information (by forest type) on the amount and quality of deadwood, density of large trees, intensity of the given management method, proportion of admixing species, and use of natural or artificial regeneration.

6. REFERENCES (not complete)

Aakala, T., & Keto-Tokoi, P. (2011). The old Norway spruce forests of northern boreal Aakala Fennoscandia are alive and well: A review of Sirén (1955). Scandinavian journal of forest research, 26(S10), 25-33.

Aakala, T., Pasanen, L., Helama, S., Vakkari, V., Drobyshev, I., Seppä, H., ... & Holmström, L. (2018). Multiscale variation in drought controlled historical forest fire activity in the boreal forests of eastern Fennoscandia. Ecological Monographs, 88(1), 74-91.

Angelstam P, Kuuluvainen T (2004) Boreal forest disturbance regimes, successional dynamics and landscape structures—a European perspective. Ecol Bull 51:117–136

Angelstam, P. K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of vegetation science, 9(4), 593-602.

Aplet, G.H. and W.S. Keeton. 1999. Application of historical range of variability concepts to biodiversity conservation. Pages 71-86 in: R. Baydack, H. Campa, and J. Haufler (eds.). Practical Approaches to the Conservation of Biological Diversity. Island Press, Washington, D.C. 313 pp.

Brang, P., Spathelf, P., Larsen, J. B., Bauhus, J., Boncčìna, A., Chauvin, C., ... & Lexer, M. J. (2014). Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry: An International Journal of Forest Research, 87(4), 492-503.

Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. Forest Ecology and Management 258:525–537.

Björse G, Bradshaw R (1998) 2000 years of forest dynamics in southern Sweden: suggestions for forest management. For Ecol Manag 104:15–26

Bobiec, A., Reif, A., & Öllerer, K. (2018). Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. Landscape ecology, 33(4), 513-528.

Boncina, A. (2011). Conceptual approaches to integrate nature conservation into forest management: a Central European perspective. International Forestry Review, 13(1), 13-22.

Bollmann, K., & Braunisch, V. (2013). To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. Integrative approaches as an opportunity for the conservation of forest biodiversity. In: Integrative approaches as an opportunity for the conservation of forest biodiversity, edited by: Kraus, D. and Krumm, F., EFI, Joensuu, 18–31, 2013.

Brang, P., P. Spathelf, J. B. Larsen, J. Bauhus, A. Bončína, C. Chauvin, L. Drössler, C. García-Güemes, C. Heiri, G. Kerr, M. J. Lexer, B. Mason, F. Mohren, U. Mühlethaler, S. Nocentini, and M. Svoboda. 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87: 492–503.

Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luyssaert, S., Sabatini, F. M., & Blasi, C. (2016). Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. Biological Conservation, 201, 370– 376.

Čada, V., R. C. Morrissey, Z. Michalová, R. Bače, P. Janda, and M. Svoboda. 2016. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. Forest Ecology and Management 363:169–178.

Čada, V., Trotsiuk, V., Janda, P., Mikoláš, M., Bače, R., Nagel, T. A., ... & Chaskovskyy, O. (2020). Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. Ecological Applications.

Caron, M. N., Kneeshaw, D. D., De Grandpré, L., Kauhanen, H., & Kuuluvainen, T. (2009, August). Canopy gap characteristics and disturbance dynamics in old-growth Picea abies stands in northern Fennoscandia: Is the forest in quasi-equilibrium?. In Annales Botanici Fennici (Vol. 46, No. 4, pp. 251-262). Finnish Zoological and Botanical Publishing Board.

Caudullo, G., Tinner, W., & de Rigo, D. (2016). *Picea abies* in Europe: distribution, habitat, usage and threats.

Diaci, J. (2006). Nature-based silviculture in Slovenia: origins, development and future trends. Nature-Based Forestry in Central Europe, 119.

Diaci, J., Rozenbergar, D., Fidej, G., & Nagel, T. A. (2017). Challenges for uneven-aged silviculture in restoration of post-disturbance forests in central Europe: A synthesis. Forests, 8(10), 378.

Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 126, 173-189.

Europe, Forest (2015). State of Europe's Forests 2015. Food and Agriculture Organization of the European Nations, EFI. In Ministerial Conference on the Protection of Forest in Europe. Disponible en: http://www. foresteurope. org/state-europes-forests-2015-report.

FAO. (2000). FRA 2000: On Definitions of Forest and Forest Change. Forest Resource Assessment Programe Working Paper# 33.

Fahey, R.T., B. C. Alvesherea, J.I. Burton, A.W. D'Amato, Y.L. Dickinson, W.S. Keeton, C.C. Kerne, A.J. Larson, B.J. Palik, K.J. Puettmann, M.R. Saunders, C.R. Webster, J.W. Atkins, C.M. Gough, and B.S. Hardimani. 2018. Shifting conceptions of complexity in forest management and silviculture. Forest Ecology and Management 421: 59-71

Fox, J., S. Weisberg, B. Price, D. Adler, D. Bates, G. Baud-bovy, B. Bolker, S. Ellison, D. Firth, M. Friendly, S. Graves, R. Heiberger, P. Krivitsky, R. Laboissiere, M. Maechler, G. Monette, D. Murdoch, D. Ogle, B. Ripley, W. Venables, S. Walker, D. Winsemius, A. Zeileis, and R-Core. 2019. Package 'car.'

Frank, G., & Parviainen, J. (2006). MCPFE information document on data collection and compiling the statistics on protected and protective forest and other wooded land in Europe. Ministerial Conference on the Protection of Forests in Europe, Liaison Unit. Warsaw

Franklin, J.F., K.N. Johnson, and D.L. Johnson. 2018. Ecological Forest Management. 646 pp. Waveland Press, Inc. Long Grove, IL.

Franklin, J.F., Mitchell, R.J., Palik, B., 2007. Natural Disturbance and Stand Development Principles for Ecological Forestry. US Department of Agriculture, Forest Service, Northern Research Station. General Technical Report NRS-19.

Franklin, J.F., T.A. Spies, R. Van Pelt, A. Carey, D. Thornburgh, D.R. Berg, D. Lindenmayer, M. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and the structural development of natural forest ecosystems with some implications for silviculture. Forest Ecology and Management 155:399-423.

Gustafsson et al. 2019. Ambio

Gustafsson, L., S. C. Baker, J. Bauhus, W. J. Beese, A. Brodie, J. Kouki, D. B. Lindenmayer, A. Lohmus, G. M. Pastur, C. Messier, M. Neyland, B. Palik, A. Sverdrup-Thygeson, W. J. A. Volney, A. Wayne, and J. F. Franklin. 2012. Retention forestry to maintain multifunctional forests: A world perspective. BioScience 62:6 33-645.

Harvey, B. D., Leduc, A., Gauthier, S., & Bergeron, Y. (2002). Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest ecology and management, 155(1-3), 369-385.

Hlásny, T., Krokene, P., Liebhold, A., Montagné-Huck, C., Müller, J., Qin, H., ... & Viiri, H. (2019). Living with bark beetles: impacts, outlook and management options (No. 8). European Forest Institute.

https://www.foresteurope.org/docs/reporting/MCPFE_INFO_DOC_on_data_collection_on_Protected_forests.pdf

Janda, P., V. Trotsiuk, M. Mikoláš, R. Bače, T. A. Nagel, R. Seidl, M. Seedre, R. C. Morrissey, S. Kucbel, P. Jaloviar, M. Jasík, J. Vysoký, P. Šamonil, V. Čada, H. Mrhalová, J. Lábusová, M. H. Nováková, M. Rydval, L. Matějů, and M. Svoboda. 2017. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. Forest Ecology and Management 388:67–78.

Johann, E. (2006). Historical development of nature-based forestry in Central Europe. Nature-based forestry in Central Europe. Alternatives to industrial forestry and strict preservation. Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Ljubljana, Slovenia, 1-17.

Kameniar, O., Baláž, M., Svitok, M., Reif, J., Mikoláš, M., Pettit, J. L., ... & Trotsiuk, V. Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition. Forest Ecology and Management, 481, 118647.

Ondrej Kameniar, Michal Baláž, Marek Svitok, Jiří Reif, Martin Mikoláš, Joseph L. Pettit, William S. Keeton, Jessika M. Pettit, Ondřej Vostarek, Thomas Langbehn, Volodymyr Trotsiuk, Federico Morelli, Michal Frankovič, Daniel Kozák, Pavel Janda, Vojtěch Čada, Matej Ferenčík, Jakub Málek, Krešimir Begovič, Michal Synek, Jana Lábusová, Kristýna Svobodová, Miroslav Svoboda,

Keeton, W.S. 2007. Role of managed forestlands and models for sustainable forest management: perspectives from North America. George Wright Forum 24(3):38-53.

Keeton, W.S., P. Angelstam, M. Baumflek, Y. Bihun, M. Chernyavskyy, S. M. Crow, A, Deyneka, M. Elbakidze, J. Farley, V. Kovalyshyn, B. Mahura, S Myklush, J. R. Nunery, I. Solovity, and L. Zahvoyska. 2013. Sustainable forest management alternatives for the Carpathian Mountain region, with a focus on Ukraine. Pages 331-352 in J. Kozak, K. Ostapowicz, A. Bytnerowicz, and B. Wyzga (eds.) The Carpathians: Integrating Nature and Society Towards Sustainability. Springer-Verlag, Berlin and Heidelberg, Germany.

Keeton, W.S., C. Lorimer, B. Palik, and F. Doyon. Silviculture for old-growth in the context of global change. Pages 237-265 in: Barton, A. and W.S. Keeton (eds.). Ecology and Recovery of Eastern Old-Growth Forests. Island Press, Washington, D.C. 340 pp

Kern, C. C., J. Burton, P. Raymond, A. D'Amato, W.S. Keeton, A.A. Royo, M.B. Walters, C.R. Webster, and J.L. Willis. 2016. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. Forestry 90: 4-17.

Khakimulina, T., Fraver, S., & Drobyshev, I. (2016). Mixed-severity natural disturbance regime dominates in an old-growth Norway spruce forest of northwest Russia. Journal of Vegetation Science, 27(2), 400-413.

Kohler, M., Pyttel, P., Kuehne, C., Modrow, T., & Bauhus, J. (2020). On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (Quercus petraea (Matt.) Liebl.) forests—a literature review. Annals of Forest Science, 77(4), 1-19.

Korpel, S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.

Kraus D., Krumm F. (eds) 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute. 284 pp

Kral, K., McMahon, S.M., Janik, D., Adam, D., Vrska, T., 2014. Patch mosaic of developmental stages in central European natural forests along vegetation gradient. Forest Ecology and Management 330, 17-28.

Krumm, F.; Schuck, A.; Rigling, A. (eds), 2020: How to balance forestry and biodiversity conservation – A view across Europe. European Forest Institute (EFI); Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf. 640 p.

Kulakowski, D., R. Seidl, J. Holeksa, T. Kuuluvainen, T. A. Nagel, M. Panayotov, M. Svoboda, S. Thorn, G. Vacchiano, C. Whitlock, T. Wohlgemuth, and P. Bebi. 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. Forest Ecology and Management 388:120–131.

Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica, 36(1), 97-125.

Kuuluvainen, T., and R. Grenfell. 2012. Natural disturbance emulation in boreal forest ecosystem management — theories, strategies, and a comparison with conventional even-aged management. Canadian Journal of Forest Research 42: 1185–1203.

Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological conservation, 131(3), 433-445.

Long, J. N. (2009). Emulating natural disturbance regimes as a basis for forest management: a North American view. Forest Ecology and Management, 257(9), 1868-1873.

Meigs et al. 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. Forest Ecology and Management 406: 410-426.

Messier, C., K. Puettmann, and D. Coates. (2013). Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, New York, NY.

Meyer, P., P. Janda, M. Mikoláš, V. Trotsiuk, F. Krumm, H. Mrhalová, M. Synek, J. Lábusová, D. Kraus, J. Brandes, and M. Svoboda. (2017). A matter of time: self-regulated tree regeneration in a natural Norway spruce (*Picea abies)* forest at Mt. Brocken, Germany. European Journal of Forest Research 136:907–921.

Mikoláš, M. M. Svoboda, V. Pouska, R. C. Morrissey, D. C. Donato, W. S. Keeton, T. Nagel, V. D. Popescu, J. Müller, C. Bässler, J. Knorn, L. Rozylowicz, M. C. Enescu, V. Trotsiuk, P. Janda, H. Mrhalová, Z. Michalová, F. Krumm, and D. Kraus. 2014. Comment on the "Opinion paper: Forest management and biodiversity": The role of protected areas is greater than the sum of its number of species. Web Ecology 14:61–64.

Mikoláš, M. I. Gallay, J. Vysoký, M. Čiliak, M. Jasík, P. Polák, V. Trotsiuk, M. Svoboda, K. Ujházy, G. Meigs, W.S. Keeton. 2019. Primary forest distribution and representation in a Central European landscape: results of a large-scale field-based census. Forest Ecology and Management 449: 17466

Mori A.S. and R. Kitagawa. 2014. Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: A global meta-analysis. Biological Conservation 175: 65–73.

Murdoch, D. 2020. Package "rgl."

Müller, J., & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research, 129(6), 981-992.

Nagel, T. A., Svoboda, M., & Kobal, M. (2014). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecological Applications, 24(4), 663-679.

Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A., Paulic, V., 2017. The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. Forest Ecology and Management 388, 29-42.

Niklasson, M., & Granström, A. (2000). Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology, 81(6), 1484-1499

North, M. P., & Keeton, W. S. (2008). Emulating natural disturbance regimes: an emerging approach for sustainable forest management. In Patterns and processes in forest landscapes (pp. 341-372). Springer, Dordrecht.

Panayotov, M., D. Kulakowski, L. L. Dos Santos, and P. Bebi. 2011. Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. Forest Ecology and Management 262:470-481.

Parviainen, J., & Frank, G. (2006). MCPFE information document on data collection and compiling the statistics on protected and protective forest and other wooded land in Europe. In Ministerial Conference on the Protection of Forests in Europe, liaison unit Warsaw, Warsaw.

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. Journal of Vegetation Science 16, 13-28. pp. 22–61.

Pretzsch, H., D.I. Forrester, and J. Bauhus (eds.). 2017. Mixed-Species Forest: Ecology and Management. Springer-Verlag, Germany. 653 pp.

Puettmann, K. J., S. M. Wilson, S. C. Baker, P. J. Donoso, L. Drossler, G. Amente, B. D. Harvey, T. Knoke, Y. Lu, S. Nocentini, F. E. Putz, T. Yoshida, and J. Bauhus. 2015. Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? Forest Ecosystems 2:1-16.

Raymond, P., Bédard, S., Roy, V., Larouche, C., & Tremblay, S. (2009). The irregular shelterwood system: review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry, 107(8), 405-413.

Ryzhkova, N., Pinto, G., Kryshen, A., Bergeron, Y., Ols, C., & Drobyshev, I. (2020). Multi-century reconstruction suggests complex interactions of climate and human controls of forest fire activity in a Karelian boreal landscape, North-West Russia. Forest Ecology and Management, 459, 117770.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Potzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horvath, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikolas, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Odor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? Diversity and Distributions 24, 1426-1439.

Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., ... & Gossner, M. M. (2020). Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems?. Journal of Applied Ecology, 57(7), 1363-1375.

Schelhaas, M.J., J. Fridman, G.M. Hengeveld, H.M. Henttonen, A. Lehtonen, U. Kies, N. Krajnc, B. Lerink, Á.N. Dhubháin, H. Polley, T.A.M. Pugh, J.J. Redmond, B. Rohner, C. Temperli, J. Vayreda, G.J. Nabuurs. 2018. Actual European forest management by region, tree species and owner based on 714,000 re-measured trees in national forest inventories. PLOS ONE 13: e0207151.

Schuck, A., Parviainen, J., Bücking, W., 1994. A review of approaches to forestry research on structure, succession and biodiversity of undisturbed and semi-natural forests and woodlands in Europe. European Forest Institute, Joensuu.

Schurman, J. S., V. Trotsiuk, R. Bače, V. Čada, S. Fraver, P. Janda, D. Kulakowski, J. Labusova, M. Mikoláš, T. A. Nagel, R. Seidl, M. Synek, K. Svobodová, O. Chaskovskyy, M. Teodosiu, and M. Svoboda. 2018. Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. Global Change Biology 24:2169–2181.

Schulze, E. D., Bouriaud, L., Bussler, H., Gossner, M., Walentowski, H., Hessenmöller, D., ... & Gadow, K. V. (2014). Opinion paper: Forest management and biodiversity. Web Ecology, 14(1), 3-10.

Schutz, J.P., Saniga, M., Diaci, J., Vrska, T., 2016. Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. Annals of Forest Science 73, 911-921.

Seidl, R. et al. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change 4: 806–810

Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., ... & Hansen, W. D. (2020). Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. Ecography.

Senf, C., and R. Seidl. 2018. Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. Global Change Biology 24:1201–1211.

Senf, C., & Seidl, R. (2020). Mapping the coupled human and natural disturbance regimes of Europe's forests. bioRxiv.

Seymour, R. S., & White, A. S. (2002). Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management, 155(1-3), 357-367.

Seymour, R.S., Hunter, M.L., Jr., 1999. Principles of ecological forestry. In: Hunter Jr., M.L. (Ed.), Managing Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge,

Spiecker, H. (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe—temperate zone. Journal of Environmental Management, 67(1), 55-65.

Splechtna, B. E., Gratzer, G., & Black, B. A. (2005). Disturbance history of a European old-growth mixed-species forest—A spatial dendro-ecological analysis. Journal of Vegetation Science, 16(5), 511-522.

Standovár, T., & Kenderes, K. (2003). A review on natural stand dynamics in beechwoods of East Central Europe. Applied ecology and environmental research, 1(1), 19-46.

Svoboda, M., P. Janda, R. Bače, S. Fraver, T. A. Nagel, J. Rejzek, M. Mikoláš, J. Douda, K. Boublík, P. Šamonil, V. Čada, V. Trotsiuk, M. Teodosiu, O. Bouriaud, A. I. Biriş, O. Sýkora, P. Uzel, J. Zelenka, V. Sedlák, and J. Lehejček. 2014. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania. Journal of Vegetation Science 25:386–401.

Svoboda, M., P. Janda, T. A. Nagel, S. Fraver, J. Rejzek, and R. Bace. 2012. Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science 23:86-97.

Szewczyk, J., J. Szwagrzyk, and E. Muter. 2011. Tree growth and disturbance dynamics in old-growth subalpine spruce forests of the Western Carpathians. Canadian Journal of Forest Research 41:938-944.

Szwagrzyk J, Gazda A. 2007. Aboveground standing biomass and tree species diversity in natural stands of Central Europe. J Vegetat Sci 18: 563–570.

Thom, D., R. Seidl, G. Steyrer, H. Krehan, and H. Formayer. 2013. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. Forest Ecology and Management 307:293–302.

Thom, D, Seidl, R. (2016): Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews, 91: 760-781.

Thom, D, Rammer, W, Seidl, R (2017): The impact of future forest dynamics on climate: Interactive effects of changing vegetation and disturbance regimes. Ecological Monographs, 87: 665-684.

Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., ... & Keeton, W. S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. Global change biology, 25(7), 2446-2458.

Thom, D., Taylor, A. R., Seidl, R., Thuiller, W., Wang, J., Robideau, M., & Keeton, W. S. (2020). Forest structure, not climate, is the primary driver of functional diversity in northeastern North America. Science of The Total Environment, 143070.

Trotsiuk, V., M. Svoboda, P. Janda, M. Mikolas, R. Bace, J. Rejzek, P. Samonil, O. Chaskovskyy, M. Korol, and S. Myklush. 2014. A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians. Forest Ecology and Management 334:144–153.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. Ecology, 91(10), 2833-2849.

Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems, 1(6), 511-523.

Vera FWM (2000) Grazing ecology and forest history. CABI Publishing, Wallingford.

Vítková, L., Bače, R., Kjučukov, P., & Svoboda, M. (2018). Deadwood management in Central European forests: Key considerations for practical implementation. Forest Ecology and Management, 429, 394-405.

Wallenius, T. H., Kauhanen, H., Herva, H., & Pennanen, J. (2010). Long fire cycle in northern boreal Pinus forests in Finnish Lapland. Canadian Journal of Forest Research, 40(10), 2027-2035.

White, P. S., & Jentsch, A. (2001). The search for generality in studies of disturbance and ecosystem dynamics. In Progress in botany (pp. 399-450). Springer, Berlin, Heidelberg.

Wolfslehner, B., and R. Seidl. 2010. Harnessing ecosystem models and multi-criteria decision analysis for the support of forest management. Environmental Management 46:850–861.

Zielonka, T., J. Holeksa, P. Fleischer, and P. Kapusta. 2009. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. Journal of Vegetation Science 21:31-42.

Supplement Table 1 – the Questionnaire

Supplement Table 2 – sources of the national management data besides expert opinion and expert synthesis

Austria	[1] : https://www.waldwissen.net/technik/inventur/bfw_altersklassen1_oewi/index_DE [2] : https://www.waldwissen.net/technik/inventur/bfw_altersklassen2_oewi/index_DE *[1] and [2] are special reports from the results of the austrian forest inventory 2007-2009 (this is the latest inventory)* [3] Austrian forest inventory – Online Database: http://bfw.ac.at/rz/wi.home Latest data from the inventory 2007-2009 was used [4] Silvicultural guidelines for Austria; Published by the Chamber of Agriculture Austria; https://www.waldverband.at/wp-content/uploads/2015/07/Titelblatt-Einleitung-Inhaltsverzeichnis.pdf [5] Austrian Forest Law: https://www.ris.bka.gv.at/GeltendeFassung.wxe?Abfrage=Bundesnormen&Gesetzesnummer=10010371 [in German]
Czech Republic	Ministry of Agriculture report on the Forests in Czech Republic for 2017. Accessed here (only in CZ): http://eagri.cz/public/web/file/609179/Zprava_o_stavu_lesa_2017.pdf
Finland	Kujala, M. 2017. The popularity of Different Harvesting Methods after The New Forest Act. Bachelor's thesis, Tampere University of Applied Sciences, 56 p Forest use declarations database of the Finnish Forest Centre Finnish National Forest Inventory 11/12
France	Expertise based on Maaf, I.G.N., 2016. Indicateurs de gestion durable des forêts françaises métropolitaines, édition 2015. ONF, 2017. Bilan patrimonial des forêts domaniales (hors DOM). Editions 2015. 250 p

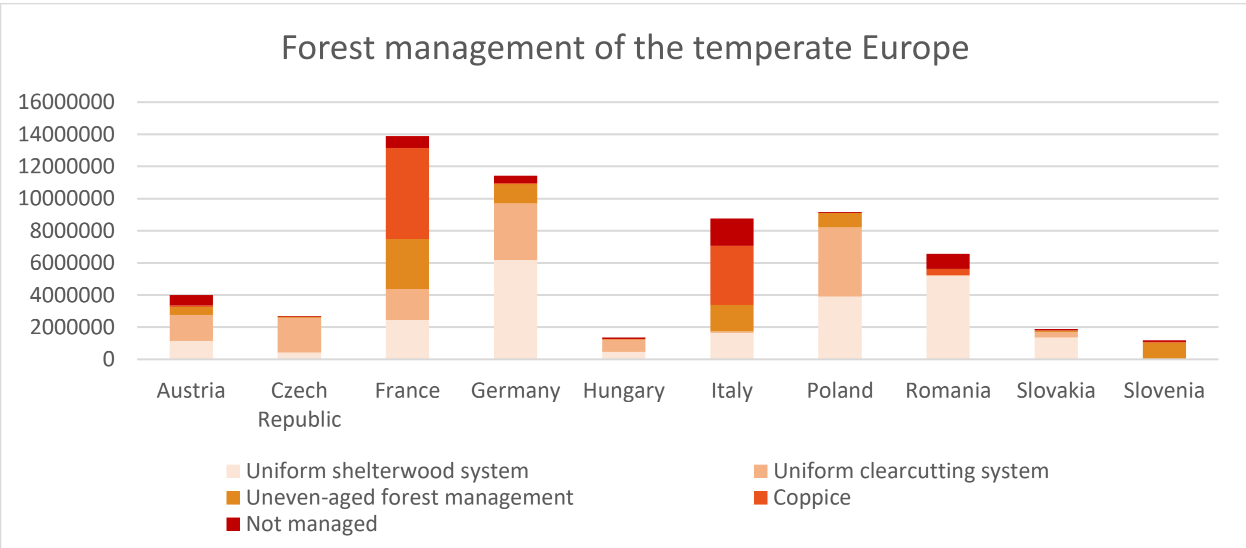
	Delord P., Mandret X. (coord.) 2018. Mémento sylvicole de conduit des peuplements. Chênaies atlantiques. Futaie régulière et conversion en futaie régulière. ONF. 58 p Abt D. & Cerf JF. 2014. Guide des sylvicultures Arc Jurassien. Sapin et épicéa. ONF. 34 p. Guillon M., Sardin T., Viry B., Wright J. 2013. Référentiels sylvicoles. Massif vosgien. Sapin, épicéa et pin sylvestre. ONF. 39 p. Chabaud L. & Nicolas L. 2009. Guide des sylvicultures. Pineraies des plaines du Centre et du Nord-Ouest. ONF. 401 p. Susse R., Allegrini C., Bruciamacchie M. Burrus R. 2009. Le traitement des futaies irrégulières. AFI. 144 p. Sardin (coord.) 2018. Conduite en futaie irrégulière des chênaies d'île de France. ONF. 60p.
Germany	Thünen-Institut, Dritte Bundeswaldinventur - Ergebnisdatenbank, https://bwi.info https://www.baysf.de/fileadmin/user_upload/04-wald_verstehen/Publikationen/Fichtenrichtlinie.pdf https://www.baysf.de/fileadmin/user_upload/04-wald_verstehen/Publikationen/WNJF-RL-005_Kiefernrichtlinie.pdf https://www.baysf.de/fileadmin/user_upload/04-wald_verstehen/Publikationen/Buchengrundsaetze.pdf
Hungary	National Forestry Database (NFD) Forest Code (2009) and a secondary legislation (2016)
Italy	INFC 2005 National Forest Inventory https://www.sian.it/inventarioforestale/jsp/home_en.jsp
Latvia	Data from State Forest Service: taken from restrictions on harvest data. http://www.vmd.gov.lv/valsts-meza-dienests/statiskas-lapas/publikacijas-un-statistika/meza-statistikas-cd?nid=1809#jump

	State Forest Service Statistics http://www.vmd.gov.lv/valsts-meza-dienests/statiskas-lapas/publikacijas-un-statistika?nid=1717#jump Maximum size set by regultions: https://likumi.lv/doc.php?id=253760 Rotation minimal diameter set in regulations: https://likumi.lv/doc.php?id=253760 Rotation age set in the Forest Law: https://likumi.lv/doc.php?id=2825
Poland	National Forest Inventory 2015 Manual for Forest Management Principles of Silviculture Bureau for the Forest Management and Geodesy 2015. The National Forest Inventory. Results of cycle II (2010-2014). State Forests National Forest Holding, Sękocin Stary. Bureau for the Forest management and Geodesy 2012. Manual for Forest Management. Centrum Informacyjne Lasów Państwowych, Warszawa. General Directorate of the State Forests National Forest Holding 2012. Zasady Hodowli Lasu (Principles of Silviculture). Warszawa. Jaworski A. 2011. Hodowla Lasu (Silviculture). PWRiL, Warszawa Sabatini F., Burrascano S., Keeton W. S., Levers C., Lindner M., Pötzschner F., Verkerk P. J., Bauhus J., Buchwald E., Chaskovsky E., Devbaive N., Horváth F., Garbarino M., Grigoriadis N., Lombardi F., Duerte I. M., Meyer P., Midteng R., Mikac S., Mikolaš M., Motta R., Mozgeris G., Nunes L., Panayotov M., Ódor P., Ruete A., Simovski B., Stillhard J., Svoboda M., Szwagrzyk J., Tikkanen O.-P., Volosyanchuk R., Vrska T., Zlatanov T., Kummerle T. 2018. Where are Europe's last primary forests?. Diversity and Distributions DOI: 10.1111/ddi.12778
Romania	Ministry of Waters and Forests (2018). State of Romanian forests in 2017 Carcea, F., Leahu, I., Guiman, G. (2013) Realities and perspectives on the application of selection systems in the Romanian forests. Revista Padurilor 128 (2): 11-17 http://roifn.ro/site/rezultate-ifn-2/ Romanian Technical Normatives (no. 3 and no. 5)

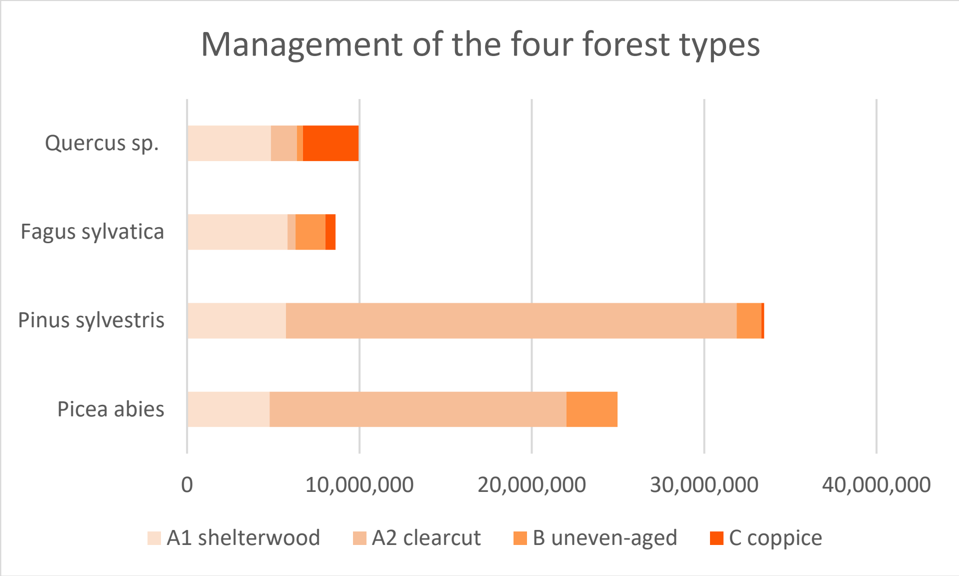
Slovakia	Ministry of agriculture and rural development of the Slovak Republic. 2018. Green Report 2018. Bratislava, Slovak Republic Green report 2018; Forest Portal; National Forest Centre Zvolen, Slovakia
Slovenia	SFS (2017) Forest inventory database. Slovenian Forest Service, Ljubljana Adamic, M., Diaci, J., Rozman, A. & Hladnik, D. (2017). Long-term use of uneven-aged silviculture in mixed mountain Dinaric forests: a comparison of old-growth and managed stands. Forestry, 90, 279-291. Diaci, J. 2006 Silviculture: old-growth forest, forest stands, silvicultural systems, silvicultural planning and selected topics. University of Ljubljana, Biotechnical Faculty, Department for Forestry and Renewable Forest Resources: Ljubljana, 348 p. Diaci, J., Govedar, Z., Krstić, M. & Motta, R. (2012). IMPORTANCE AND PERSPECTIVES OF SILVICULTURE FOR THE SCIENCE AND PRACTICE OF FORESTRY. In: Forestry science and practice for the purpose of sustainable development of forestry 20 years of the Faculty of forestry in Banja Luka Banja Luka, pp. 23-40. O'Hara, K.L., Bonĉina, A., Diaci, J., Anić, I., Boydak, M., Curovic, M. et al. (2018). Culture and Silviculture: Origins and Evolution of Silviculture in Southeast Europe. SPIE.
Sweden	SLU. 2018. Skogsdata. Institutionen för skoglig resurshushållning, SLU, Umeå Källa: Naturvårdsverket och Skogsstyrelsen 2017. Värdefulla skogar. Skrivelse. Naturvårdsverket diarienummer NV-00110-16. Skogsstyrelsen diarienummer 2019/479. Källa: Skogsstyrelsen 2017. Avrapportering av regeringsuppdrag om frivilliga avsättningar. Skogsstyrelsen Meddelande 4/2017. Källa: Skogsstyrelsen 2015. Skogliga konsekvensanalyser 2015 – SKA 15. Rapport 10/2015

	Axelsson, R., Angelstam, P., Svensson, J. 2007. Natural forest and cultural woodland with continuous tree cover in Sweden: How much remains and how is it managed? Scandinavian Journal of Forest Research 22: 545-558. Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51(6): 1669-1679. Surendra Joshi. 2017. Notified areas of final felling in 2016 Data from Statistiska meddelanden, JO0314 SM 1701 Surendra.joshi@skogsstyrelsen.se Clas Fries, Jonas Bergquist, Peder Wikström. 2015. Lägsta ålder för föryngringsavverkning (LÅF) – en analys av följder av att sänka åldrarna i norra Sverige till samma nivå som i södra Sverige. Skogsstyrelsen, Rapport 6.

Supplement Table 3 – the raw database of national data (should be attached)



Supplement Fig. 1 Forest management of the temperate Europe (if we need this fig, the same colour palette should be used as Fig2)



Supplement Fig. 2 Forest management of forests dominated by the four focal species of boreal and temperate Europe

Supplement Table 4. Proportion of silvicultural systems across 13 target countries. Data are shown for totals and separately by boreal and temperate zone as well as for unmanaged forests.

	%	total	temperate	boreal	total without D
A1	Uniform shelterwood system	21.0	37.4	0.4	22.9
A2	Uniform clearcutting system	51.9	24.3	86.7	56.6
B	Uneven-aged forest management	9.7	14.1	4.2	10.6
C	Coppice systems	9.1	16.4	0.0	9.9
D	Unmanaged	8.3	7.9	8.7	

Supplement Note 1 – literature review