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More wood but less biodiversity in forests in Finland: a historical evaluation

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National forest inventories (NFI) in Finland provide empirical evidence for a marked increase in tree growth, total forest area, and total timber volume over the past century. Meanwhile, the assessments of threatened forest species and habitats indicate continuous degradation of biodiversity in Finnish forests. To shed light on this seeming paradox, we summarized the temporal patterns of forest characteristics (indicators) that have major influence on biodiversity, comparing the structure of current Finnish forests with natural and historical references. Using a variety of data sources, we estimated the proportion of area of old-growth forest and of deciduous-dominated forests, the density of large trees, and the amount of dead wood in Finnish forests under natural reference conditions, in the 1750s, 1920s (NFI1), and 2010s (NFI12). Our results show that levels of the forest structures essential to maintain ecologically diverse forests are below those that likely prevailed in Finland under natural reference conditions and in the 1750s. This scarcity is particularly pronounced for dead wood volumes and old forest area. The marked increase in the volume of living trees during the last century did not translate into improved biodiversity indicators and has not been effective for turning the tide of biodiversity loss in Finnish forests. We discuss actions that are necessary to safeguard forest biodiversity in Finland both in terms of protected areas and management in production forest.

Introduction

The hundred years of forest inventories in Nordic countries provide an exceptional time series on forest resources and their structure, allowing researchers to assess long-term changes over large spatial scales. These data from Finland show that during the past century forest growth has doubled, average per hectare growing stock (FAO 2020) has increased >50%, and drainage of millions of hectares of peatlands has provided more productive forest area. As a result, the current volume of growing stock is 1.7 times the growing stock 100 years ago (Korhonen et al. 2021). Simultaneously, three quarters of the forest habitat types are threatened (Kouki et al. 2018, 2019),

there are more than 800 threatened species in Finnish forests, and forest-dwelling species is the largest group among all the threatened species (Hyvärinen et al. 2019). Moreover, the threat status of species has not improved between the two most recent assessments (2010 and 2019) and species are becoming more threatened in all habitats including forests (Hyvärinen et al. 2019). The paradox of having more wood but less biodiversity should be understood if we aim to sustainably manage forests.

Hundred years is still a short perspective to document forest history. To explore and understand this paradox, relevant time horizons are required that link natural forest successions to the impact of forest use. For example, human land use in the Nordic countries started many centuries ago, and therefore the changes we see in our forests over the past 100 years are contingent upon forest use during longer historical times.

To provide perspective regarding the changes in Finnish forests during the past 100 years, we compare their structure with those under natural reference conditions (no major human influence) and in 1750. The latter time point is used to assess threats and monitor the historical declines of ecosystems in the IUCN Red List of Ecosystems (IUCN 2015), and justified by the earliest onset of industrial-scale exploitation of ecosystems (Keith et al. 2013). In Finland, human population remained very low until the mid-18th century, after which population growth accelerated strongly. Simultaneously, slash-and-burn cultivation and human settlement expanded to more remote areas (Keto-Tokoi 2014a). Slash-and-burn cultivation, tar extraction, clearing forests for fields and meadows, and timber logging increased strongly, resulting in large-scale decline of primeval forests in the latter half of the 18th century and in the 19th century (Keto-Tokoi 2014a).

The early phases of intensive forest use were regionally highly variable. They had clear effects on forest characteristics, but these changes were most evident in southern Finland near the human population. Additionally, land clearing and slash-and-burn cultivation primarily affected the most fertile forest habitats first (Keto-Tokoi 2014a). Consequently, the forest landscapes in the late 1800s and early 1900s were quite heterogeneous and diverse, although the volumes of living trees were low in southern parts of the country. In fact, the historical analyses of forest use and timber supplies suggest that standing timber volumes were at a historical low in the early 1900s (Myllyntaus & Mattila 2002) when the Finnish national forest inventories (NFIs) began.

During the 1900s, intensive forest use expanded to even the most remote areas in northern Finland (Lihtonen 1949). Forest management and timber extraction occurred across all types of forests, regardless of their fertility or location (Kouki et al. 2001). This resulted in large-scale alteration of forest habitats. Forestry and management activities are the direct or indirect causes for changes in forest structure, threatening forest species (Hyvärinen et al. 2019) and habitats (Kouki et al. 2018). The major consequences of human use of forest resources are the decrease in old-growth forest area, number of large trees, amount of dead wood, and proportion of deciduous trees and deciduous-dominated forests, which are critical characteristics for biodiversity in boreal forests.

To understand the paradox of "more wood but less biodiversity", we explored the temporal patterns of forest characteristics that have major influence on biodiversity, comparing the structure of current Finnish forests with their structure in the past. We entitle these forest characteristics as forest biodiversity indicators. We evaluated these changes using the data produced by the Red List evaluation of forest habitat types in Finland and Finnish NFIs. Provided the regional differences in forestry history, we made this assessment separately for southern Finland (including hemiboreal, southern, and middle boreal zones) and northern Finland (northern boreal zone) which represent 15.2 and 5 million ha of total productive forest land area, respectively (productive forest land refers to land where the annual tree growth is more than one cubic metre per hectare). Our study is closely related to the Red List assessment of forest habitats in Finland by Kouki et al. (2018, 2019). To that assessment, our current study adds a longer time perspective (the NFIs were only used for the period of 1960s onward in Kouki et al. (2018), i.e., for the last 50 years) and uses natural forests as a reference point to explore habitat changes (the farthest historical reference point in Kouki et al. was the year 1750). In

addition, we are not aiming at a habitat type level analysis. Instead, we explore more thoroughly the overall country-level patterns from the natural state through 1750s to the 1920s, and finally, during the 100-year period that is covered by the NFIs, i.e., by comparing NFI1 (1920) and NFI12 (2014-2018).

Data and methods

Using a variety of data sources, we estimated the proportion of area of old-growth forest and deciduous-dominated forests, the density of large trees, and the amount of dead wood (Table 1). Site fertility and successional stage are strong drivers of the development of these forest features, of human use of forest resources, and of the historical distribution of natural forests. Therefore, the forest biodiversity indicators were estimated considering the observed or estimated proportion of various forest habitat types. We used the forest habitat classification from the Red List, which includes 15 heath forest habitat types (Kouki et al. 2018). The classification was based on site-fertility class (herb-rich heath, mesic, sub-xeric, xeric and barren heath forests), successional stage (young, mature and old), and partly on dominant tree species (conifer- vs. deciduous-dominated). We concentrated on the 12 major habitat types of heath forests, excluding the barren and considering deciduous-dominated heath as conifer-dominated forests. These exceptions cover only 3.2% of all heath forests in Finland according to NFI 11 (2009–2013, background data of Kouki et al. 2018).

Table 1. Overview of the different data sources used to compile the historic reference levels and the present situation as measured in the national forest inventory (NFI12). For the data, we concentrate on the 12 major heath forest habitat types (out of 15, Kouki et al. 2018).

Forest characteristics (biodiversity indicators)	Natural reference	1750s	NFI1 (1921–1924)	NFI12 (2014–2018)
Share of old-growth forest area (> 150 years)	Covering between 50% – 95% of the area; here, a conservative estimate of 50% was adopted (Berglund & Kuuluvainen 2021)	Estimates for southern and northern Finland (Kouki et al. 2018) based on historical maps of natural forests (Keto-Tokoi, 2014b) and on the age-class distribution suggested by the review of Berglund & Kuuluvainen (2021)	Percentage share of forests older than 160 years for NFI1 (due to coarser age class reporting for northern Finland) and 150 years for NFI12	
Share of deciduous-dominated forests	• In mesic & herb-rich heath forests all young forests and 50% of mature forests are deciduous-dominated and all old forests are conifer dominated • Forests on less fertile soils are conifer dominated irrespective of age (Berglund & Kuuluvainen 2021) • Relative share of site-fertility classes: NFI5 (1964–1970) (Kouki et al. 2018)	No estimates available	Values for whole Finland	
Number of large living trees	• Southern Finland: research data from natural forests (Kouki et al. 2018) • Northern Finland: research data from natural forests and data of NFI1 (1921–1924) (Kouki et al. 2018)	Estimates of Kouki et al. (2018); based on values for natural reference conditions, adjusted to reflect the distribution of natural forests and climatic conditions in 1750; 75% of natural reference in North, and 25% in South	Estimates of Henttonen et al. (2019); with threshold values of diameter at breast height >40 cm for South, and >30 cm for North	
Amount of dead wood	Research data from natural forests (Kouki et al. 2018)		Dead wood has been monitored from NFI9 (1996–2003) onwards; NFI9 data were used in place of NFI1	

Natural reference conditions

Berglund and Kuuluvainen (2021) estimated the natural reference conditions of boreal forests in northern Europe, indicating that old forests (at least 150 years old) were a prevalent or even dominant age-class, typically covering between 50% and 95% of the area. We adopted a conservative estimate of 50%. The remaining forest area was divided between young and mature forests following the age-class classification in Kouki et al. (2018): young forests (<40 years) covering 13% of the forest area, mature forests (40–150 years) covering 37%.

For the percentage share of deciduous-dominated forests we adopted the age distribution from Berglund and Kuuluvainen (2021) and assumed that in mesic and herb-rich heath forests all young forests and 50% of mature forests are deciduous-dominated, and that all old forests are conifer dominated. Forests on less fertile soils are assumed to be conifer-dominated irrespective of forest age. Eutrophication has changed the relative share of different site-fertility classes from 1960s onwards and thus, their shares under natural reference conditions were approximated using the data of the fifth NFI (1964–1970; see Kouki et al. 2018).

The densities of large living trees by each habitat types are based on empirical data from natural forests (Ilvessalo 1937, Rouvinen & Kouki 2002, Rouvinen & Kuuluvainen 2005, Aakala et al. 2009, Kreutz et al. 2015, Aakala et al. 2016, Punttila & Siitonen unpublished data), and, additionally, the data of the first NFI (1921–1924) in northern Finland as explained in Kouki et al. (2018). There is very little information on the densities of surviving large trees after wildfires in early successional stages. For this, it was assumed that the variation in the number of large trees depends on site fertility and, consequently, density of large trees in early successional forests decreases with increasing site fertility (see Kouki et al. 2018).

Similarly, the assessment of the amount of dead wood in the habitat types under natural reference conditions is based on data from natural forests (Siitonen 2001, Karjalainen & Kuuluvainen 2002, Rouvinen et al. 2002; Gibb et al. 2005; Rouvinen et al. 2005; Dahlström & Nilsson 2006; Ekbom et al. 2006; Ylläsjärvi & Kuuluvainen 2009; Aakala 2010; Josefsson et al. 2010; Ylisirniö et al. 2012) also considering site-fertility class and location (see Kouki et al. 2018). Estimates for the density of large trees and amount of dead wood were calculated as weighted mean values across age and site-fertility classes.

Forests and their structures in the 1750s

We used the share of old-growth forests in the 1750s estimated by Kouki et al. (2018). For that, they combined the historical distribution of natural forests from Keto-Tokoi (2014b) with site-fertility classes in different parts of Finland, and their varying likelihood of being used for slash-and-burn cultivation (Kouki et al. 2018). Information on tree species composition in Finnish forests is not available before NFIs started in 1920s, and thus we could not provide an estimate for the percentage share of deciduous-dominated forests in 1750s.

The densities of large trees and dead wood volumes were estimated by Kouki et al. (2018). Their estimation relied on corresponding values for forests under natural reference conditions for different site-fertility classes and successional stages (see above). Their approach makes the conservative assumption that dead wood and large trees were completely missing outside natural forests owing to human impact. Further, the expected amount of dead wood and large trees in natural forests was adjusted by a factor of 0.75 due to lower temperatures during the Little Ice Age (from ca. 15th to 19th century) (and hence slower tree growth) and more frequent fires (Kouki et al. 2018).

National forest inventory (NFI) data

For changes in forest characteristics important for biodiversity over the past 100 years, we used the first NFI (NFI1, 1921–24) and the most recent published NFI data (NFI12, 2014–2018) (Ilvessalo 1927, Korhonen et al. 2021). While for natural state and the 1750s the reporting for north and south strictly followed ecoregions, for NFIs we aggregated the county or municipality-level reporting to best fit the ecoregions. To obtain the share of old-growth forest, and due to reporting issues from the NFI (reported in 20-year age bins,

except NFI1 for northern Finland that reports in 40-year bins), we made the conservative assumption that the area between age classes decreases linearly (e.g., we divided by half forest cover reported under 141–160 years to obtain estimate >150 years). We used Henttonen et al. (2019) to get NFI-derived estimates for the density of large trees. Dead wood has been only exhaustively monitored in NFI starting at NFI9 (1996–2003), therefore these data were used.

Results

Area of old and deciduous-dominated forests.
Under natural reference conditions, old forests (>150 years) covered at least 50% of the forest area. In southern Finland, their share had already shrunk by 50% by the 1750s (Table 2). Currently in southern Finland, old forest coverage is a small fraction compared with natural reference conditions (3%) and the 1750s (7%; Fig. 1) but slightly larger than in the 1920s (Table 2). In northern Finland, the decline in old forest coverage only started in the 20th century (Table 2), and their current cover is one-fifth of the forest area, and <40% of the coverage prior to the 1920s (Fig. 1).

Under natural reference conditions, deciduous-dominated forests covered >20% of forest area. There has been a 40–50% decline in their cover over the past century (Table 1) and current coverage is 35–50% from the natural reference condition (Fig. 1).

Large trees
Under natural reference conditions, the density of large trees has been several tens of stems per hectare (Table 1). By the 1750s in the south, the density had declined by 75% and continued declining till 1920s (NFI1) to a level that corresponds to <2% of natural density. NFI data shows marked recovery (>7-fold increase) in the density of large trees over the last 100 years, but still, current densities are only one sixth of the natural reference values and approximately 60% of the den-

Table 2. Values of forest characteristics important for biodiversity in Finland under natural reference conditions, in the 1750s, and according to national forest inventories in the 1920s (NFI1) and 2010s (NFI12). Relative change denotes the change between NFI1 and NFI12 except for dead wood volumes, for which it represents changes between NFI9 and NFI12. To facilitate comparison, two threshold level values of % old forests in NFI12 is given.

	Natural reference	1750s	NFI1 (1921–1924)	NFI12 (2014–2018)		Relative change (NFI1–NFI12)
% Old forests	>150 years	>150 years	>160 years	>150 years	>160 years	
North	50%	50%	39%	18.9%	17.1%	–56%*
South	50%	25%	0.7%	1.7%	1.1%	57%*
Whole of Finland	50%	32%	10%	5.9%	5%	–51%*
% Deciduous-dominated forests						
North	17.2%	NA	12.8%	6.3%		–51%
South	23.3%	NA	19.3%	11.1%		–42%
Whole of Finland	21.6%	NA	17.9%	10.0%		–45%
Large trees #/ha						
North	56	42	11.8	12.9		9%
South	36	9	0.6	5.1		743%
Whole of Finland	42	18	3.7	7.3		97%
Dead wood m^3/ha						
North	50	38	9.5**	7.5		–21%
South	110	27	2.8**	4.5		61%
Whole of Finland	94	30	5.8**	5.8		0%

* for forests >160 years. **NFI9 (1996-2003) estimate.

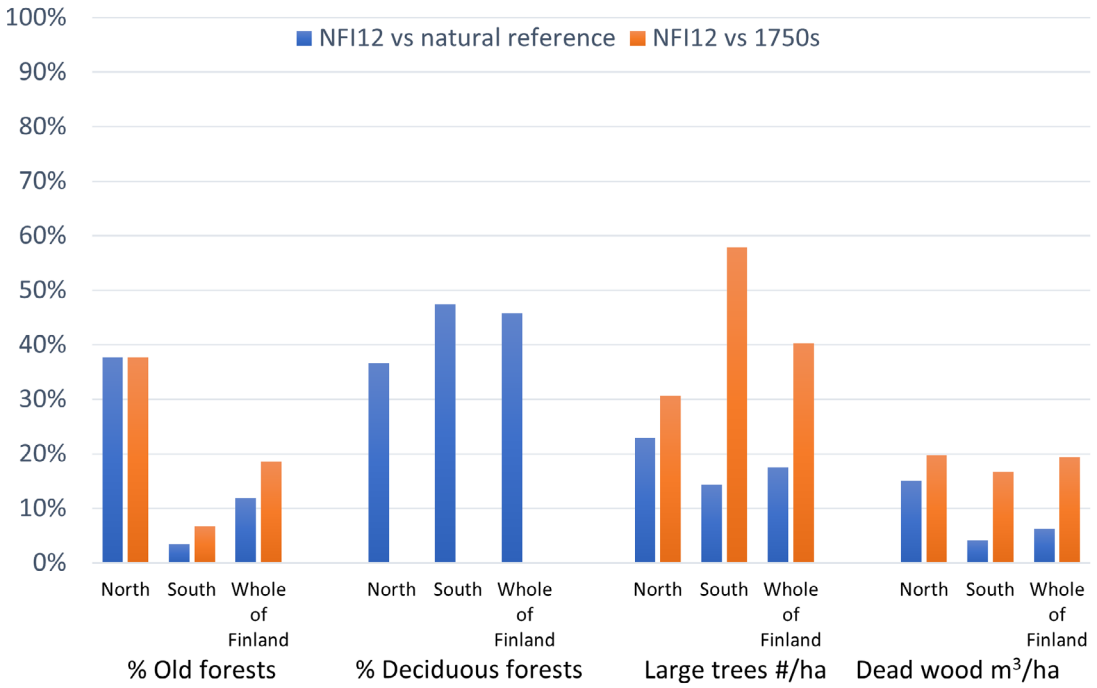

Figure 1. Percentage cover of old forests and deciduous forests, density of large trees and dead wood volumes in Finland according to NFI12 relative to values under natural reference conditions (blue bars) and in the 1750s (orange bars). The values are given for North (northern boreal forests), South (middle- & south- & hemiboreal forests), and for whole Finland.

sity in the 1750s (Fig. 1). In the north, the density of large trees markedly declined prior to the NFIs started in the 1920s and has ever since remained at a level that corresponds 25–30% of values under natural reference conditions and in the 1750s.

Amount of dead wood

Under natural reference conditions, dead wood volumes are >90 m^3/ha on average, with higher values in the south than in the north of Finland (Table 1). By the 1750s in southern Finland, dead wood volume had decreased considerably, and somewhat also declined in the north. Between NFI9 (1996–2003) and NFI12 (2014–2018) – the period for which NFI provides data of the amount of dead wood in Finnish forest – dead wood volume has increased in southern Finland but decreased in northern Finland, where it has yet remained higher than in the south. Considering the historical range, there has not been a remarkable change since NFI9 (Table 1). Current dead wood volume in the south is <5% of the natural reference value. In the north, the decline is more recent and effectively started in the 20th century, with current volume being 15% of the dead wood volume relative to the natural reference value, and about 20% relative to the 1750s value (Fig. 1).

Discussion

Current Finnish forests largely depart from natural state

Forest structures essential to maintain ecologically diverse biota are below those that likely prevailed in Finland under natural reference conditions and in the 1750s. This scarcity is particularly pronounced for dead wood volumes, and old forest area in southern Finland (Fig. 1). Korhonen et al. (2016) suggested that in the south, dead wood volume has been constantly low since 1920s and declining in the north until the 1980s. They concluded this from the NFI data concerning the volumes of hard dead wood (still usable as fuel wood) since the late 1930s (from NFI2 (1936–1938) to present).

Despite recent positive trends in the density of large trees and dead wood volumes particularly in the south, simultaneous negative trends in the threat status of forest species (Hyvärinen et al. 2019) and high numbers of threatened habitats (Kouki et al. 2018) indicate that these improvements have not been effective enough to turn the tide of biodiversity loss. Moreover, positive development in these structural indicators may be tempered by negative trends in the cover of old forests (at the whole country-level) and deciduous-dominated forests over the past 100 years. While the area of old forest in southern Finland started to increase after being only 0.7% in the 1920s (Table 2), it has declined both in the south and in the north over the past four decades (Korhonen et al. 2020). At the same time, the area of deciduous-dominated forests has increased in the south (Korhonen et al. 2020).

The current levels in the density of large trees and in dead wood volume remain clearly below natural reference conditions. It should be noted that large trees are not necessarily old, as current forest management regimes and timber pricing favor fast diameter growth. Also, climate change and the fertilizing effect of nitrogen deposition has accelerated tree growth in boreal forests (see Henttonen et al. 2017). Consequently, in southern Finland, only a small proportion (11%) of current large trees are old (>150 years), whereas in the north most (95%) large trees are old (Henttonen et al. 2019). Many species require trees that are both large and old (Pykälä 2019). Thus, as tree size is a poor proxy for its age in the present human-modified conditions, monitoring only the density of large trees does not sufficiently reveal changes in forest structures that are important for species.

Protected areas foster forest recovery

In southern Finland, the density of large trees and volumes of dead wood have been increasing since the late 1990s. For deadwood, this increase is largely due to positive development within protected areas, while the contribution of production forests is negligible (Korhonen et al. 2020). Dead wood volume in southern protected areas has doubled from 10 m^3/ha to about 20 m^3/ha, but in managed forests increased only slightly (from 2.7 to 3.9 m^3/ha) between NFI9 and NFI12 (Korhonen et al. 2020, 2021). In both managed and protected forests, the amount of dead wood still remains far below natural reference values, although it is above its historical lowest level. Despite the small cover (10%) of protected forests, 43% of large old trees are in forest reserves (Henttonen et al. 2019). These results indicate the ongoing but partial recovery of forest ecosystems from very intensive management in the past and emphasize the role of conservation areas in protecting biodiversity. As a large share of the protected forests area were previously managed and are gradually recovering, the density of large old trees and volumes of dead wood will continue to increase in forest reserves. In contrast, in managed forests the density of old trees may continue to decline following regeneration felling of the oldest age classes.

In terms of management strategy this means that first, more protected areas are necessary (Kouki et al. 2018, 2019). This is particularly important in southern Finland where only 2.7% of forest land is strictly protected (nature reserves and sites reserved for nature conservation and other statutory protected areas where no felling is allowed, stat.luke.fi/metsa), and where most forests are intensively managed for timber production. Second, the remaining biodiversity-rich natural or semi-natural unprotected forests should be prioritized when expanding the existing protected area network. As the recovery process of forests takes decades or centuries, the loss of these remnant forests is practically irreversible and hard to replace in the foreseeable future. As a complement, currently degraded or young forests could be spared so that they get a chance to recover their integrity in the future (Kotiaho & Mönkkönen 2017, Kouki et al. 2018).

The biodiversity value of managed forests can be increased

As managed forests cover nearly 90% of the country, they will inevitably have a major role in facilitating biodiversity recovery. However, their role critically depends on the management methods applied. Even though protection of biodiversity has been an important aim in managed forests in Finland since the 1990s, management for tim-

ber production in unprotected forests is still too intensive to allow the amount of dead wood to recover and trees to grow old. It is also noteworthy that although 6% of large, old trees are living retention trees in managed forests (Henttonen et al. 2019), most large, old trees are still subject to logging in ordinary production forests. Management practices can facilitate the recovery of essential structures to maintain ecologically diverse biota, such as increasing the numbers of – preferably large and old – retention trees left behind in logging operations and by emulating natural disturbances with prescribed post-harvest burnings (Heikkala et al. 2016, Suominen et al. 2019, Kouki & Salo 2020). This would primarily slow down the loss of important legacy trees from the landscape, and eventually facilitate the formation of large diameter dead wood in managed forests (Kouki et al. 2018).

The most cost-efficient means to maintain habitats for dead-wood dependent species in managed forests is to retain all the existing dead wood during logging operations by avoiding the destruction of snags and logs, and by refraining from harvesting dead trees for energy wood. The loss of existing dead wood may be very high, up to 80%, during logging and site preparation operations (Hautala et al. 2004). Refraining from all logging, including selective cutting, in valuable woodland key-habitats of managed forests will support maintaining valuable habitat features and their connectivity in managed landscapes (Laita et al. 2010). Finally, landowners have been shown to voluntarily conserve small forest patches occupied by charismatic species such as birds-of-prey (Santangeli et al. 2012), which will benefit also other species (Burgas et al. 2014). It has been suggested that this approach could be further developed to cover other types of biodiversity values and larger patches via compensation schemes (Santangeli & Laaksonen 2015).

Natural disturbances are opportunities for restoration

Our analyses are based on ecologically simplistic assumptions that forests and their features evolve gradually over decades and centuries. However, strong pulsed disturbances, such as wildfires, large storms or outbreaking insects may rapidly affect forest characteristics, including biodiversity indicators we have analyzed in this study. However, due to insufficient knowledge of the spatio-temporal distribution of disturbances, it is impossible to reveal their exact role in the past. Even more importantly, such disturbances are predicted to increase in the future, and their role may deviate and increase from their historical occurrence (Venäläinen et al. 2020). For the maintenance of biodiversity, large-scale and intensive disturbance provide opportunities to quickly restore some of the features lost from forests, or even restore fully functioning forest habitat types that are currently threatened. Further, disturbances create forest structures and habitats that are targeted in artificial restoration, often at a high cost (e.g., restoration burnings).

We strongly recommend developing strategic plans to take advantage of positive effects of natural disturbances to enhance ecological integrity inside production forests. Disturbances are spatially and temporally unpredictable, and, thus, it is crucial to have agreed forest policies on how to deal with them once the events occur (Thorn et al. 2020). This is of crucial importance for species that are dependent on dead, injured or charred wood. There is an obvious need to reconsider the Finnish Forest Damages Prevention Act, which obligates a forest owner to remove large-diameter conifers from forest stands if there are more than 10 m^3/ha of freshly damaged spruce trees or more than 20 m^3/ha of damaged pine trees. This Act effectively precludes rapid and cost-efficient accumulation of dead wood in unprotected forests, is detrimental to biodiversity and has unclear biological justification in preventing further damages particularly in pine forests (Martikainen et al. 2006, Komonen & Kouki 2008, Siitonen & Heliövaara 2013). Disturbances and their effects on tree mortality must not only be seen as economic losses but considered as highly potential and rapid investment opportunities in natural capital (sensu Dasgupta 2021) because of the positive biodiversity effects.

Conclusions

Forests in Finland have largely lost their ecosystem integrity and are faring poorly in a global comparison (Grantham et al. 2020). Our re-

sults show that this loss of ecological integrity in southern Finland is a result of a long process that spans over several centuries. Changes in forest habitats accelerated and were especially widespread and intensive during 1900s when currently applied intensive forestry expanded to the whole country and targeted all forest habitat types. Recent decades show slow recovery of degraded forest characteristics important for biodiversity. This recovery is an indication that forest management can be adjusted so that forest habitats and biodiversity are maintained better in the future. However, the future condition of Finnish boreal forests critically hinges on the management decisions we make today. The assessments of forest-dwelling species (Hyvärinen et al. 2019) and habitats (Kouki et al. 2018, 2019, this study) provide ecologically comprehensive and up-to-date background to improve ecological integrity in the Finnish forests.

Additionally, a recent analysis of alternative policy scenarios shows that forest policy can be tailored to meet the goal of biodiversity maintenance in Finland (Blattert et al. 2022). For example, the amount of dead wood and density of large trees can be increased but requires a policy that gives proper weight on both economic and ecological objectives and that has realistic tools to implement measures needed. Clearly, however, further coordinated efforts on how to maintain biodiversity in managed and protected forests will be required if the Finnish society wants to achieve genuinely sustainable forests and forestry (Kouki et al. 2018, Kuuluvainen et al. 2019, Korhonen et al. 2020).

The principles of sustainable forest management emphasize the value of ecosystem services and their value for people (Vanhanen et al. 2012). As the functioning of ecosystems is based on their structure and underlying biodiversity, there are opportunities to reconcile the maintenance of biodiversity with multiple benefits obtained by human communities from forest ecosystems (e.g., water quality or health and recreational value). A critical challenge in this context is how to balance biodiversity requirements with timber production and the flow of non-timber ecosystem services from forests over the long term.

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