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

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(Article begins on next page)

1

2 **Natural disturbance regimes as a guide for sustainable forest** 3 **management in Europe**

4

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25 **ABSTRACT**

26 In Europe, there has long been interest in natural dynamics silviculture, although the vast
27 majority of forests remain tightly regulated under a variety of production-driven silvicultural
28 systems. A major barrier has been incomplete understanding of the ranges of variability in
29 disturbance regimes, including frequencies, spatial attributes, and severities. Addressing this
30 constraint in European forest management, we adapted a “comparability index” that was first

31 developed in the US to compare natural disturbances and forest management effects based on
32 disturbance size and frequency. We extended the original concept by adding residual structure of
33 canopy trees after disturbance (i.e. retention in case of forest management and the inverse of
34 disturbance severity) as a third dimension. We populated the model by compiling published data
35 on disturbance dynamics from 13 countries, covering four major forest types (i.e. spruce, beech,
36 oak, and pine-dominated). Expert-derived data on harvesting effects by country and forest type
37 for a variety of silvicultural systems were obtained through a questionnaire, with standardized
38 estimation protocol, distributed to collaborators. The data for both natural and harvest
39 disturbances were visualized in two- and three-dimensional plots indicating ranges for
40 frequency, size, and severity. “Comparability Lines (CL)” were fit as the central tendency among
41 all two-dimensional combinations of disturbance attributes while controlling for the third
42 dimension. Congruence of common silvicultural systems with the CL was then calculated as a
43 Comparability Index (CI). Specifically, we computed the CI as the relative distance between the
44 centroids of each silvicultural system to the respective CL. Natural disturbances are highly
45 variable in size, frequency, and severity, but European forest management does not reflect this
46 complexity. The CI indicates the highest congruence between uneven-aged silvicultural systems
47 and key natural disturbance attributes. Other silvicultural systems perform poorly in terms of
48 retention as compared to tree survivorship after natural disturbances. Applying the CI to a variety
49 of forest management contexts will help European silviculturists determine how to adjust
50 harvesting regimes to better approximate the complexity of natural disturbance dynamics. This,
51 in turn, may aid efforts to provide a broader array of ecosystem services and habitat conditions in
52 managed forests.

53

54 **1. INTRODUCTION**

55 Forest scientists in many regions are exploring innovative ways of managing forests both for a
56 greater variety of services and biodiversity than in the past and for enhanced resilience and
57 adaptive capacity to global change (Gustafsson et al. 2012, 2019; Mori and Kitagawa 2014,
58 Fahey et al. 2018). For example, there is growing interest in the development of forest
59 management techniques designed to approximate the structural and compositional dynamics of
60 ‘natural’ (or less human-influenced) ecosystems (Keeton 2007, Kuuluvainen and Grenfell 2012,
61 Puettmann et al. 2015). Here we use the term “natural dynamics” silviculture to refer to these
62 approaches, recognizing this as part of a larger trend towards “ecological silviculture” as

63 described by Franklin et al. (2018) and others (e.g. D’Amato et al. 2017, Keeton et al. 2018). In
64 Europe, there has long been interest in ecological or multi-functional forest management
65 approaches (Diaci et al. 2006, Wolfslehner and Seidl. 2010, Kraus and Krum 2013, Brang et al.
66 2014, Pretzsch et al. 2017). However, growth, composition, structure, and age class distributions
67 of the vast majority of European forests remain tightly regulated under a variety of production
68 driven, even-aged and continuous cover systems (Schelhaas et al. 2018). As Gustafsson et al.
69 (2019) suggest, the former may be more common in boreal regions and the latter more dominant
70 in temperate regions of Europe.

71

72 However, a major barrier to implementing natural dynamics silviculture has been the lack of
73 comprehensive understanding of the ranges of variability (whether historic, contemporary, or
74 future) in disturbance regimes, including frequencies, spatial attributes, and severities
75 (Kulakowski et al. 2017). Moreover, the distribution, composition, and dynamics of European
76 forests have been fundamentally altered by centuries, even millennia, of human influence
77 (Keeton et al 2013, Pretzsch et al. 2017). Consequently, finding reference forests in which to
78 observe baseline disturbance dynamics is highly challenging, since only small fragments of
79 primary or old forests remain in most places (Szwagrzyk and Gazda 2007, Mikoláš et al. 2019).
80 The proportion of remnant old-growth (primary) forests is very low in Europe (0.7% of the forest
81 cover); montane beech forests are overrepresented relative to other forest types (Sabatini et al.
82 2018). However, in recent decades great progress has been made in describing the disturbance
83 regimes of European forests (e.g. Seidl et al. 2011, Kuuluvainen and Aakala 2011, Thom et al.
84 2013, Kulakowski et al. 2017, Thom and Seidl 2016; Senf and Seidl 2020). Our study advances
85 the science by comparing such literature derived data on disturbance dynamics with a
86 comprehensive database on forest management effects across 13 countries. The analysis
87 encompasses four of the major European forest types, including those dominated by European
88 beech (*Fagus sylvatica*), spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and oak (*Quercus*
89 *spp.*) respectively.

90

91 [1.1 Comparing natural disturbance dynamics to forest management](#)

92

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

96 from the processes and dynamics occurring in primary and less human-influenced forests. A
97 consistent comparative framework is needed. This framework must acknowledge the alteration
98 of disturbance regimes caused by centuries of human influence as well as shifting boundary
99 conditions associated with climate change (Seidl et al. 2014, Kulakowski et al. 2017, Thom et al.
100 2017, Senf and Seidl 2020). It must also consider the broad range of forest management
101 approaches and harvesting intensities in Europe, varying by region, forest type, ownership and
102 subsidy programs, local conditions and accessibility, importance of non-timber services, and
103 other factors (Schelhass et al. 2018).

104 We explore this potential by assembling data on pan-European forest disturbances and
105 management effects. We use those data to adapt for Europe the “Comparability Index” (CI) first
106 proposed by Seymour et al. (2002) in North America and later modified by North and Keeton
107 (2008). The CI plots the relative frequencies and sizes of dominant disturbance types – such as
108 gap forming, intermediate severity, and stand replacing wind events – against the frequencies
109 and scales of regeneration harvesting methods, such as clearcutting or selection systems. Using
110 the current version of the index, silviculturists can determine how to adjust harvesting regimes to
111 better approximate natural disturbance dynamics in terms of scale and frequency.

112 In this study we expand the CI framework by adding a critical third dimension or axis (see, for
113 example, Turner et al. 1998), namely residual structure, survival of canopy trees (i.e., the inverse
114 of disturbance severity). This results in a 3-dimensional framework showing ranges of variability
115 both for disturbance dynamics and forest management, based on the shared parameters of spatial
116 extent, frequency, and residual structure. A similar framework was employed for boreal forests
117 in Canada (Bergeron et al. 2002). With this innovation, the framework now provides a rigorous
118 basis for assessing the congruence between forest management and natural disturbances in both
119 temperate and boreal European forest ecosystems. With all three parameters represented, the
120 framework will capture more completely the variation in both natural disturbance effects and
121 silvicultural regimes. Furthermore, we hypothesize that contemporary European forest
122 management is likely to exhibit very low congruence with past and present natural disturbance
123 regimes. We predict that the divergence between natural disturbances and forest management
124 will increase by adding a new axis (residual structure) to our comparative framework.

125

126 1.2 Understanding variability in disturbance regimes

127

128 How should management approaches be modified to more closely emulate natural disturbances?
129 And furthermore, how does management differ from the ranges of variability in disturbance
130 processes for different forest types? To answer these questions we synthesize research on
131 disturbance dynamics obtained from both a survey of expert knowledge on the forest
132 management of 13 European countries and a literature review on natural disturbance regime of
133 European forests. For example, relevant research has utilized (i) stand level structural
134 observations of remnant old-growth stands (Korpel 1995, Standovár and Kenderes 2003, Aakala
135 2018, Schutz et al. 2018), (ii) dendrochronological studies (Splechtna 2005, Svoboda et al. 2012,
136 Nagel et al. 2014, Čada et al. 2016), and (iii) historical and remote sensing studies (Nagel et al.
137 2017). There are many studies in the first group, describing composition and structure or short-
138 term dynamics in old-growth forests, based on repeated measurements, but these have yielded
139 only limited information on long-term and landscape scaled dynamics. Dendrochronological
140 studies have longer (e.g. multiple centuries) time-frames, but explore primarily stand level
141 processes; while the third group includes areas with forests under strong human influences.
142 Therefore, in our study we relied on expert knowledge to synthesize and triangulate data from
143 multiple types of natural disturbance studies and for all four of the major forest types.

144 There are multiple sources of spatial variability in European disturbance processes (Senf and
145 Seidl 2018, 2020); these differ among forest types and between boreal and temperate forested
146 biomes (Thom and Seidl 2016). For instance, fire plays a greater role in boreal forests as
147 compared to European temperate systems but is typically infrequent and stand replacing in
148 Norway spruce (Aakala et al. 2009, 2018), whereas fire more frequent and of low to mixed
149 severity in Scots pine (Niklasson and Granström 2000, Aakala 2018). This contrast differs from
150 wind disturbances, which are a dominant structuring process across all European forests, though
151 varying greatly in intensity (e.g. gap forming, diffuse low severity, mixed severity, or stand
152 replacing) and temporal dynamics, for example exhibiting periods when high intensity wind
153 storms are of greater prevalence (Zielonka et al. 2009; Svoboda et al. 2012, Čada et al. 2016).
154 And finally, recent research on the role of intermediate severity disturbances suggests a much
155 broader range of variability in potential age class structures than previously recognized for
156 European forests (Svoboda et al. 2014, Trotsiuk et al. 2014). Thus, rather than conceptualizing
157 forest management as a choice between even or uneven-aged approaches, silviculturists are
158 challenged to manage for a range of multi-aged or multi-cohort forest structures as well. These
159 are more analogous to the stand structures created by periodic partial mortality events and
160 associated pulses of tree recruitment (Meigs et al. 2017). The comparative framework we

161 propose synthesizes the current knowledge of these ranges of variability, presenting a basis for
162 consistent comparisons against forest management.

163

164 **2. METHODS**

165

166 **2.1 A Scope of the Study**

167

168 The scope of this study spans the boreal and temperate forest regions of Europe. We excluded
169 the Mediterranean zone because of the greater variability and fragmentation of the region's
170 extant forests and fundamental differences in forest history and contemporary management.
171 Within the scope of our study were four main forest types, dominated by four focal species
172 respectively; Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), European beech (*Fagus*
173 *sylvatica*) and European oak species (*Quercus robur*, *Q. petraea*, *Q. pubescens*, *Q. cerris*). These
174 forest types are the most common ones in the boreal and temperate zones of Europe, and
175 represent different points on the disturbance continuum. Our study compared human and natural
176 disturbances both in aggregate for all forests continent-wide, and individually within each forest
177 type, quantitatively for the former and qualitatively for the latter.

178

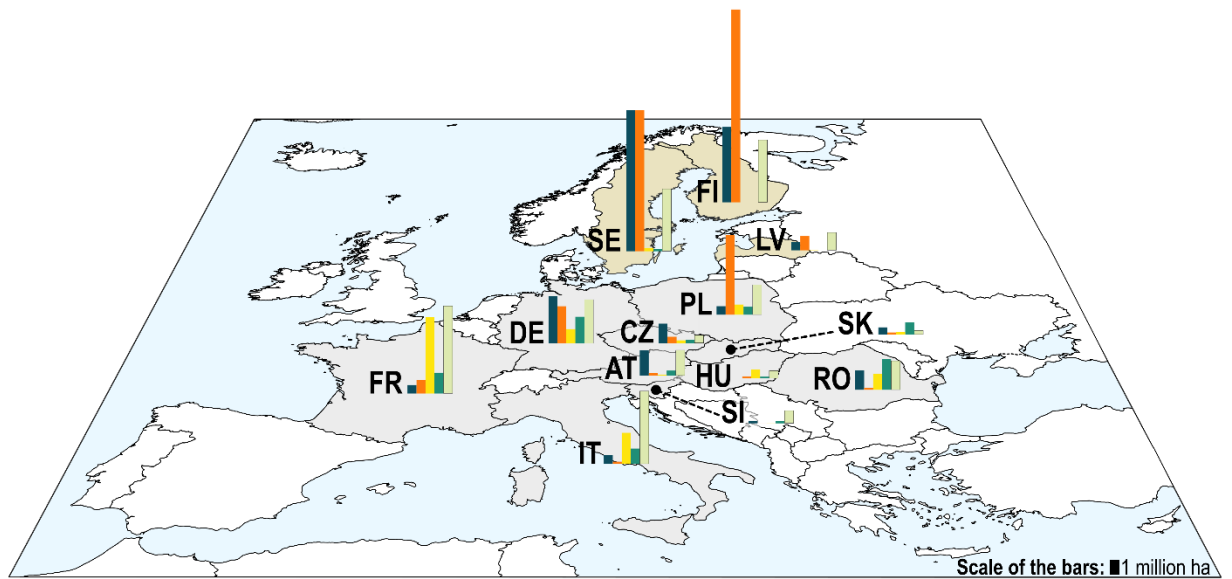
179 **2.2 Compiling the dataset**

180

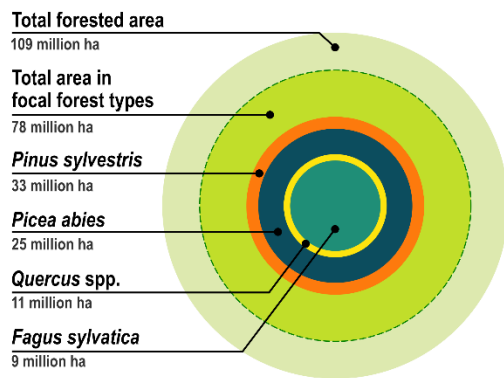
181 2.2.1 National forest management data for 13 target countries

182

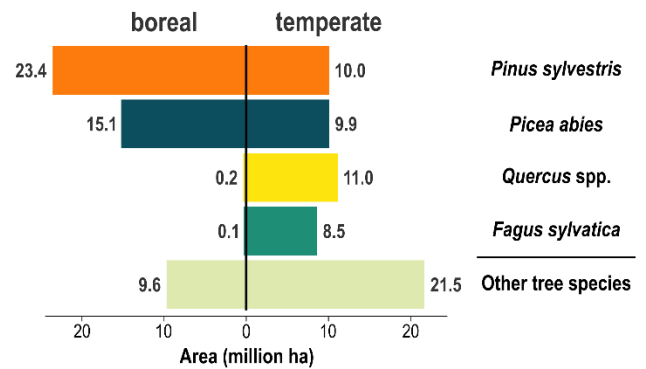
183 To assess European forest management practices, we selected 13 target countries, representing
184 West-, Central-, and North-Europe (Fig 1), and asked forest experts of each country to complete
185 a standardized questionnaire (Supplement Table 1). The questionnaire (Q) was designed to
186 assess four groups of questions: 1) silvicultural systems used by a given country; 2) the ratio and
187 land area under different silvicultural systems as well as forests with no management or managed
188 primarily for non-timber objective ("unmanaged" henceforward); 3) the area and ratio of forest
189 types dominated by the four focal species and their typical management methods; and 4) harvest
190 size, rotation period, and residual structure (live tree retention) for these silvicultural systems.



Area of focal forest types across 13 countries



Area of dominant species by biome



191

192

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

195

196 Our classification of silvicultural systems encompasses four main categories of forest
 197 management (Table 1): A) even-aged forest management methods, such as uniform shelterwood
 198 and uniform clearcutting systems; B) uneven-aged and multi-aged forest management methods,
 199 represented by a variety of selection and irregular shelterwood systems (see Raymond et al.
 200 2009); C) regular coppice and coppice with standards; and D) no management or management
 201 primarily for non-timber objectives (EU MCPFE categories 1.1, 1.2, 1.3, see Frank & Parviainen
 202 2006).

203 The survey excluded “other wooded lands” (see definition in FAO 2000) and non-productive
 204 forests (defined as annual increment < 1 m³/ha/yr). Mediterranean forests, like evergreen oak

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

207 To produce a standardized database, we also excluded the short-rotation clearcutting systems (\leq
 208 40 years). Short-rotation systems, usually intensively managed plantations, are considered as
 209 forest in some countries (France, Slovakia, Hungary, Latvia), but not so in others (Austria, Italy),
 210 where they are instead classified as agroforestry. For consistency, we harmonized the
 211 silvicultural terminology across country-specific data. The area and ratio of the forest types
 212 dominated by the four focal species and their typical management methods were also assessed by
 213 the questionnaire. Forests not covered by these four types were assigned to an “other” category.

214 The intervention sizes for the different silvicultural systems were defined as the area of the final
 215 harvest in the case of shelterwood-, clearcut-, and coppice systems (Cat. A1, A2, C1, C2).

216 Intervention size in the case of uneven-aged systems (Cat. B) was defined as the size of the
 217 canopy gaps created by the intervention of the single-tree-, group- or multicohort selection. This
 218 was necessary to compare forestry practices with their natural analogues.

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

221 Residual structure (retention) was defined as the percentage of living woody biomass volume
 222 (m^3) compared to the pre-harvest volume left on a 1 ha site after the final cutting operation
 223 (clearcutting system, shelterwood system) or after the regular entry (uneven-aged forestry).

224 Intermediate treatments, such as thinnings were not considered in the determination of harvest
 225 frequency and residual structure.

226 Multiple primary data sources were used by the national experts we surveyed in response to the
 227 questionnaire. Sources included national forest inventories, national silvicultural guidelines,
 228 ministry reports, data archived by national research institutes, scientific papers, state forest
 229 service statistics, original datasets maintained by survey participants, and expert opinion.

230 Sources varied by country depending on data availability (see Supplement Table 2).

231

232 Table 1. Classification and the definition of the silvicultural systems

233

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

A1	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • single tree selection 	Scattered individual trees of multiple age classes are harvested
B2	<ul style="list-style-type: none"> • group selection 	Small to medium sized openings created by the removal of several adjacent trees
B3	<ul style="list-style-type: none"> • multi-cohort (irregular shelterwood) system 	Multi-aged forestry, permanent retention with $\geq 10\%$ 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

234

235

236 [2.2.2 Natural disturbance attributes of European forests](#)

237

238 Our analysis was based on parameters describing the frequency, severity, and spatial extent of
 239 natural disturbances in Europe. For this part of the assessment, we compiled a literature review
 240 by collecting and extracting data from, (i) long-term studies of primary and old-growth forests
 241 (see Sabatini et al. 2018 for definitions), (ii) dendrochronological studies, and (iii) and other
 242 studies defining the ranges of variability in disturbance dynamics for the four forest types
 243 (Supplement Note 1). Then, the categories of the natural disturbance types of European boreal
 244 and temperate zones were defined by adapting the classification of Kuuluvainen and Aakala
 245 (2011). We grouped natural disturbance regimes into four categories; 1) high-severity, stand-
 246 replacing disturbances, like major windstorms or fire events, 2) intermediate severity
 247 disturbances driven by partial disturbances, like microbursts, ice storms, and bark beetle
 248 outbreaks, 3) low severity diffuse disturbances, like low severity fires, windstorms, ice storms,
 249 bark beetle outbreaks, 4) low severity, aggregated disturbances, such as “gap dynamics” driven

250 by tree mortality at fine scales (< 200 m²). Finally, ranges for size, frequency, and severity
251 parameters were attributed to these categories by expert consensus, on the basis of the literature
252 review.

253

254 2.3 Data Analysis

255

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

260 Next, we designed a 3D figure for visualization purposes, populated with the data obtained from
261 our forest management survey and natural disturbance literature review. The 3D figure compares
262 disturbance size, frequency, and residual structure simultaneously, with each parameter
263 displayed along an independent axis. For each silvicultural system, we obtained country-level
264 averages of the given silvicultural system. Then, we visualized the volume (within the 3D figure)
265 of natural disturbance types and silvicultural systems by drawing ellipsoids with the outer
266 bounds concurring with the data ranges. To facilitate the derivation and interpretation of the CI,
267 we used the same approach to populate three, 2D figures presenting size and frequency, size and
268 residual structure, and frequency and residual structure (*sensu* Seymour et al. 2002). The 3D and
269 2D figures were visualized in R using the rgl (Murdoch 2020) and car package (Fox et al. 2019),
270 respectively.

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

281

282 3. RESULTS

283

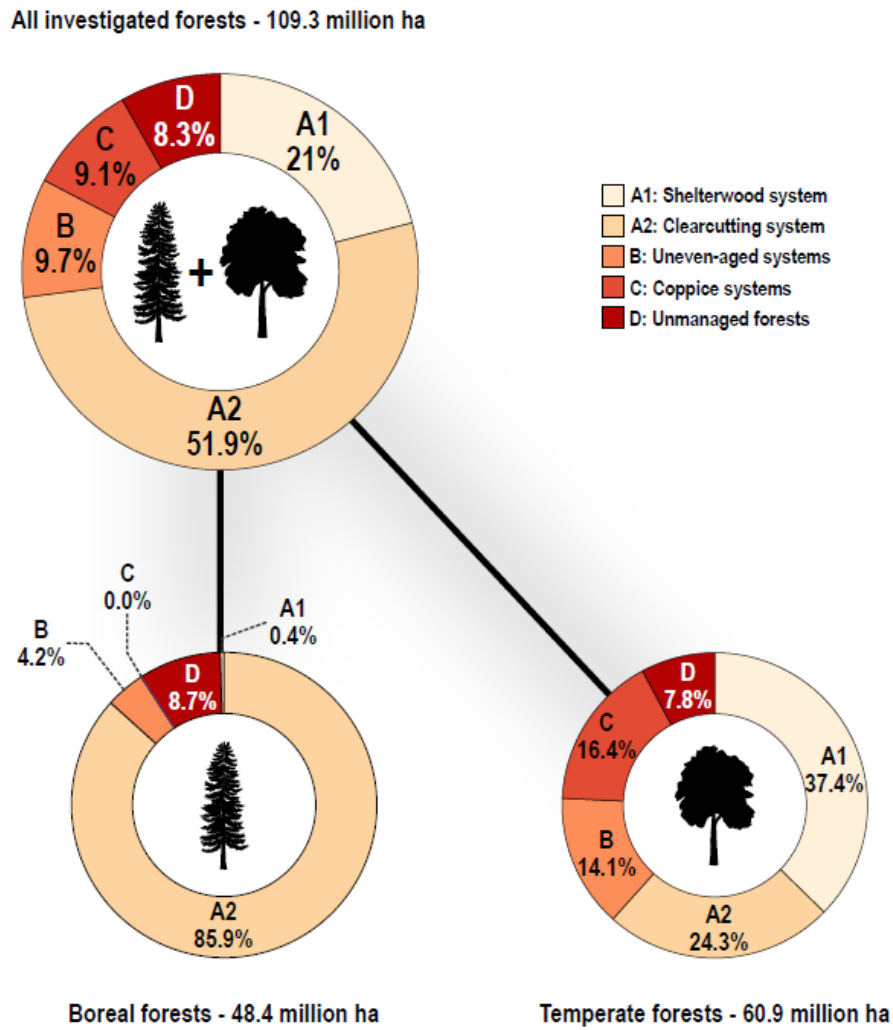
284 3.1 Silvicultural systems and dominant tree species of European forests

285

286 Our results showed that use of silvicultural systems in Europe is skewed disproportionately
287 towards even-aged systems. Even-aged silvicultural systems (Cat. A, see Table 1 for categories)
288 dominate (proportion of all studied forests: 72.9%) across all the target countries. More than half
289 of the investigated forests are managed by uniform clearcutting systems (51.9%, Cat. A2), and
290 approximately one-fifth by shelterwood systems (21%, Cat. A1). Uneven-aged systems, by
291 comparison, are employed to a far lesser degree. In our dataset 9.7% are managed using uneven-
292 aged systems (Cat. B), whereas coppice systems (Cat. C) are applied to 9.1% of forests. Only
293 8.3% of the forest included within the scope of our study is unmanaged or managed primarily for
294 non-timber objectives (Fig. 2, Supplement Table 4).

295 However, there is a marked difference between boreal and temperate countries (Supplement Fig.
296 1). Clearcutting systems (Cat. A2) are utilized across 85.9% of forests in the boreal zone, which
297 are predominantly coniferous. For the three boreal countries included in our dataset, all other
298 management methods represent minor components. Uneven-aged management is applied on only
299 4.2% of forests, whereas 8.7% are unmanaged. By comparison, in the temperate zone
300 shelterwood (Cat. A1), uneven-aged (Cat. B), and coppice systems (Cat. C) have higher ratios,
301 employed at 37.4%, 14.1%, and 16.4% of all forests, respectively (Fig 2, Supplement Table 4).
302 Within the temperate biome, however, dominant silvicultural systems vary by country. For
303 example, coppice and uneven-aged systems are more prevalent in France and Italy; shelterwood
304 systems are more common in Slovakia and Romania. This compares to Czech Republic,
305 Germany, Poland, Austria, and Hungary, where clearcutting and/or uniform shelterwood systems
306 are more widely represented. The majority of Slovenian forests are managed by irregular
307 shelterwood systems (Supplement Fig. 1).

308



309

310

311 Fig. 2 Silvicultural systems used by target European countries.

312

313

314 **3.2 Frequencies, spatial attributes, and severities of natural disturbances in European**
 315 **forests**

316

317 The literature review (Supplement X) revealed that disturbance sizes, frequencies and severities
 318 in European temperate and boreal forests are highly variable across space and time (Table 2).
 319 Small, aggregated canopy openings, where gap size usually does not exceed 200 m² (Mountford
 320 et al. 2001, Kuuluvainen and Aakala 2011) most commonly are of low severity, with less than
 321 20% of the canopy removed (Nagel et al. 2014, Hobi et al. 2013). Individual low severity,
 322 diffuse disturbance events affect larger spatial extents, as is the case, for example, with the low

323 severity fires typical in boreal forests and low severity ice storms in temperate Europe. The total
 324 area of scattered canopy openings, tree mortality, and tree damage for an event may range from
 325 200 m² to 100 ha. Return intervals for low severity, diffuse disturbances are relatively short,
 326 ranging between 10-100 years. Intermediate severity wind and ice storms, having return intervals
 327 of approximately 100-500 years (Nagel et al. 2014, 2017), generate a diverse mosaic with 25-
 328 75% canopy loss (Nagel et al. 2014, Čada et al. 2020) suggesting a very broad range of
 329 variability. Disturbance patches resulting from intermediate severity disturbances are irregularly
 330 structured (i.e. often having variable residual tree survivorship densities and patterns) and range
 331 in size from 200 m² up to 10 ha (Kuuluvainen and Aakala 2011, Kameniar et al. 2021). Stand-
 332 replacing, high severity events are rare, returning at intervals usually of more than 300-500 years
 333 (Aakala 2018, Nagel et al. 2014). However, severe disturbances in mountain ecosystems, like in
 334 the conifer forests of the Carpathians, can have rotation periods as short as 174 years (Čada et al.
 335 2016). The size of such disturbance areas varies widely, ranging from 1 up to thousands of
 336 hectares (Kuuluvainen and Aakala 2011).

337

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

Disturbance type	Size (m²)	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

339

340

341

3.3 Congruence of silvicultural systems with natural disturbances

342

343 We identified a low congruence of silvicultural systems with natural disturbance regimes,
 344 referring to the attributes size, frequency, and residual structure (Table 3, Table 4, Fig. 3, Fig. 4).
 345 With an average CI of 0.07 (7% congruence), clearcutting and shelterwood systems had the

346 lowest congruence with natural disturbances, followed by coppice systems (on average 13 %).
347 Uneven-aged systems were most similar to natural disturbances (on average 53 %) among all
348 silvicultural systems investigated.

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

354 Ellipsoids – representing the attribute space occupied by a given disturbance type or silvicultural
355 system relative to the three axes – for clearcutting and shelterwood systems had large
356 overlapping zones (Fig 3, Fig 4 A, B, C). The mean harvest sizes of these systems (2.84, 3.72 ha
357 respectively, Table 3) were intermediate between the mean size of low severity aggregated and
358 diffuse natural disturbances, however their return intervals were higher (100 years). The even-
359 aged management systems overlapped with coppice systems in the size to residual structure
360 comparison. Ellipsoids of uneven-aged systems are detached from the three other silvicultural
361 systems on each plot, but were often close to, or overlapping with, low severity aggregated
362 natural disturbances (Fig. 3, Fig. 4 A, B, C).

363 The 2D plots add more detail to the relationship between natural disturbance and silvicultural
364 systems (Fig. 4). The size-frequency plot shows an overlap of the ellipsoids of uneven-aged
365 systems and low severity aggregated disturbance, indicating that uneven-aged systems are partly
366 within the range low severity aggregated disturbance. Coppice systems, and, to some degree,
367 even-aged silviculture systems, overlapped with low severity diffuse disturbance (Fig 4 A). We
368 found the highest congruence between uneven-aged forestry and natural disturbance for size
369 relative to frequency, and frequency relative to size with CIs of 0.5 and 0.79 (i.e., 50 % and 79 %
370 congruency), respectively (Table 4). CI values of other silvicultural systems ranged from 0.1 to
371 0.4 (i.e., 10% to 40% congruence with natural disturbance). Lowest CI values (i.e., the largest
372 divergence) were detected for size relative to residual structure and frequency relative to residual
373 structure (Fig 4 B, C). In particular, CI values for even-aged and coppice systems were only 0.01
374 or smaller. Further, these silvicultural systems diverged strongly from natural disturbance
375 comparing residual structure relative to size and residual structure relative to frequency (Fig 4 B,
376 C) with CIs of 0.03 and 0.06, respectively. In contrast with CIs of 0.7 and 0.8 uneven-aged
377 systems were considerably more similar to natural disturbance in the same pairwise comparisons.

378

379

380

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

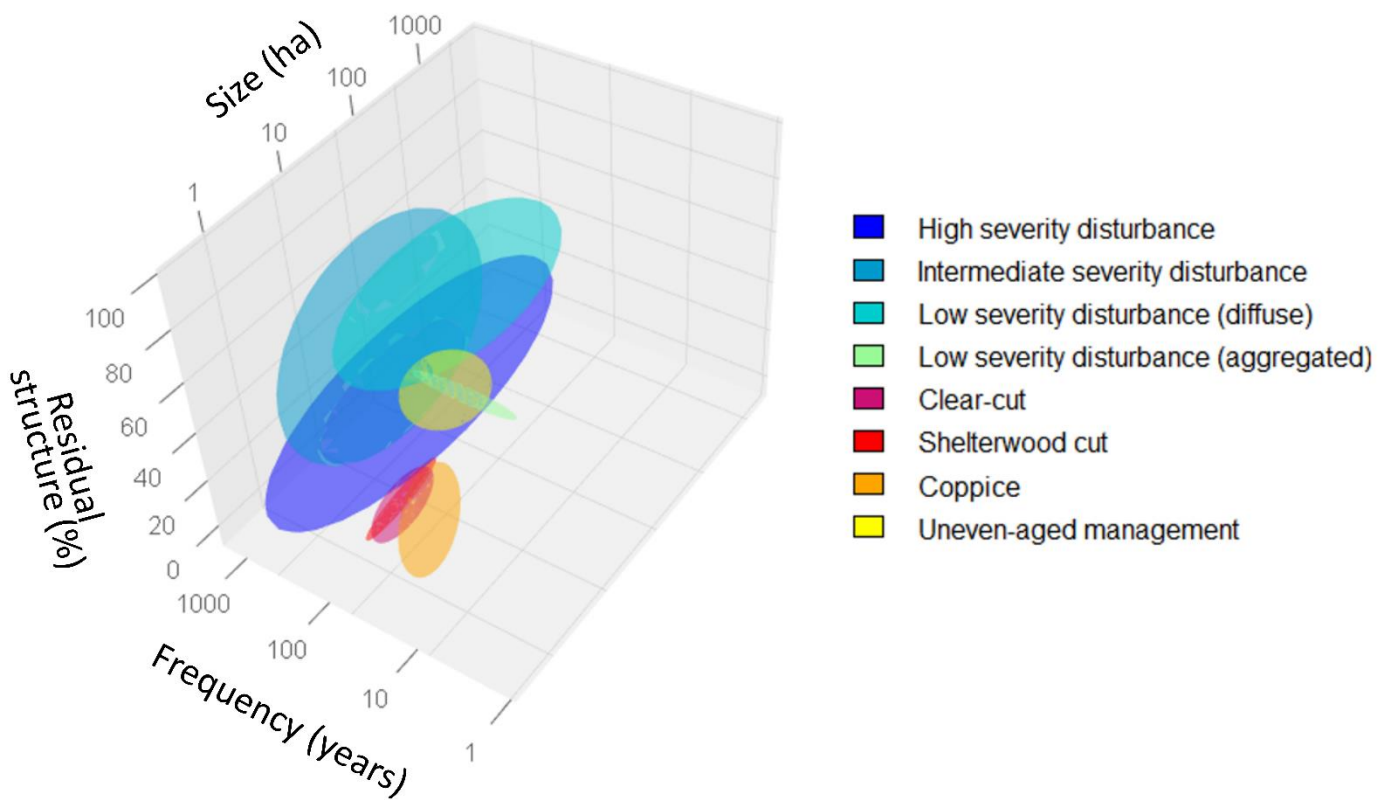
Silvicultural system	Size (ha)	Frequency (years)	Residual structure (%)
A1 Shelterwood system	3.72	103.98	1.56
A2 Clearcutting system	2.84	91.42	1.89
B Uneven-aged system	0.12	8.36	78.70
C Coppice system	3.27	48.04	1.66
Natural disturbance			
High severity	500.50	575.00	12.50
Intermediate severity	50.01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

383

384 Table 4. Comparability Index (CI) values, representing the congruence between silvicultural
 385 systems and natural disturbance regimes. As shown in Fig. 4, each attribute (size, frequency, and
 386 residual structure) was assessed relative to another attribute to derive the CI values, measuring
 387 the distance from the centroids to the CL. The final row of the table presents the average CI
 388 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

389

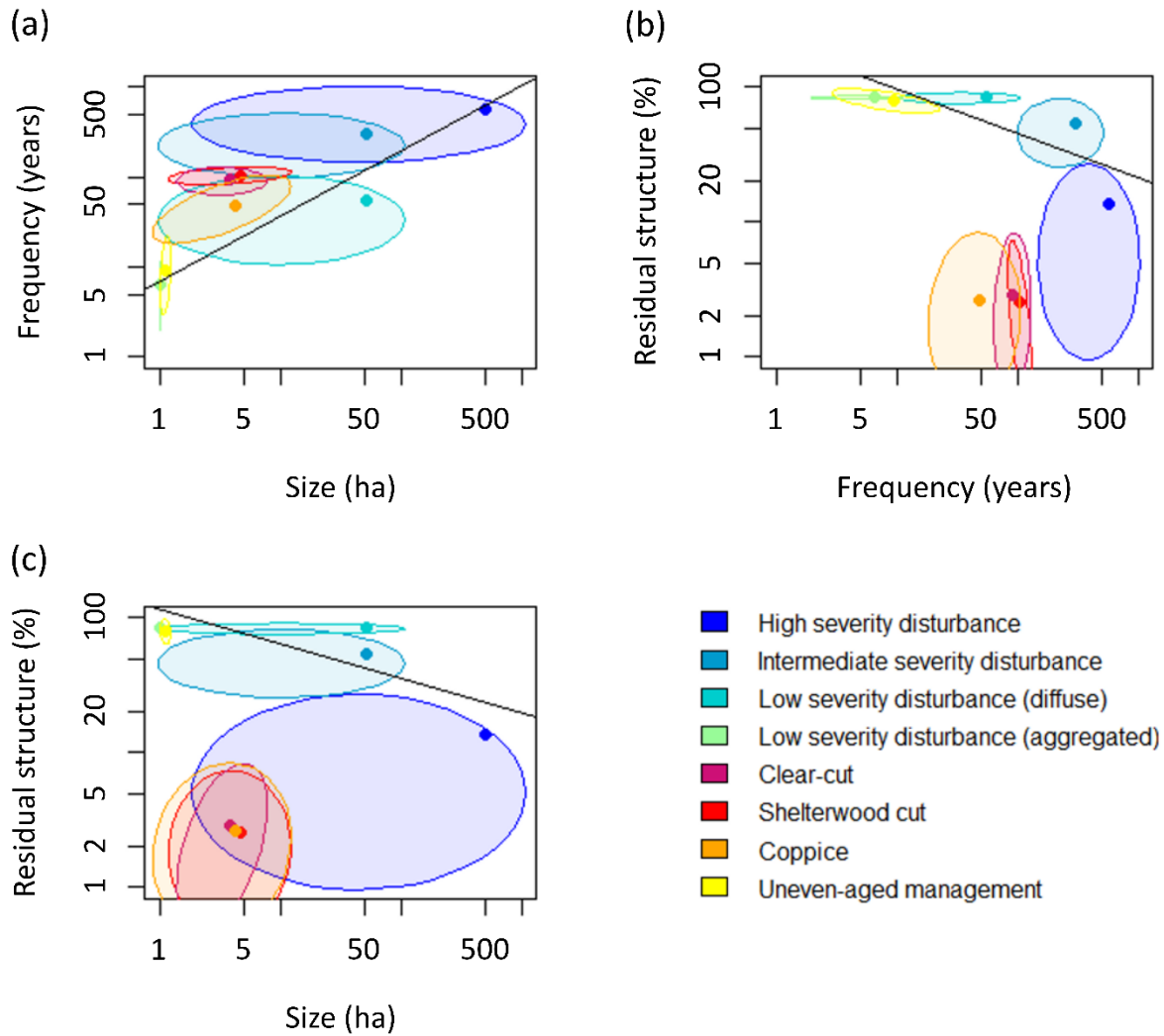


390

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

394

395



396
 397 Fig 4. Size, frequency, and residual structure attributes for natural disturbance regimes and
 398 silvicultural systems in Europe. Shown are: (a) size and frequency; (b) frequency and residual
 399 structure; and (c) size and residual structure comparisons. Dots indicate the centroids of natural
 400 disturbance types and silvicultural systems. The CL is based on the centroids of all the natural
 401 disturbance types assessed. Axes were log+1 transformed.

402

403 3.4 Silvicultural systems applied to four of the most common European forest types

404

405 The total forest cover of the 13 target countries – without the Mediterranean forests and short-
 406 rotation systems – is approximately 109 M hectares (109 298 966 hectare) based on assessment.

407 According to the national forest management data we examined (Supplement Table 3), the

408 forested area of the three boreal countries (Sweden, Finland and Latvia) accounts for 44% of this
409 total, and the 10 temperate countries encompass the remaining 56%.

410 In Norway spruce and Scots pine forests, the primary management system is even-aged with
411 clearcutting system, applied to 68.9% and 78.1% of the area respectively (Table 5). Less than
412 one fifth of these two forest types is managed by shelterwood systems across all of the 13 target
413 countries. However, in temperate Norway spruce stands, shelterwood cutting has the highest
414 representation among silvicultural systems (45.1%), and uneven-aged methods, such as single-
415 tree and group selection, are also common (24.7%) (Table 5). The majority of European beech
416 and oak dominated forests are managed with shelterwood systems (67.7% and 48.9%
417 respectively), indicating that natural regeneration (advanced regeneration) and subsequent
418 release through overstory removal are the typical silvicultural techniques applied to these forest
419 types. Beech dominated forests have a fairly high ratio of uneven-aged management on
420 European scale and in the temperate countries, nearly 20% of beech forests in our dataset are
421 managed with selection methods on both scales. One-third of temperate oak dominated forests
422 are managed with a variety of coppice systems (Table 5, Supplement Fig. 2).

423

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

426

	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Fagus sylvatica</i>	<i>Quercus sp.</i>	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

427

428

429

430 **4. DISCUSSION**

431

432 **4.1 Significance of the residual structure axis**

433

434 Based on our findings, the majority of European forests are managed outside the range of their
435 natural disturbance regimes, showing low congruences with past and present natural
436 disturbances. While previous studies have described natural disturbance regimes according to
437 their size, frequency, and severity ranges (Turner et al. 1998, Bergeron et al 2010), ours is among
438 the first to populate this framework with real data for both forest management and disturbances.
439 The expanded framework employed in our study defines the critical third axis, severity, as
440 percent residual canopy structure left on a site following management or disturbance. Adding
441 this third axis to the forest disturbance conceptual model significantly improved the basis for
442 comparison and proved critical in understanding incongruences. Silvicultural systems in Europe,
443 excepting selection systems, typically retain very low densities of biological legacies, such as
444 residual live, dead, and downed trees, either dispersed or aggregated. Our model incorporated
445 only residual living trees – but even this resulted in high divergence from natural dynamics.

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

462 through the European forest disturbance regimes as reference line. Using the expanded index,
463 forest managers can determine the divergence of a given harvesting regime from natural
464 disturbance dynamics.

465

466 4.2 Uneven-aged silvicultural systems are most similar to natural disturbances

467

468 The vast majority of the 109 million ha of temperate and boreal forests included within the scope
469 of this study are managed under even-aged systems, having only 7% congruence with natural
470 disturbances on average. Uneven-aged systems had the highest CI values, with 53% similarity to
471 natural disturbances, but this silvicultural system constitutes only approximately 10% of all
472 human management of the investigated forest land. The 3-dimensional ellipsoid for uneven-aged
473 forest systems occupied an attribute space close to the ellipsoids for natural disturbances,
474 whereas the three other silvicultural systems were located well outside the range of natural
475 disturbances. Clearcutting and shelterwood systems had the lowest CI in almost all comparisons,
476 coppice systems was intermediate, and uneven-aged system had the highest CI values in all
477 paired comparisons. Using only axes for size and frequency, and disregarding structural
478 complexity, the similarity of silvicultural systems with natural disturbances was markedly
479 higher. However, both size and frequency attributes for clearcut, shelterwood, and coppice
480 systems exhibited large departure with the residual structure axis included, with CI values
481 dropping to only 0.01 or less congruence with natural disturbances.

482 This analysis clearly showed that Europe's natural disturbance regimes have great complexity
483 and variability across the multiple dimensions of spatial extent, frequency, and severity. In
484 contrast, forest management perpetuates a landscape-scale condition incorporating little of this
485 diversity (Angelstam et al. 1998?). This mismatch has been noted in other regions of the world
486 subject to intensive forest management practices as well (Bergeron et al 2010, Messier et al.
487 2013).

488

489 4.3 Congruence of natural disturbance and human management for Europe's four most 490 dominant forest types

491

492 The relative merits of intensive forest management, such as high yield, even-aged forestry
493 practices, has been the subject of debate in Europe as in any parts of the world (Bollan and

494 Braunisch 2013; Schulze et al. 2014). Points of contention include tradeoffs among economic
495 efficiency, hydrologic regulation, abiotic disturbance risks, susceptibility to insects and
496 pathogens, carbon uptake and storage, and habitat provisioning (Mikolas et al. 2014, Burrascano
497 et al. 2016). In this context comparison with natural disturbance analogues is particularly
498 informative, for instance in developing forest management approaches that integrate competing
499 objectives (Franklin et al. 2018; Schall et al. 2020). We found that even-aged management with
500 clearcut regeneration harvesting is the most prevalent system in the boreal zone of Europe, and
501 yet has results in very low (7%) congruence with natural dynamics. Primary or unmanaged
502 boreal Norway spruce forests are dominated by finely-scaled, low severity aggregated gap
503 openings, together with less frequent intermediate severity disturbance events (Caron et al. 2009,
504 Aakala et al. 2009, Aakala et al. 2011, Khakimulina et al. 2016). Boreal Scots pine stands also
505 experience mixed-severity fire disturbances, leaving irregular age-class structures and high
506 amounts of deadwood in a variability distributed spatial pattern (Niklasson and Granström 2000,
507 Wallenius et al. 2010, Aakala 2018, Rhyzkova et al. 2020). Natural disturbance effects contrast
508 starkly with the dominant forest management regimes of boreal pine and spruce dominated forest
509 types; these create mosaics of 2-10 hectare stands that are predominately even-aged, harvested
510 on 80-90 year rotations, and have extremely low volumes and densities of post-harvest residual
511 structure (i.e. biological legacies).

512 The temperate zone of Europe has a more diverse portfolio of harvest regimes, and consequently
513 the congruence with natural disturbances greatly varies between countries and forest types.
514 Forests dominated by Scots pine (more than half are in Poland), like the boreal zone, are
515 predominantly managed by clearcutting systems. Regional studies from the Carpathians, Rila
516 Mountains (Bulgaria), and Bohemia (Czech Republic) suggest that mixed-severity disturbance
517 regimes with wide variation of low to high disturbance severities historically operated in
518 temperate mountain spruce forests (Panayotov et al. 2011, Svoboda et al. 2014, Trotsiuk et al.
519 2014, Čada et al. 2016, Janda et al. 2017). This variability is not emulated by contemporary
520 forest management (Citations). And yet, almost 25% of temperate Norway spruce stands are
521 managed by uneven-aged systems, having 53% similarity to natural processes, which suggests
522 that the management of this forest type has the largest congruence with natural disturbances. On
523 the other hand, Norway spruce has been planted widely outside its natural distribution in
524 temperate Europe (Caudullo et al. 2016). These stands are highly susceptible to climate change
525 and bark beetle outbreaks; foresters have responded by salvaging or “sanitary cutting” thousands
526 of hectares of beetle or wind disturbed forests in recent decades (Schelhaas et al. 2003, Thom et
527 al. 2013, Seidl et al. 2014, Hlásny et al. 2019). Beech dominated forests are usually managed

528 with even-aged shelterwood systems, but on 20% uneven-aged silviculture is applied, emulating
529 more closely the pattern created by the low severity aggregated disturbances (gap dynamics)
530 associated with beech forests (Schuck et al. 1994, Emborg et al. 2000, Standovár and Kenderes
531 2003, Kral et al. 2014). However, intermediate and mixed severity disturbances are also common
532 in beech-dominated forests (Splechtna et al. 2005, Nagel et al. 2014, 2017), and these are not
533 well emulated by the present harvest system of Europe based on our results. Natural dynamics
534 for oak forests in Europe are difficult to separate from anthropogenic influences, as the latter
535 have shaped the oak-zone landscapes since pre-historic times (Vera 2000, Bobiec et al. 2018).
536 Lacking robust natural reference stands, researchers have only a limited understanding natural
537 regeneration and stand dynamics in European oak forests (Kohler et al. 2020). Light demanding
538 oak species (*Quercus pubescens*, *Q. robur*, *Q. petraea*) require open habitats resulting from of
539 poor site productivity or strong human/natural disturbances that enhance natural regeneration
540 (“oakspace” see Bobiec et al. 2018). In the contrast to their natural regeneration strategy, much
541 of the contemporary oak management employs closed coppice and high forest systems which
542 have very low congruence with natural dynamics for this forest type.

543

544 4.4 Natural dynamics silviculture

545

546 The comparative framework and index presented in this paper are intended as a reference to help
547 guide “natural dynamics silviculture,” including retention forestry approaches (see, for example,
548 Mori and Kitagawa 2014; Puettmann et al. 2015, Gustafsson et al. 2019). Natural dynamics
549 silviculture has the objective of emulating natural disturbance dynamics to better provide the
550 environmental conditions to which organisms are evolutionarily adapted (Aplet and Keeton
551 1999, Franklin et al. 2007, Keeton 2007). In some cases, provisioning of ecosystem services,
552 such as carbon storage and hydrologic regulation, may be a co-benefit (Ford and Keeton 2018).
553 A further goal is to enhance resilience to global change (through adaptive capacity) by providing
554 a broader array of plant functional traits and functional complexity in managed forests (Messier
555 et al. 2013, Thom et al. 2019, 2020). This is compared to the trait and functional diversity
556 representation offered by more intensive management practices, such as short rotation, even-
557 aged forestry, which tend to simplify and homogenize forest stands and landscapes (Fahey et al.
558 2018).

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

561 2006, Franklin et al. 2007, Krumm et al. 2020). But there are key differences. In North America,
562 ecological forest management increasingly looks to baselines provided by primary (i.e. never
563 cleared by humans) forests, comparing forest dynamics driven by natural disturbances (e.g.
564 wind, fire, insects, floods) with the impacts of different forest harvesting approaches (Franklin et
565 al. 2002, Keeton 2006, Fahey et al. 2018, Keeton et al. 2018, Thom and Keeton 2019). In Europe
566 interest in ecological forestry is also high (e.g. Bauhus et al. 2009, Pretzsch et al. 2017), but the
567 common European approaches, variably termed “close-to-nature,” “Plenterwald”, or “Pro Silva”
568 are quite different, being primarily modifications of conventional selection systems (Johann
569 2006, Brang et al. 2014). They are used primarily for either conversion cutting in spruce
570 plantations – promoting replacement by endemic mixed species or deciduous forest types – or as
571 uneven-aged management (e.g. the “Plenterwald” and “Dauerwald” systems) in European beech
572 (*Fagus sylvatica*) and other temperate deciduous or mixed species forest types. Close-to-nature
573 silviculture, as commonly practiced, only partially replicates natural disturbance effects (Diaci
574 2006, Schutz et al. 2016), because it rarely maintains irregular age-class structure or retention
575 trees within patches and often neglects the dead wood (both standing and downed) component of
576 structural complexity. It does provide a mosaic of structurally variable patches as well as tree
577 age class diversity at the aggregate or stand scale. Moreover, in parts of Central Europe
578 deliberate efforts have been made to incorporate natural processes observed in old-growth stands
579 (Kraus and Krum 2013, Schutz et al. 2016), such as retention of downed woody debris and other
580 structures (Johann 2006). For example, research of the old-growth forest reserves has constantly
581 helped the development of flexible irregular shelterwood system in Slovenia, by defining unique
582 combinations of forest sites, stands, and social environments (see Diaci 2006, Boncina 2011).
583 The potential to incorporate a broader range of dynamics and structures, including old, dead, and
584 downed trees, based on research on natural disturbance effects is true both for European even-
585 aged and continuous cover forest management (Kern et al. 2016).

586 Simplification and homogenization of European forests, for example through the widespread
587 planting of mono-specific *Picea abies* plantations across formerly diverse landscapes and on
588 non-endemic sites, is a well-documented phenomenon (Angelstam 1998, Björse and Bradshaw
589 1998, Keeton et al. 2013). This practice, implemented over centuries, has contributed to the high
590 susceptibility of some European forests to spruce bark beetle (*Ips typographus*) outbreaks as well
591 as forest dieback associated with fungal pathogens, such as root rots (e.g. *Armillaria sp.*;
592 *Heterobasidion annosum*). Also as a result of homogenization, European forests may be more
593 vulnerable to increased disturbance intensity and frequency associated with climate change
594 (Seidl et al. 2014), leading to interest in management to restore greater heterogeneity in forest

595 composition at landscape scales (Angelstam and Kuuluvainen 2004, Seidl et al. 2018).
596 Improved understanding of baseline disturbance dynamics – from both studies of reference
597 stands as well as dendrochronological reconstructions – could guide this endeavor (Bauhus et al.
598 2009, Paillet et al. 2010).

599

600 4.5 Management implications

601

602 We present this conceptual model to help inform silvicultural practices designed to more closely
603 emulate natural disturbance effects, and in so doing provide a broader range of ecosystem goods,
604 services, and habitats compared to conventional practices. The Comparability Line and
605 Comparability Index, which helps to compare natural and human disturbances, highlights the
606 importance of understanding the three main attributes of disturbances: size, frequency, and
607 severity. These must be considered jointly, both for understanding natural disturbance baselines
608 and while developing and testing ecologically-based, sustainable forest management practices in
609 Europe.

610 Natural disturbances create much broader range of variability for all the three attributes as
611 compared to human disturbances. Forest practitioners could approximate the Comparability Line
612 at any point of the continuum represented by the ranges of variability for the three attributes.
613 However, to apply the entire range of disturbance processes to a landscape heavily altered by
614 millennia of land-use history will be challenging. For example, intermediate and mixed-severity
615 disturbances play a formative structuring role in many European forest types (Svoboda et al.
616 2014, Trotsiuk et al. 2014, Khakimulina et al. 2016, Nagel et al. 2017, Aakala 2018, Čada et al.
617 2020). However, emulation of intermediate and mixed-severity disturbances, with broad range of
618 age classes and high level of biological legacy needs will require a fundamental change in forest
619 practices. Advances in multi-cohort and retention silvicultural practices in North America,
620 derived from efforts to emulate natural disturbance regime, may prove informative in this regard
621 (Harvey et al. 2002, North and Keeton 2008, Long 2009). The forestry community's perceptions
622 of the role of natural disturbances are also vital (Nagel et al. 2017). Foresters will need to feel
623 comfortable emulating certain aspects of natural disturbance effects, such as deliberating
624 creating (or retaining following natural disturbances) variability in residual structure, both live
625 and dead, without defaulting always to sanitary cutting (Diaci et al. 2017).

626 Natural dynamics silviculture must incorporate deadwood management and tree retention to
627 decrease the divergence from natural disturbances by increasing the amount and type of

628 biological legacies (Krumm et al. 2020). The net amount of deadwood is considerably low in
629 European forests; according to the national reported values, the estimates at country level, for
630 both standing and lying deadwood range between 5 and 15 m³/ha for most countries (Europe,
631 Forest, 2015). However, effective deadwood management not only increases the amount, but
632 also considers/manipulates the size, position and arrangement, and decay stage of retained trees
633 (Vítková et al. 2018). As climate change intensifies bark beetle outbreaks, deadwood
634 management, tree retention, and disturbance-based forestry efforts should be harmonized with
635 bark beetle management strategies in forests most susceptible for bark beetle (Hlásny et al.
636 2019).

637

638 4.6 Limitation of the study

639

640 Human presence and influence on forest ecosystems has been continuous since the last ice age in
641 Europe. Hence the structure, composition, and natural dynamics of European forests have been
642 fundamentally altered across millennia. This particularly concerns certain forest types, like oak
643 dominated forests at lower elevations. Other forest types survived in small old-growth fragments,
644 often in places with low accessibility (Sabatini et al. 2018). These remnants provided only
645 limited capacity to reconstruct historical ranges of variability, particularly for landscape-scale
646 processes. Consequently, reconstructing or inferring baseline disturbance dynamics is fraught
647 with uncertainty, though dendrochronological approaches (Svoboda et al. 2012, Nagel et al.
648 2014, Čada et al. 2020) and retrospective modeling (Citation) are proving increasingly robust.
649 The Comparability Index presented here must be applied within this context, acknowledging
650 human influences our estimation of natural disturbance regime characteristics.

651 Disturbance regimes are changing rapidly (Turner 2010). Recent studies indicate a significant
652 increase in disturbance rates across Europe's natural and managed forests (Schelhaas et al., 2003,
653 Seidl 2014). However, it remains unknown how they will change in the future, and how they will
654 be affected by climate change. The strong yet complex linkage between natural and human
655 processes are already shaping the forested landscapes of Europe (Senf and Seidl 2020), making
656 the separation of human and natural dynamics very challenging.

657 Further research could strengthen the Comparability Index by incorporating more detailed
658 information (by forest type) on the amount and quality of deadwood, density of large trees,
659 intensity of the given management method, proportion of admixing species, and use of natural or
660 artificial regeneration.

661

662 **6. REFERENCES (not complete)**

663

- 664 Aakala, T., & Keto-Tokoi, P. (2011). The old Norway spruce forests of northern boreal Aakala
665 Fennoscandia are alive and well: A review of Sirén (1955). *Scandinavian journal of forest*
666 *research*, 26(S10), 25-33.
- 667 Aakala, T., Pasanen, L., Helama, S., Vakkari, V., Drobyshev, I., Seppä, H., ... & Holmström, L.
668 (2018). Multiscale variation in drought controlled historical forest fire activity in the boreal
669 forests of eastern Fennoscandia. *Ecological Monographs*, 88(1), 74-91.
- 670 Angelstam P, Kuuluvainen T (2004) Boreal forest disturbance regimes, successional dynamics and
671 landscape structures—a European perspective. *Ecol Bull* 51:117–136
- 672 Angelstam, P. K. (1998). Maintaining and restoring biodiversity in European boreal forests by
673 developing natural disturbance regimes. *Journal of vegetation science*, 9(4), 593-602.
- 674 Aplet, G.H. and W.S. Keeton. 1999. Application of historical range of variability concepts to
675 biodiversity conservation. Pages 71-86 in: R. Baydack, H. Campa, and J. Haufler (eds.). *Practical*
676 *Approaches to the Conservation of Biological Diversity*. Island Press, Washington, D.C. 313 pp.
- 677 Brang, P., Spathelf, P., Larsen, J. B., Bauhus, J., Bončina, A., Chauvin, C., ... & Lexer, M. J. (2014).
678 Suitability of close-to-nature silviculture for adapting temperate European forests to climate
679 change. *Forestry: An International Journal of Forest Research*, 87(4), 492-503.
- 680 Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. *Forest*
681 *Ecology and Management* 258:525–537.
- 682 Björse G, Bradshaw R (1998) 2000 years of forest dynamics in southern Sweden: suggestions for
683 forest management. *For Ecol Manag* 104:15–26
- 684 Bobiec, A., Reif, A., & Öllerer, K. (2018). Seeing the oakscape beyond the forest: a landscape
685 approach to the oak regeneration in Europe. *Landscape ecology*, 33(4), 513-528.
- 686 Boncina, A. (2011). Conceptual approaches to integrate nature conservation into forest management:
687 a Central European perspective. *International Forestry Review*, 13(1), 13-22.
- 688 Bollmann, K., & Braunisch, V. (2013). To integrate or to segregate: balancing commodity
689 production and biodiversity conservation in European forests. Integrative approaches as an
690 opportunity for the conservation of forest biodiversity. In: *Integrative approaches as an*
691 *opportunity for the conservation of forest biodiversity*, edited by: Kraus, D. and Krumm, F., EFI,
692 Joensuu, 18–31, 2013.
- 693 Brang, P., P. Spathelf, J. B. Larsen, J. Bauhus, A. Bončina, C. Chauvin, L. Drössler, C. García-
694 Güemes, C. Heiri, G. Kerr, M. J. Lexer, B. Mason, F. Mohren, U. Mühlethaler, S. Nocentini,
695 and M. Svoboda. 2014. Suitability of close-to-nature silviculture for adapting temperate
696 European forests to climate change. *Forestry* 87: 492–503.

- 697 Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luyssaert, S., Sabatini, F. M., & Blasi,
698 C. (2016). Current European policies are unlikely to jointly foster carbon sequestration and
699 protect biodiversity. *Biological Conservation*, 201, 370–376.
- 700 Čada, V., R. C. Morrissey, Z. Michalová, R. Bače, P. Janda, and M. Svoboda. 2016. Frequent severe
701 natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest
702 in central Europe. *Forest Ecology and Management* 363:169–178.
- 703 Čada, V., Trotsiuk, V., Janda, P., Mikoláš, M., Bače, R., Nagel, T. A., ... & Chaskovskyy, O. (2020).
704 Quantifying natural disturbances using a large-scale dendrochronological reconstruction to
705 guide forest management. *Ecological Applications*.
- 706 Caron, M. N., Kneeshaw, D. D., De Grandpré, L., Kauhanen, H., & Kuuluvainen, T. (2009, August).
707 Canopy gap characteristics and disturbance dynamics in old-growth *Picea abies* stands in
708 northern Fennoscandia: Is the forest in quasi-equilibrium?. In *Annales Botanici Fennici* (Vol.
709 46, No. 4, pp. 251-262). Finnish Zoological and Botanical Publishing Board.
- 710 Caudullo, G., Tinner, W., & de Rigo, D. (2016). *Picea abies* in Europe: distribution, habitat, usage
711 and threats.
- 712 Diaci, J. (2006). Nature-based silviculture in Slovenia: origins, development and future trends.
713 *Nature-Based Forestry in Central Europe*, 119.
- 714 Diaci, J., Rozenbergar, D., Fidej, G., & Nagel, T. A. (2017). Challenges for uneven-aged silviculture
715 in restoration of post-disturbance forests in central Europe: A synthesis. *Forests*, 8(10), 378.
- 716 Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov,
717 a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management* 126,
718 173-189.
- 719 Europe, Forest (2015). State of Europe's Forests 2015. Food and Agriculture Organization of the
720 European Nations, EFI. In Ministerial Conference on the Protection of Forest in Europe.
721 Disponible en: [http://www. foresteurope. org/state-europes-forests-2015-report](http://www.foresteurope.org/state-europes-forests-2015-report).
- 722 FAO. (2000). FRA 2000: On Definitions of Forest and Forest Change. Forest Resource Assessment
723 Programme Working Paper# 33.
- 724 Fahey, R.T., B. C. Alvsherea, J.I. Burton, A.W. D'Amato, Y.L. Dickinson, W.S. Keeton, C.C.
725 Kerne, A.J. Larson, B.J. Palik, K.J. Puettmann, M.R. Saunders, C.R. Webster, J.W. Atkins, C.M.
726 Gough, and B.S. Hardimani. 2018. Shifting conceptions of complexity in forest management
727 and silviculture. *Forest Ecology and Management* 421: 59-71
- 728 Fox, J., S. Weisberg, B. Price, D. Adler, D. Bates, G. Baud-bovy, B. Bolker, S. Ellison, D. Firth, M.
729 Friendly, S. Graves, R. Heiberger, P. Krivitsky, R. Laboissiere, M. Maechler, G. Monette, D.
730 Murdoch, D. Ogle, B. Ripley, W. Venables, S. Walker, D. Winsemius, A. Zeileis, and R-Core.
731 2019. Package 'car.'
- 732 Frank, G., & Parviainen, J. (2006). MCPFE information document on data collection and compiling
733 the statistics on protected and protective forest and other wooded land in Europe. Ministerial
734 Conference on the Protection of Forests in Europe, Liaison Unit. Warsaw
- 735 Franklin, J.F., K.N. Johnson, and D.L. Johnson. 2018. *Ecological Forest Management*. 646 pp.
736 Waveland Press, Inc. Long Grove, IL.

- 737 Franklin, J.F., Mitchell, R.J., Palik, B., 2007. Natural Disturbance and Stand Development Principles
738 for Ecological Forestry. US Department of Agriculture, Forest Service, Northern Research
739 Station. General Technical Report NRS-19.
- 740 Franklin, J.F., T.A. Spies, R. Van Pelt, A. Carey, D. Thornburgh, D.R. Berg, D. Lindenmayer, M.
741 Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and the structural
742 development of natural forest ecosystems with some implications for silviculture. *Forest
743 Ecology and Management* 155:399-423.
- 744 Gustafsson et al. 2019. **Ambio**
- 745 Gustafsson, L., S. C. Baker, J. Bauhus, W. J. Beese, A. Brodie, J. Kouki, D. B. Lindenmayer, A.
746 Lohmus, G. M. Pastur, C. Messier, M. Neyland, B. Palik, A. Sverdrup-Thygeson, W. J. A.
747 Volney, A. Wayne, and J. F. Franklin. 2012. Retention forestry to maintain multifunctional
748 forests: A world perspective. *BioScience* 62:6 33-645.
- 749 Harvey, B. D., Leduc, A., Gauthier, S., & Bergeron, Y. (2002). Stand-landscape integration in
750 natural disturbance-based management of the southern boreal forest. *Forest ecology and
751 management*, 155(1-3), 369-385.
- 752 Hlásny, T., Krokene, P., Liebhold, A., Montagné-Huck, C., Müller, J., Qin, H., ... & Viiri, H. (2019).
753 Living with bark beetles: impacts, outlook and management options (No. 8). European Forest
754 Institute.
- 755 https://www.foresteurope.org/docs/reporting/MCPFE_INFO_DOC_on_data_collection_on_Protected_forests.pdf
756
- 757 Janda, P., V. Trotsiuk, M. Mikoláš, R. Bače, T. A. Nagel, R. Seidl, M. Seedre, R. C. Morrissey, S.
758 Kucbel, P. Jaloviar, M. Jasík, J. Vysoký, P. Šamonil, V. Čada, H. Mrhalová, J. Lábusová, M. H.
759 Nováková, M. Rydval, L. Matějů, and M. Svoboda. 2017. The historical disturbance regime of
760 mountain Norway spruce forests in the Western Carpathians and its influence on current forest
761 structure and composition. *Forest Ecology and Management* 388:67–78.
- 762 Johann, E. (2006). Historical development of nature-based forestry in Central Europe. Nature-based
763 forestry in Central Europe. Alternatives to industrial forestry and strict preservation.
764 Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Ljubljana,
765 Slovenia, 1-17.
- 766 Kameniar, O., Baláž, M., Svitok, M., Reif, J., Mikoláš, M., Pettit, J. L., ... & Trotsiuk, V. Historical
767 natural disturbances shape spruce primary forest structure and indirectly influence bird
768 assemblage composition. *Forest Ecology and Management*, 481, 118647.
- 769 Ondrej Kameniar, Michal Baláž, Marek Svitok, Jiří Reif, Martin Mikoláš, Joseph L. Pettit, William
770 S. Keeton, Jessika M. Pettit, Ondřej Vostarek, Thomas Langbehn, Volodymyr Trotsiuk, Federico
771 Morelli, Michal Frankovič, Daniel Kozák, Pavel Janda, Vojtěch Čada, Matej Ferenčík, Jakub
772 Málek, Krešimir Begovič, Michal Synek, Jana Lábusová, Kristýna Svobodová, Miroslav
773 Svoboda,
- 774 Keeton, W.S. 2007. Role of managed forestlands and models for sustainable forest management:
775 perspectives from North America. *George Wright Forum* 24(3):38-53.

- 776 Keeton, W.S., P. Angelstam, M. Baumflek, Y. Bihun, M. Chernyavskyy, S. M. Crow, A. Deyneka,
777 M. Elbakidze, J. Farley, V. Kovalyshyn, B. Mahura, S Myklush, J. R. Nunery, I. Solovity, and
778 L. Zahvoyska. 2013. Sustainable forest management alternatives for the Carpathian Mountain
779 region, with a focus on Ukraine. Pages 331-352 in J. Kozak, K. Ostapowicz, A. Bytnerowicz,
780 and B. Wyzga (eds.) *The Carpathians: Integrating Nature and Society Towards Sustainability*.
781 Springer-Verlag, Berlin and Heidelberg, Germany.
- 782 Keeton, W.S., C. Lorimer, B. Palik, and F. Doyon. Silviculture for old-growth in the context of
783 global change. Pages 237-265 in: Barton, A. and W.S. Keeton (eds.). *Ecology and Recovery of*
784 *Eastern Old-Growth Forests*. Island Press, Washington, D.C. 340 pp
- 785 Kern, C. C., J. Burton, P. Raymond, A. D'Amato, W.S. Keeton, A.A. Royo, M.B. Walters, C.R.
786 Webster, and J.L. Willis. 2016. Challenges facing gap-based silviculture and possible solutions
787 for mesic northern forests in North America. *Forestry* 90: 4-17.
- 788 Khakimulina, T., Fraver, S., & Drobyshev, I. (2016). Mixed-severity natural disturbance regime
789 dominates in an old-growth Norway spruce forest of northwest Russia. *Journal of Vegetation*
790 *Science*, 27(2), 400-413.
- 791 Kohler, M., Pyttel, P., Kuehne, C., Modrow, T., & Bauhus, J. (2020). On the knowns and unknowns
792 of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.)
793 forests—a literature review. *Annals of Forest Science*, 77(4), 1-19.
- 794 Korpel, S., 1995. *Die Urwälder der Westkarpaten*. Gustav Fischer Verlag, Stuttgart.
- 795 Kraus D., Krumm F. (eds) 2013. Integrative approaches as an opportunity for the conservation of
796 forest biodiversity. European Forest Institute. 284 pp
- 797 Kral, K., McMahon, S.M., Janik, D., Adam, D., Vrska, T., 2014. Patch mosaic of developmental
798 stages in central European natural forests along vegetation gradient. *Forest Ecology and*
799 *Management* 330, 17-28.
- 800 Krumm, F.; Schuck, A.; Rigling, A. (eds), 2020: How to balance forestry and biodiversity
801 conservation – A view across Europe. European Forest Institute (EFI); Swiss Federal Institute
802 for Forest, Snow and Landscape Research (WSL), Birmensdorf. 640 p.
- 803 Kulakowski, D., R. Seidl, J. Holeksa, T. Kuuluvainen, T. A. Nagel, M. Panayotov, M. Svoboda, S.
804 Thorn, G. Vacchiano, C. Whitlock, T. Wohlgemuth, and P. Bebi. 2017. A walk on the wild side:
805 Disturbance dynamics and the conservation and management of European mountain forest
806 ecosystems. *Forest Ecology and Management* 388:120–131.
- 807 Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing
808 biological diversity in boreal Fennoscandia. *Silva Fennica*, 36(1), 97-125.
- 809 Kuuluvainen, T., and R. Grenfell. 2012. Natural disturbance emulation in boreal forest ecosystem
810 management — theories, strategies, and a comparison with conventional even-aged
811 management. *Canadian Journal of Forest Research* 42: 1185–1203.
- 812 Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a
813 checklist of strategies to guide forest biodiversity conservation. *Biological conservation*, 131(3),
814 433-445.

- 815 Long, J. N. (2009). Emulating natural disturbance regimes as a basis for forest management: a North
816 American view. *Forest Ecology and Management*, 257(9), 1868-1873.
- 817 Meigs et al. 2017. More ways than one: Mixed-severity disturbance regimes foster structural
818 complexity via multiple developmental pathways. *Forest Ecology and Management* 406: 410-
819 426.
- 820 Messier, C., K. Puettmann, and D. Coates. (2013). *Managing forests as complex adaptive systems:
821 building resilience to the challenge of global change*. Routledge, New York, NY.
- 822 Meyer, P., P. Janda, M. Mikoláš, V. Trotsiuk, F. Krumm, H. Mrhalová, M. Synek, J. Lábusová, D.
823 Kraus, J. Brandes, and M. Svoboda. (2017). A matter of time: self-regulated tree regeneration in
824 a natural Norway spruce (*Picea abies*) forest at Mt. Brocken, Germany. *European Journal of
825 Forest Research* 136:907–921.
- 826 Mikoláš, M. M. Svoboda, V. Pouska, R. C. Morrissey, D. C. Donato, W. S. Keeton, T. Nagel, V. D.
827 Popescu, J. Müller, C. Bässler, J. Knorn, L. Rozyłowicz, M. C. Enescu, V. Trotsiuk, P. Janda,
828 H. Mrhalová, Z. Michalová, F. Krumm, and D. Kraus. 2014. Comment on the “Opinion paper:
829 Forest management and biodiversity”: The role of protected areas is greater than the sum of its
830 number of species. *Web Ecology* 14:61–64.
- 831 Mikoláš, M. I. Gallay, J. Vysoký, M. Čiliak, M. Jasík, P. Polák, V. Trotsiuk, M. Svoboda, K. Ujházy,
832 G. Meigs, W.S. Keeton. 2019. Primary forest distribution and representation in a Central
833 European landscape: results of a large-scale field-based census. *Forest Ecology and Management*
834 449: 17466
- 835 Mori A.S. and R. Kitagawa. 2014. Retention forestry as a major paradigm for safeguarding forest
836 biodiversity in productive landscapes: A global meta-analysis. *Biological Conservation* 175: 65–
837 73.
- 838 Murdoch, D. 2020. Package “rgl.”
- 839 Müller, J., & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline for
840 management recommendations in European forests. *European Journal of Forest Research*,
841 129(6), 981-992.
- 842 Nagel, T. A., Svoboda, M., & Kopal, M. (2014). Disturbance, life history traits, and dynamics in an
843 old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24(4), 663-679.
- 844 Nagel, T.A., Mikac, S., Dolinar, M., Klopčič, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A.,
845 Paulic, V., 2017. The natural disturbance regime in forests of the Dinaric Mountains: A synthesis
846 of evidence. *Forest Ecology and Management* 388, 29-42.
- 847 Niklasson, M., & Granström, A. (2000). Numbers and sizes of fires: long-term spatially explicit fire
848 history in a Swedish boreal landscape. *Ecology*, 81(6), 1484-1499
- 849 North, M. P., & Keeton, W. S. (2008). Emulating natural disturbance regimes: an emerging approach
850 for sustainable forest management. In *Patterns and processes in forest landscapes* (pp. 341-372).
851 Springer, Dordrecht.
- 852 Panayotov, M., D. Kulakowski, L. L. Dos Santos, and P. Bebi. 2011. Wind disturbances shape old
853 Norway spruce-dominated forest in Bulgaria. *Forest Ecology and Management* 262:470-481.

- 854 Parviainen, J., & Frank, G. (2006). MCPFE information document on data collection and compiling
855 the statistics on protected and protective forest and other wooded land in Europe. In Ministerial
856 Conference on the Protection of Forests in Europe, liaison unit Warsaw, Warsaw.
- 857 Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, dynamics
858 and dendroecology of an old-growth *Fagus* forest in the Apennines. *Journal of Vegetation*
859 *Science* 16, 13-28. pp. 22–61.
- 860 Pretzsch, H., D.I. Forrester, and J. Bauhus (eds.). 2017. *Mixed-Species Forest: Ecology and*
861 *Management*. Springer-Verlag, Germany. 653 pp.
- 862 Puettmann, K. J., S. M. Wilson, S. C. Baker, P. J. Donoso, L. Drossler, G. Amente, B. D. Harvey,
863 T. Knoke, Y. Lu, S. Nocentini, F. E. Putz, T. Yoshida, and J. Bauhus. 2015. Silvicultural
864 alternatives to conventional even-aged forest management - what limits global adoption? *Forest*
865 *Ecosystems* 2:1-16.
- 866 Raymond, P., Bédard, S., Roy, V., Larouche, C., & Tremblay, S. (2009). The irregular shelterwood
867 system: review, classification, and potential application to forests affected by partial
868 disturbances. *Journal of Forestry*, 107(8), 405-413.
- 869 Ryzhkova, N., Pinto, G., Kryshen, A., Bergeron, Y., Ols, C., & Drobyshev, I. (2020). Multi-century
870 reconstruction suggests complex interactions of climate and human controls of forest fire activity
871 in a Karelian boreal landscape, North-West Russia. *Forest Ecology and Management*, 459,
872 117770.
- 873 Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Potzschner, F., Verkerk, P.J.,
874 Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horvath, F., Garbarino, M., Grigoriadis,
875 N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikolas, M., Motta, R.,
876 Mozgeris, G., Nunes, L., Panayotov, M., Odor, P., Ruete, A., Simovski, B., Stillhard, J.,
877 Svoboda, M., Szwagrzyk, J., Tikkanen, O.P., Volosyanchuk, R., Vrska, T., Zlatanov, T.,
878 Kuemmerle, T., 2018. Where are Europe's last primary forests? *Diversity and Distributions* 24,
879 1426-1439.
- 880 Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., ... & Gossner, M. M. (2020).
881 Can multi-taxa diversity in European beech forest landscapes be increased by combining
882 different management systems?. *Journal of Applied Ecology*, 57(7), 1363-1375.
- 883 Schelhaas, M.J., J. Fridman, G.M. Hengeveld, H.M. Henttonen, A. Lehtonen, U. Kies, N. Krajnc,
884 B. Lerink, Á.N. Dhubháin, H. Polley, T.A.M. Pugh, J.J. Redmond, B. Rohner, C. Temperli, J.
885 Vayreda, G.J. Nabuurs. 2018. Actual European forest management by region, tree species and
886 owner based on 714,000 re-measured trees in national forest inventories. *PLOS ONE* 13:
887 e0207151.
- 888 Schuck, A., Parviainen, J., Bücking, W., 1994. A review of approaches to forestry research on
889 structure, succession and biodiversity of undisturbed and semi-natural forests and woodlands in
890 Europe. European Forest Institute, Joensuu.
- 891 Schurman, J. S., V. Trotsiuk, R. Bače, V. Čada, S. Fraver, P. Janda, D. Kulakowski, J. Labusova,
892 M. Mikoláš, T. A. Nagel, R. Seidl, M. Synek, K. Svobodová, O. Chaskovskyy, M. Teodosiu,
893 and M. Svoboda. 2018. Large-scale disturbance legacies and the climate sensitivity of primary
894 *Picea abies* forests. *Global Change Biology* 24:2169–2181.

- 895 Schulze, E. D., Bouriaud, L., Bussler, H., Gossner, M., Walentowski, H., Hessenmöller, D., ... &
896 Gadow, K. V. (2014). Opinion paper: Forest management and biodiversity. *Web Ecology*, 14(1),
897 3-10.
- 898 Schutz, J.P., Saniga, M., Diaci, J., Vrska, T., 2016. Comparing close-to-nature silviculture with
899 processes in pristine forests: lessons from Central Europe. *Annals of Forest Science* 73, 911-
900 921.
- 901 Seidl, R. et al. (2014) Increasing forest disturbances in Europe and their impact on carbon storage.
902 *Nature Climate Change* 4: 806–810
- 903 Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., ... & Hansen, W.
904 D. (2020). Globally consistent climate sensitivity of natural disturbances across boreal and
905 temperate forest ecosystems. *Ecography*.
- 906 Senf, C., and R. Seidl. 2018. Natural disturbances are spatially diverse but temporally synchronized
907 across temperate forest landscapes in Europe. *Global Change Biology* 24:1201–1211.
- 908 Senf, C., & Seidl, R. (2020). Mapping the coupled human and natural disturbance regimes of
909 Europe's forests. *bioRxiv*.
- 910 Seymour, R. S., & White, A. S. (2002). Natural disturbance regimes in northeastern North
911 America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology*
912 *and Management*, 155(1-3), 357-367.
- 913 Seymour, R.S., Hunter, M.L., Jr., 1999. Principles of ecological forestry. In: Hunter Jr., M.L. (Ed.),
914 *Managing Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge,
- 915 Spiecker, H. (2003). Silvicultural management in maintaining biodiversity and resistance of forests
916 in Europe—temperate zone. *Journal of Environmental Management*, 67(1), 55-65.
- 917 Splachtna, B. E., Gratzer, G., & Black, B. A. (2005). Disturbance history of a European old-growth
918 mixed-species forest—A spatial dendro-ecological analysis. *Journal of Vegetation Science*,
919 16(5), 511-522.
- 920 Standovár, T., & Kenderes, K. (2003). A review on natural stand dynamics in beechwoods of East
921 Central Europe. *Applied ecology and environmental research*, 1(1), 19-46.
- 922 Svoboda, M., P. Janda, R. Bače, S. Fraver, T. A. Nagel, J. Rejzek, M. Mikoláš, J. Douša, K. Boublík,
923 P. Šamonil, V. Čada, V. Trotsiuk, M. Teodosiu, O. Bouriaud, A. I. Biriş, O. Sýkora, P. Uzel, J.
924 Zelenka, V. Sedlák, and J. Lehejček. 2014. Landscape-level variability in historical disturbance
925 in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. *Journal of*
926 *Vegetation Science* 25:386–401.
- 927 Svoboda, M., P. Janda, T. A. Nagel, S. Fraver, J. Rejzek, and R. Bace. 2012. Disturbance history of
928 an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. *Journal of*
929 *Vegetation Science* 23:86-97.
- 930 Szewczyk, J., J. Szwagrzyk, and E. Muter. 2011. Tree growth and disturbance dynamics in old-
931 growth subalpine spruce forests of the Western Carpathians. *Canadian Journal of Forest*
932 *Research* 41:938-944.

- 933 Szwagrzyk J, Gazda A. 2007. Aboveground standing biomass and tree species diversity in natural
934 stands of Central Europe. *J Vegetat Sci* 18: 563–570.
- 935 Thom, D., R. Seidl, G. Steyrer, H. Krehan, and H. Formayer. 2013. Slow and fast drivers of the
936 natural disturbance regime in Central European forest ecosystems. *Forest Ecology and*
937 *Management* 307:293–302.
- 938 Thom, D, Seidl, R. (2016): Natural disturbance impacts on ecosystem services and biodiversity in
939 temperate and boreal forests. *Biological Reviews*, 91: 760-781.
- 940 Thom, D, Rammer, W, Seidl, R (2017): The impact of future forest dynamics on climate: Interactive
941 effects of changing vegetation and disturbance regimes. *Ecological Monographs*, 87: 665-684.
- 942 Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., ... & Keeton, W.
943 S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest
944 age in boreal–temperate North America. *Global change biology*, 25(7), 2446-2458.
- 945 Thom, D., Taylor, A. R., Seidl, R., Thuiller, W., Wang, J., Robideau, M., & Keeton, W. S. (2020).
946 Forest structure, not climate, is the primary driver of functional diversity in northeastern North
947 America. *Science of The Total Environment*, 143070.
- 948 Trotsiuk, V., M. Svoboda, P. Janda, M. Mikolas, R. Bace, J. Rejzek, P. Samonil, O. Chaskovskyy,
949 M. Korol, and S. Myklush. 2014. A mixed severity disturbance regime in the primary *Picea*
950 *abies* (L.) Karst. forests of the Ukrainian Carpathians. *Forest Ecology and Management*
951 334:144–153.
- 952 Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91(10),
953 2833-2849.
- 954 Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors influencing succession:
955 lessons from large, infrequent natural disturbances. *Ecosystems*, 1(6), 511-523.
- 956 Vera FWM (2000) *Grazing ecology and forest history*. CABI Publishing, Wallingford.
- 957 Vítková, L., Bače, R., Kjučukov, P., & Svoboda, M. (2018). Deadwood management in Central
958 European forests: Key considerations for practical implementation. *Forest Ecology and*
959 *Management*, 429, 394-405.
- 960 Wallenius, T. H., Kauhanen, H., Herva, H., & Pennanen, J. (2010). Long fire cycle in northern boreal
961 *Pinus* forests in Finnish Lapland. *Canadian Journal of Forest Research*, 40(10), 2027-2035.
- 962 White, P. S., & Jentsch, A. (2001). The search for generality in studies of disturbance and ecosystem
963 dynamics. In *Progress in botany* (pp. 399-450). Springer, Berlin, Heidelberg.
- 964 Wolfslehner, B., and R. Seidl. 2010. Harnessing ecosystem models and multi-criteria decision
965 analysis for the support of forest management. *Environmental Management* 46:850–861.
- 966 Zielonka, T., J. Holeksa, P. Fleischer, and P. Kapusta. 2009. A tree-ring reconstruction of wind
967 disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. *Journal of*
968 *Vegetation Science* 21:31-42.
- 969
- 970

971 Supplement Table 1 – the Questionnaire

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

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Austria	<p>[1] : https://www.waldwissen.net/technik/inventur/bfw_altersklassen1_oewi/index_DE</p> <p>[2] : https://www.waldwissen.net/technik/inventur/bfw_altersklassen2_oewi/index_DE</p> <p><i>[1] and [2] are special reports from the results of the austrian forest inventory 2007-2009 (this is the latest inventory)</i></p> <p>[3] Austrian forest inventory – Online Database: http://bfw.ac.at/rz/wi.home Latest data from the inventory 2007-2009 was used</p> <p>[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</p> <p>[5] Austrian Forest Law: https://www.ris.bka.gv.at/GeltendeFassung.wxe?Abfrage=Bundesnormen&Gesetzesnummer=10010371 [in German]</p>
Czech Republic	<p>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</p>
Finland	<p>Kujala, M. 2017. The popularity of Different Harvesting Methods after The New Forest Act. Bachelor's thesis, Tampere University of Applied Sciences, 56 p</p> <p>Forest use declarations database of the Finnish Forest Centre</p> <p>Finnish National Forest Inventory 11/12</p>
France	<p>Expertise based on Maaf, I.G.N., 2016. Indicateurs de gestion durable des forêts françaises métropolitaines, édition 2015.</p> <p>ONF, 2017. Bilan patrimonial des forêts domaniales (hors DOM). Editions 2015. 250 p</p>

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

	<p>State Forest Service Statistics http://www.vmd.gov.lv/valsts-meza-dienests/statiskas-lapas/publikacijas-un-statistika?nid=1717#jump</p> <p>Maximum size set by regulations: https://likumi.lv/doc.php?id=253760</p> <p>Rotation minimal diameter set in regulations: https://likumi.lv/doc.php?id=253760</p> <p>Rotation age set in the Forest Law: https://likumi.lv/doc.php?id=2825</p>
Poland	<p>National Forest Inventory 2015</p> <p>Manual for Forest Management</p> <p>Principles of Silviculture</p> <p>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.</p> <p>Bureau for the Forest management and Geodesy 2012. Manual for Forest Management. Centrum Informacyjne Lasów Państwowych, Warszawa.</p> <p>General Directorate of the State Forests National Forest Holding 2012. Zasady Hodowli Lasu (Principles of Silviculture). Warszawa.</p> <p>Jaworski A. 2011. Hodowla Lasu (Silviculture). PWRiL, Warszawa</p> <p>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</p>
Romania	<p>Ministry of Waters and Forests (2018). State of Romanian forests in 2017</p> <p>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</p> <p>http://roifn.ro/site/rezultate-ifn-2/</p> <p>Romanian Technical Normatives (no. 3 and no. 5)</p>

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

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.

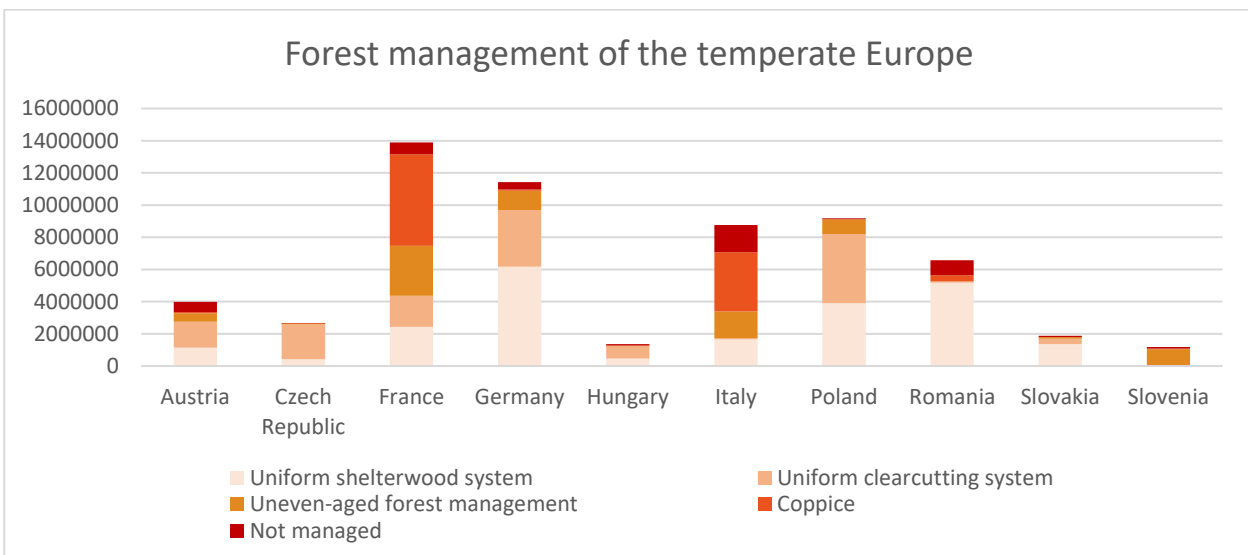
Surendra Joshi. 2017. Notified areas of final felling in 2016 Data from Statistiska meddelanden, JO0314 SM 1701 Surendra.joshi@skogsstyrelsen.se

Clas Fries, Jonas Bergquist, Peder Wikström. 2015. Lägsta ålder för förnygringsavverkning (LÅF) – en analys av följder av att sänka åldrarna i norra Sverige till samma nivå som i södra Sverige. Skogsstyrelsen, Rapport 6.

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

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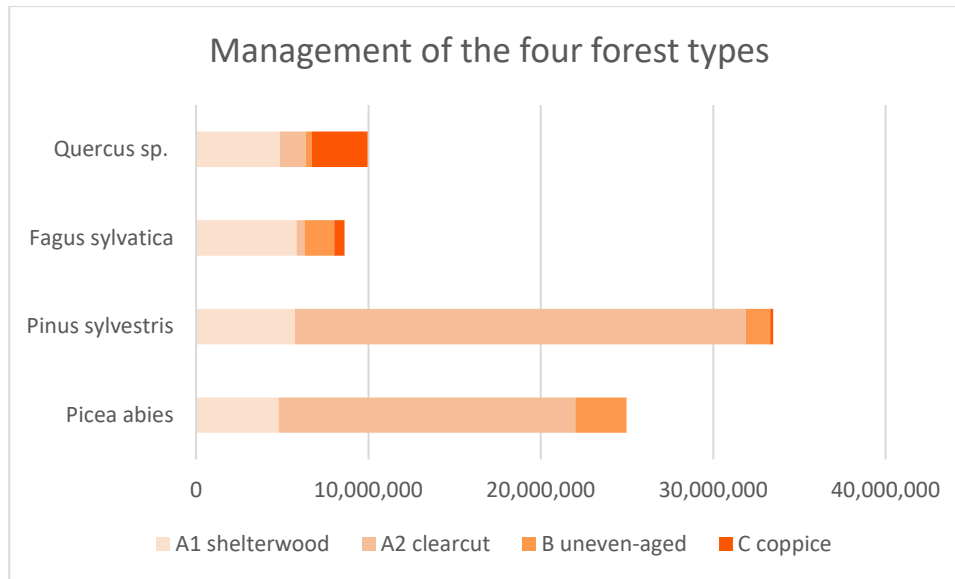
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979 Supplement Fig. 1 Forest management of the temperate Europe (if we need this fig, the same
980 colour palette should be used as Fig2)

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

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988 Supplement Table 4. Proportion of silvicultural systems across 13 target countries. Data are
989 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	

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993 Supplement Note 1 – literature review