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Natural Disturbance-Based Forest Management: Moving Beyond Retention and Continuous-Cover Forestry

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Global forest area is declining rapidly, along with degradation of the ecological condition of remaining forests. Hence it is necessary to adopt forest management approaches that can achieve a balance between (1) human management designs based on homogenization of forest structure to efficiently deliver economic values and (2) naturally emerging self-organized ecosystem dynamics that foster heterogeneity, biodiversity, resilience and adaptive capacity. Natural disturbance-based management is suggested to provide such an approach. It is grounded on the premise that disturbance is a key process maintaining diversity of ecosystem structures, species and functions, and adaptive and evolutionary potential, which functionally link to sustainability of ecosystem services supporting human well-being. We review the development, ecological and evolutionary foundations and applications of natural disturbance-based forest management. With emphasis on boreal forests, we compare this approach with two mainstream approaches to sustainable forest management, retention and continuous-cover forestry. Compared with these approaches, natural disturbance-based management provides a more comprehensive framework, which is compatible with current understanding of multiple-scale ecological processes and structures, which underlie biodiversity, resilience and adaptive potential of forest ecosystems. We conclude that natural disturbance-based management provides a comprehensive ecosystem-based framework for managing forests for human needs of commodity production and immaterial values, while maintaining forest health in the rapidly changing global environment.

Keywords: biodiversity conservation, forest dynamics, forest ecosystem, landscape management, restoration, sustainable forestry, Natural range of variation

INTRODUCTION

> *Natural disturbance emulation is based on the idea that by emulating the attributes of natural disturbances, it is possible to maintain or restore ecological structure and function …and thus maintain biodiversity along with other ecological goods and services.*
>
> Stockdale et al. (2016)

Natural ecosystem dynamics foster self-organized heterogeneity and diversity (Levin, 1998, 2005), which are fundamental in maintaining healthy, diverse and resilient ecosystems (Messier et al., 2013; Gauthier et al., 2015; IPBES, 2019). This feature contrasts with managed ecosystems, which typically are structurally and functionally homogenized for high yields of particular commodities. This is the fundamental divide between natural and anthropogenic systems, and reflects the eternal dilemma of using or protecting. To overcome this dilemma, and to enable long-term sustainability of forest management (e.g., Castañeda, 2000), it is necessary to find a balance between these two. In forest management, this means finding a balance in space and time between management system designs promoting production of specific goods and services, and natural ecosystem designs characterized by self-organized properties such as heterogeneity, biodiversity, resilience and adaptive capacity (Drever et al., 2006; Bergeron and Fenton, 2012; Kusumoto et al., 2020).

Although boreal forests have been utilized for timber and other natural goods for hundreds if not thousands of years, expansion of frontiers of industrial-scale management started to have an unprecedented impact on boreal forest landscapes after World War II, particularly in northern Europe, but increasingly also in North America. Nevertheless, the boreal forest still harbors a large share of the world's intact landscapes and also terrestrial carbon (Bradshaw et al., 2009; Potapov et al., 2008). In boreal forests managed for timber production, the dominating silvicultural approach is intensive even-aged management (Duncker et al., 2012), with some ecological considerations such as leaving retention trees (Martínez Pastur et al., 2020) and protecting valuable key habitats (Timonen et al., 2011). However, management is driven by relatively short clear-cut harvesting cycles compared with natural, usually much longer and also more diverse, cycles of natural disturbance (Kuuluvainen, 2009; Jõgiste et al., 2017, 2018). This type of intensive management results in such forest compositions, structures and functions that are beyond their natural range of variation at multiple spatial and temporal scales (Cyr et al., 2009; Kuuluvainen, 2009). This management system promotes homogeneity in pursuit of increased productivity, predictability, and logistic efficiency to provide industrial raw material (Puettmann et al., 2008).

The logical reference system for this kind of silviculture is agriculture. Management is optimized for specific, narrowly defined values, mostly timber, pulpwood and biomass volume and monetary economic return, primarily in the subsequent industrial value chain. However, it is evident that agricultural crop production cannot be the reference system, neither if ecological sustainability is taken seriously nor if value chains based on multiple material and immaterial values are to be developed and sustained (Jonsson et al., 2019). Instead, the reference must be found in a holistic site-type and region-specific understanding of key ecological features of naturally dynamic forest landscapes, including their intrinsic structure, dynamics, and species composition at multiple spatial scales (Angelstam, 1998; Bergeron et al., 1999, 2002; Messier et al., 2013).

Fennoscandian countries, notably Sweden and Finland, provide an example of a region where forest management has been intensive locally since the mid-nineteenth century, and regionally after World War II, with continued transformation of naturally dynamic forests to those focusing on intensive production for wood (Jonsson et al., 2019; Angelstam et al., 2020a). As a consequence, while hosting only 2% of the global forest area, Swedish and Finnish sawn wood and paper export make up more than 15% globally (SNS, 2020). The established model of intensive forestry is considered sustainable from the point of view of timber, pulp and biomass yield (Rytteri et al., 2016). However, such a definition of sustainability does not meet current national and international standards, in particular because it does not address the fact that a large part of forest biodiversity is in jeopardy (Hanski, 2000; Kontula and Raunio, 2018; Hyvärinen et al., 2019; SLU ArtDataBanken, 2020), nor does it recognize the steeply declining role of intensive forestry and forest industry for regional and rural sustainability (Angelstam et al., 2020b).

The root causes of issues in forest biodiversity conservation are habitat loss and degradation due to reduced structural variability and tree-species diversity over large geographic areas (Kuuluvainen, 2009; Kontula and Raunio, 2018). Secondary forests resulting from intensive management lack the natural amount and variability of legacy features and landscape connectivity, and species with specific habitat requirements, which make up forest biodiversity (Kuuluvainen, 2009). In naturally dynamic forests the so-called "ecological memory" (Bengtsson et al., 2003) is key to the resilience and adaptive capacity through disturbance cycles. This includes, for example, a high amount and diversity of dead wood, or persistent complex overstorey structures consisting of large trees (Johnstone et al., 2016).

The ongoing loss of global forest area, and degradation of natural forest ecosystems (FAO, 2020; McDowell et al., 2020), combined with the need to deliver diverse ecological and social values in forest landscapes, requires ecosystem-based approaches to forest management (Bradshaw et al., 2009; Johnstone et al., 2016). In particular, the pivotal role of disturbances in driving forest ecosystem structure, development, biodiversity, and maintenance of adaptive capacity have become highlighted since the 1980s as part of the field of disturbance ecology (Pickett and White, 1985). Forest disturbance ecology examines the occurrence and drivers of disturbances and how disturbance regimes affect the structural heterogeneity, species composition and their dynamics, and adaptive capacity of ecosystems over extensive spatial and temporal scales (Holling, 2001).

Natural disturbance-based forest management is grounded in research on disturbance ecology, and it aligns with current policies aiming at multifunctional forest landscapes

(Kuuluvainen and Grenfell, 2012; Stanturf et al., 2019). The goal is to minimize the negative impacts of focusing narrowly on wood and biomass production to forest ecosystems by identifying and maintaining key habitats and heterogeneity features, which can be expected to support biodiversity and, in turn, human well-being (Hanski et al., 2012; Pukkala, 2016). This principle forms the ecological foundation of natural disturbance-based forest management. In practical terms, it is based on the hypothesis that by mimicking natural tree mortality patterns and forest structures at multiple scales in forest management, it is possible to maintain or restore key ecological structures, and hence sustain communities, processes and biodiversity, along with associated ecosystem services in managed forest landscapes (Stockdale et al., 2016; Frelich et al., 2018; Berglund and Kuuluvainen, 2021).

Although protection of representative areas of natural forest should be prioritized, primary forests are still extensively harvested in many parts of the world (FAO, 2020). In this case, principles of natural disturbance-based management can be used to minimize the ecological damage of timber harvesting. In secondary forests, the goal can be to restore some of the once lost ecological structures and communities. Here, natural disturbance-based management comes close to ecological restoration, which is broadly defined as assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Although this definition is broad indeed, we make a distinction where ecological restoration is mainly about recovering the ecological qualities (Halme et al., 2013), whereas natural disturbance-based management aims at finding a nature-based balance and reconciliation between economic, ecological and social values in the long term. In practice, this distinction calls for management that has restorative elements while at the same time a significant share of timber is harvested in a manner to create structural variability similar to that caused by natural disturbances (Bergeron et al., 2002; Angelstam and Kuuluvainen, 2004; Vanha-Majamaa et al., 2007; Koivula et al., 2014).

The purpose of this paper is to present a synthetic overview of natural disturbance-based forest management. Specific goals are: (1) to discuss the origins and emergence of the concept of natural disturbance-based management and its current policy context, (2) to review the ecological and evolutionary foundations of the concept, (3) to analyze how it relates to and differs from two mainstream approaches to sustainable forestry, retention and continuous-cover forestry, and (4) to discuss the strengths and limitations of natural disturbance-based approach in managing adaptive and sustainable forest landscapes. Our focus is on the circumboreal forest biome, but our analysis is relevant to other biomes too.

HISTORICAL DEVELOPMENT AND CURRENT POLICY CONTEXT

To understand the historical context concerning the emergence of the natural disturbance-based management approach, it is useful to review the development of forest management methods over the past century (**Figure 1**). In general and through time, changes in management approaches have reflected societal needs for different kinds of forest resources and fears of their depletion; furthermore, they are a product of technological and methodological advances, and growing knowledge in ecological and forest sciences (Rytteri et al., 2016). The idea of natural disturbance-based management is paradoxical in that natural disturbances have typically been considered the foresters' worst enemy, and basing forest management on natural disturbance patterns may be difficult for managers to accept (Kuuluvainen and Grenfell, 2012). The current additional challenges are climate change-driven increases in frequency and severity of natural disturbances (Seidl et al., 2020). Ironically this leads us to a situation where management based on historical disturbance regimes must simultaneously be adaptive to rapidly changing environmental conditions now and in the future, in order to achieve the goals of sustainable forest management (Webster et al., 2018).

Basing forest management on knowledge of natural forest diversity and dynamics is not a novel idea, indeed it was the starting point already for the early pioneers of silviculture (Bauhus et al., 2013). Their motivation was practical, namely to find cost-efficient ways to manage the forest for timber by working along with, rather than against, developmental pathways of natural forest. This was necessary because all forest work had to be done with muscle power. Although the mainstream of development of forest management has primarily focused on timber production, there have been consistent side currents under the titles "ecological forestry" in North America and "close-to-nature" forestry in Europe, starting from the early twentieth century and continuing up to today (**Figure 1**; Angelstam, 1998; Puettmann et al., 2008; D'Amato et al., 2017). Although the practise of close-to-nature forestry, and its derivative continuous cover management, rejected even-aged management and clearcutting, they originally focused on maximizing economic return (Bauhus et al., 2013). Recently, more emphasis has been placed on the ecological and social influences of continuous-cover management (Pommerening and Murphy, 2004; Kuuluvainen et al., 2012; Bauhus et al., 2013; Peura et al., 2018; Koivula et al., 2020).

In the boreal zone, with the expansion of forest industry from the mid-nineteenth century, large-scale extraction of timber resources began in landscapes dominated by older forests. This was mostly carried out by selective harvesting (or high-grading) of large high-quality timber trees from abundant natural or near-natural forests along with expanding local and regional "timber frontiers" (Keto-Tokoi and Kuuluvainen, 2014). With decreasing sawn-timber resources, and with the emergence of the pulp and paper industry, smaller-diameter trees also became merchantable. Given sufficient institutional stability, state-driven organized forestry developed to serve the needs of a rapidly growing forest industry (**Figure 1**).

After World War II, the availability of new technology and cheap fossil fuels boosted forest extraction further. The goal was set: get rid of "nature's constraints" (Keto-Tokoi and Kuuluvainen, 2014). The reference model of silviculture was taken from agriculture, and even-aged monoculture management driven by short (e.g., 60–100 years) clear-cutting cycles became the dominant management method. The need to secure an

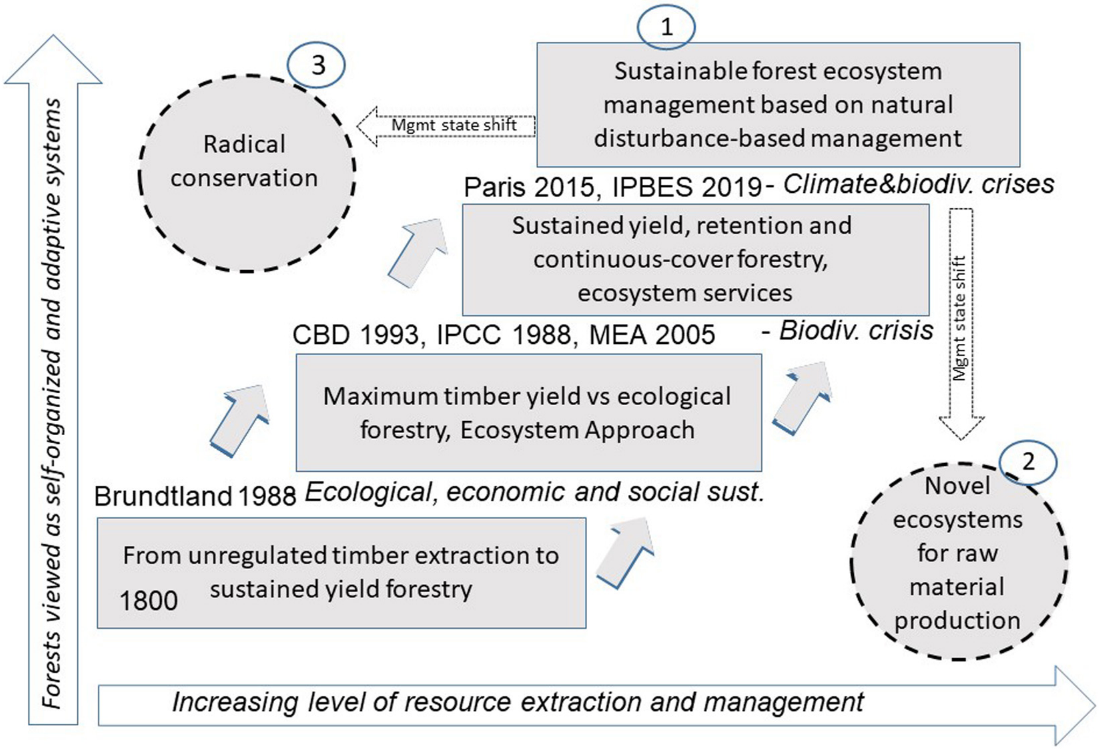

FIGURE 1 | Illustration of the historical development of forest management approaches toward sustainable forest ecosystem management (1), including some key milestones and underlying driving factors, along gradients of increasing level of resource extraction and viewing forests as self-organized adaptive systems. Two other alternative future developments are also illustrated. Escalated global change can force the abandonment of current approaches to ecosystem management and instead to design completely novel ecosystems that are hoped to better cope with new environmental conditions (2). An alternative reaction to rapid global change is to radically increase protection area, so that degraded ecosystems can recover (or rewild) either passively through adaptive self-organization processes, or more actively using, for example, the natural disturbance-based approach (3). In the future components of all these three scenarios may be needed to cope with the climate- and biodiversity crises.

increasing and sustained supply of raw material for the expanding forest industry led to the next phase, where the goal was maximum sustained yield (Puettmann et al., 2008). This approach was in line with the Brundtland commission report Our Common Future (1988) on sustainable development, emphasizing resource sustainability from the human point of view, including intergenerational equity of resource use. It is noteworthy that the concept of biodiversity was established in public discourse only in the late 1980s (Wilson, 1988).

By the 1990s, the cumulative impacts of intensive forest management on other than economic values started to become more and more evident. Loss of natural or near-natural forests, and associated ecosystem services, resulted in public concern, while mechanization of forestry resulted in declining support to rural development and human well-being (Elbakidze et al., 2018). Consequently, in addition to sustained timber yield, ecological and social sustainability issues became highlighted in forest policy and forest management. This development was punctuated by the Convention on Biological Diversity (1993), which promoted the Ecosystem Approach in all management of natural resources (CBD, 2004). At the same time, the concept of ecosystem management was formalized (Christensen et al., 1996). Ecological understanding of the key importance of disturbances in ecosystems started to accumulate (Pickett and White, 1985), and the first suggestions to use disturbances as a model for forest conservation and sustainable management were made (Angelstam et al., 1993; Attiwill, 1994).

Natural disturbance-based management was proposed to be applied at varying spatial scales (Puettmann et al., 2008). At the landscape scale, it was envisioned that natural disturbance-based management could involve harvesting patterns designed to create a landscape age distribution and spatial pattern of disturbed patches similar to that resulting from natural disturbance (Hunter, 1993). At the stand scale, it was proposed that natural disturbance-based silvicultural approaches would focus on retention of biological legacies, again, such as those created by natural disturbances (Lindenmayer and Franklin, 2002). However, in practical forestry two dominant approaches, namely variable retention and uneven-aged (or continuous-cover) forestry, have been more widely advocated as ways to achieve multiple objectives.

An important societal driver for change in forestry practices has been the emergence of environmentally increasingly conscious markets who wanted to know whether or not harvesting for products damages ecosystems and their biodiversity. These demands, along with increasing criticism of intensive forest management in many countries, led to a wide-scale application of retention forestry (Gustafsson et al., 2012; Simonsson et al., 2015; Kuuluvainen et al., 2019). Leaving retention trees aims at maintaining some of the post-disturbance structures found in older forests, such as large trees, snags, downed dead wood and damaged trees (Gustafsson et al., 2012, 2020b). The retention-forestry approach is suggested to emulate the outcome of natural disturbances, with the ultimate aim being to reconcile the goals of timber production, other ecosystem services and conservation of biodiversity (Lindenmayer et al., 2012). Also continuous-cover management has recently become prominent under the auspices of ecosystem or natural-disturbance-based management; it aims to maintain forest cover and preserve structural features in a way that might be touted as mimicking the effects of small-scale and low severity disturbances (Pommerening and Murphy, 2004; Peura et al., 2018).

Additionally, the mounting threats to forest health, posed by intensive exploitation, biodiversity loss and rapid climate change (Bradshaw et al., 2009; Gauthier et al., 2015), have prompted a number of new concepts and approaches. These include novel ecosystems (Hobbs et al., 2009), resilience-based management (Rist and Moen, 2013), and managing forests as complex adaptive systems (Kuuluvainen and Siitonen, 2013; Messier et al., 2013); all of these emphasize that holistic understanding is needed for sustainable forest ecosystem management (**Figure 1**). A common feature of these approaches is also the recognition of the unavoidable consequences of exploitation of natural resources, in terms of maintaining local biodiversity, species and habitat types, and the need to find nature-based and globally applicable solutions to sustainable forest management.

At present, environmental concerns are widely acknowledged, ecosystem management is taken as the *de facto* approach in national and international policy agendas (Burton et al., 2010; Moen et al., 2014), and new nature-based management approaches are advocated (Lindenmayer and Franklin, 2002). Still, intensive clearcutting-based forestry with low tree retention continues to dominate and cause forest loss and degradation in many regions (FAO, 2020). Moreover, the discourse about forest management versus protection has become increasingly polarized (Angelstam et al., 2020a; Sténs and Mårald, 2020). Furthermore, new policy objectives advocating further forestry intensification for the mitigation of climate change have appeared (EASAC, 2017).

Intensification of forest utilization links closely to increasingly used buzzwords like bio-economy, bio-based economy and knowledge-based bio-economy (Pülzl et al., 2014), which have the potential of becoming defining concepts of forestry discourses, replacing concepts such as ecosystem approach, sustainable ecosystem management and others that simultaneously consider economic benefits, biodiversity conservation and rural development (**Figure 1**). Because discourses can have performative power by shaping stakeholder opinions, beliefs and behavior, they can potentially trigger institutional change in a society (Feindt and Oels, 2005; Hajer and Versteeg, 2005).

In many boreal countries the use of forests is already so intensive and timber-oriented that biodiversity is in jeopardy (Hanski, 2000; Kontula and Raunio, 2018; Hyvärinen et al., 2019; SLU ArtDataBanken, 2020). The replacement of a fossil-fuel-based economy with a bio-based one in the future would inevitably lead to further intensification of management, accompanied by an even narrower focus on the wood resource. This will put additional unprecedented pressure on forests and reverse efforts to consider and reconcile a wider range of management goals, such as biodiversity conservation and rural development (Naumov et al., 2018).

Finally, we must face the possibility that climate change could result in a situation where the sustainability of the current ecological condition and values of forests is no longer achievable. In this situation we may have two scenarios to avoid collapse of ecosystems (**Figure 1**). It may become necessary to abandon current management approaches and ecosystems and to design completely novel ecosystems, possibly with genetically modified plants, which we hope will be able to cope with drastically different environmental conditions in the future (Frelich et al., 2020). Second, we may need to dramatically increase the area of protected habitats to let nature to recover with *in situ* adaptive processes. To avoid the realization of such most drastic of predicted scenarios, it is important to maintain the discourse on alternative pathways and approaches to sustainable forest management that could provide resilience and adaptive capacity now and in a rapidly changing world (**Figure 1**).

FROM ECOLOGICAL AND EVOLUTIONARY FOUNDATIONS TO APPLICATIONS

In forest ecology, disturbances refer to events of tree damage and mortality, which release growing space and resources, and change micro-climate (Pickett and White, 1985). In natural forests disturbances are caused by factors such as fire, windthrow, insects and fungi, and they occur at varying spatial scales, from deaths of single old trees, to mortality of groups of trees, to large-scale impacts. Disturbances also vary in their frequencies and severities. The functioning of varying disturbances in a landscape and over a prolonged time-period is called the disturbance regime. In naturally dynamic forests, the disturbance regime creates a successional mosaic of forests of various composition, structure and age, which is called the natural range of variation (**Figure 2**; Landres et al., 1999). This forest mosaic is affected both by site and regional conditions, and it is characterized by multi-scale structural diversity of habitats for forest-dwelling organisms. The ecosystem is developed through the processes of disturbances, self-organization and *in situ* selection (Sgrò et al., 2011). In contrast, the commonly practiced clear-cut harvesting in managed forests is characterized by little variation in severity or size and is applied with a narrow, and short, range of frequencies; this leads to loss of native biodiversity and fragmentation of natural habitats, such as young naturally

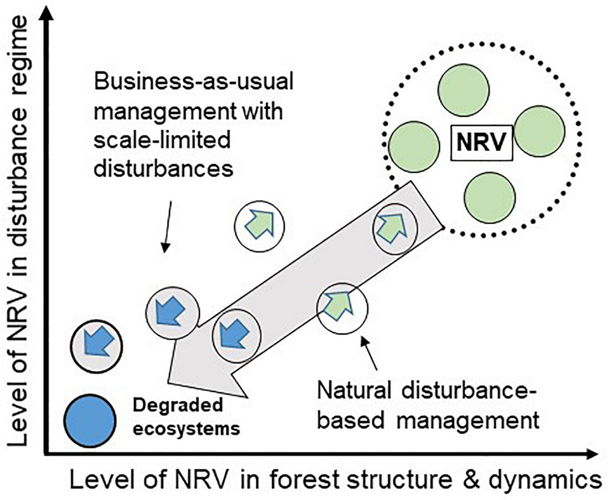

FIGURE 2 | Emulation of natural disturbances in forest management is hypothesized to play a key role in sustainable forest ecosystem management. Conventional forest management methods typically create disturbance and successional dynamics which are strongly scale-limited compared with their natural range of variation (NRV). This results in simplification and degradation of ecosystems in terms of structure, native species communities and ecological processes (Blue arrows). Natural disturbance-based management aims to restore or maintain some of the essential features of the natural forest's multiscale dynamics and heterogeneity by diversification of silvicultural treatments to mimic NRV in disturbance severity, quality, extent, and repeatability (Green arrows).

disturbed forests and old-growth forests (Kuuluvainen and Gauthier, 2018). Thus, characteristics of disturbance regimes play a pivotal role in driving ecosystem processes and in maintaining biodiversity through species re-assembly, and they should be emulated in management if the intention is to support natural processes, habitats, and species and their evolutionary potential (**Figure 2**; Bergeron et al., 2002; Kuuluvainen and Grenfell, 2012; LaRue et al., 2016). This is the ecological premise of natural disturbance-based management.

Fundamentally, the natural disturbance-based management approach is grounded on the properties of forest ecosystems, which are shaped by large-scale pressures of evolutionary selection. These processes are reflected in species-pool properties (taxonomic and phylogenetic assembly), including abundance of common tree species that are often targeted in forestry (Kubota et al., 2018a). Local forest communities can be regarded as samples filtered from regional species pools, shaped by historical macro-evolutionary processes. The species, communities and ecosystems we wish to preserve have emerged through such large-scale processes (Kubota et al., 2018a), although micro-evolutionary processes may also be important (Rice and Emery, 2003). From the evolutionary point of view, disturbances, which are characterized by region-specific climatic (abiotic) conditions, can be seen as environmental filters. The evolutionary premise of natural disturbance-based management is that adaptations and assemblies of specific species, communities and ecosystems have arisen through multiple environmental filters (Kubota et al., 2018b), prominently driven by natural disturbance, and more recently including anthropogenic disturbance. Thus, ecosystems and landscapes are characterized by resilience and adaptive capacity within the natural range of variation in environmental conditions (Sgrò et al., 2011).

From the conservation point of view, it is notable that human actions in forests can also affect evolution, and such effects could perhaps be faster than we think. There is evidence that rapid evolution can take place in short-lived species within tens of years (LaRue et al., 2016). Human impacts on forests and particular timber tree species, although currently strong, are relatively recent in an evolutionary time perspective. However, it is possible that changing properties of environmental filters, e.g., due to region-scale clear-cut harvesting and tree breeding, together with local-scale forest management targeting particular tree species, may affect the evolutionary potential via deteriorating genetic and species-pool properties (Rice and Emery, 2003; Sgrò et al., 2011). Also, climate change-driven shifts in local-scale natural disturbance regimes could be another major driver related to evolutionary processes (Rice and Emery, 2003). So far, research on natural disturbance-based management has focused mainly on restoring and/or maintaining structural and functional attributes related to taxonomic diversity. In the future, emphasis is also needed on clarifying the roles of *in situ* selection and phylogenetic diversity that reflect the evolutionary assembly processes affecting resilience and adaptive capacity of forest ecosystems (Rice and Emery, 2003; Sgrò et al., 2011).

In practical forest planning and management, the natural disturbance-based management approach can be grounded on knowledge and assumptions of species and ecosystem adaptations to local and/or temporal environmental changes (Stokland et al., 2012; Angelstam et al., 2021b). It is an ecosystem approach that focuses holistically on restoring and maintaining near-to-natural dynamics in managed forests by mimicking natural disturbances with forest harvesting (**Figure 3**). This approach acknowledges that the current knowledge on habitat requirements of most forest species is poor, and that this situation will not significantly improve for most ecosystems in the foreseeable future. Moreover, it recognizes that we may not well understand the current or past conditions to which the current species have adapted. A further complication is the possibility of rapid epigenetic and eco-evolutionary adaptation in some species populations (Sgrò et al., 2011). All this makes comprehensive species-by-species (fine filter) conservation difficult or even impossible, and thus motivates the call for habitat structure-based (coarse filter) approaches, such as natural disturbance-based management (Hunter, 1993; Lemelin and Darveau, 2006).

Natural disturbance-based management relies on the key ecological premise that disturbance-driven forest structure is a major determinant ("proxy") of species diversity and ecosystem functioning (**Figure 3**; LaRue et al., 2019; Lelli et al., 2019). This is illustrated by, for example, the close links between disturbances, dead wood, deadwood-dependent species diversity, and cycling of carbon and other nutrients (Stokland et al., 2012).

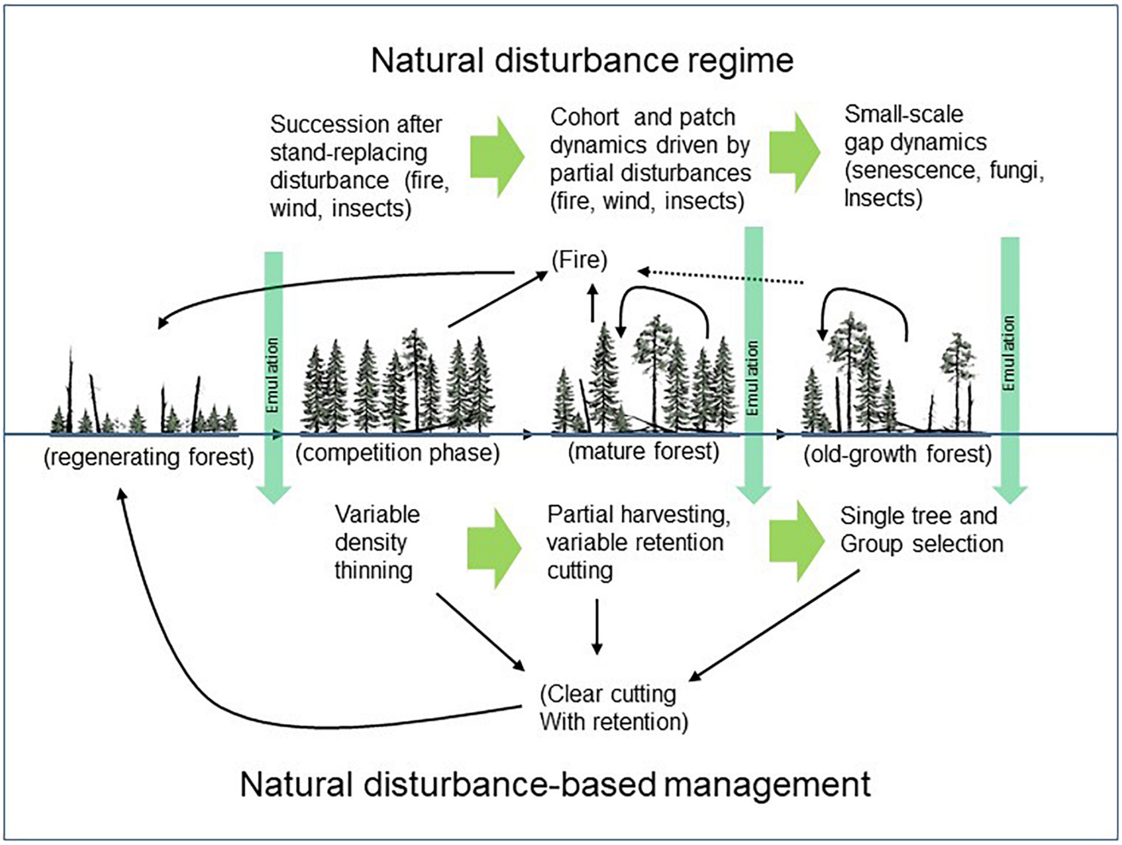

FIGURE 3 | Illustration on how knowledge about natural disturbance regimes can be used in natural disturbance-based management (Bergeron et al., 2002). Here the forest successional sequence is divided into four developmental phases after stand-replacing disturbance, with their typical internal dynamics: regeneration, competition, mature and old-growth. Silvicultural tools are used in each phase to emulate natural disturbances. Retention of ecological legacies (living and dead trees) is applied in regeneration cutting, variable-density thinning is used to emulate competition-phase dynamics, partial harvesting and high-retention cutting can be used to imitate opening up of canopy, and structure and dynamics of old forests are emulated by selective and group harvesting. The desired proportions of developmental phases are derived from a reference landscape (if available) or from the historical reference-disturbance regime (Drawing by J. Karsisto, modified from Kuuluvainen et al., 2017).

Managing for natural forest structures at multiple scales can also be regarded as a precautionary approach to managing a complex system for ecological sustainability (Messier et al., 2013). The coarse filter created by natural disturbance-based management (**Figures 4**, **5**) likely supports a more natural and wider range of ecosystem structures, native species and ecological processes, compared with variants of conventional even-aged management (biodiversity hypothesis).

Maintenance of native biodiversity (involving taxonomic, functional and phylogenetic assembly), promoted by natural disturbance-based management, can be expected to enhance ecosystem resilience and ecosystem adaptations to changing environmental conditions (resilience hypothesis, Gunderson, 2000), as well as a higher range of ecosystem services, compared with conventional even-aged management (ecosystem service hypothesis, Balvanera et al., 2006). What is notable for forestry aimed at wood production is that higher tree-species diversity resulting from various phylogenetic clades has been linked to both higher productivity through redundant functional structure (Knoke et al., 2009; Paquette and Messier, 2011) and increased resistance and resilience (Drever et al., 2006). These effects may potentially compensate for potential economic losses associated with natural disturbance-based management (Rist and Moen, 2013).

WHAT IS DIFFERENT IN NATURAL DISTURBANCE-BASED MANAGEMENT?

In managed forests, leaving retention trees has globally become a common approach in reconciling the conflicting goals of timber production and biodiversity conservation (Gustafsson et al., 2010, 2012, 2020b; Lindenmayer et al., 2012; Martínez Pastur et al., 2020). The ecological impact of logging depends on retention level and its range of variability (**Table 1**). In retention forestry the focus in most cases is on production of wood and biomass, and low retention can be seen as an "entrance fee" to the environmentally aware markets (Kuuluvainen et al., 2019). However, low retention levels may fail to address the root problems of the clearcutting practice

TABLE 1 | Comparison of basic properties of natural disturbance-based management, retention forestry, and continuous-cover management.

Property of approach	Natural disturbance-based approach	Retention approach	Continuous-cover approach
Spatial scale of management	Multi-scale: from microsites to trees to stands to landscapes	Retention patch, stand	Individual tree, tree group (stand)
Temporal scale of management	Diverse range from years to centuries	Same range as for even-aged rotation	Intermittent local disturbances
Reference disturbance regime	Defined, representative of NRV of disturbance type, severity, size, and repeatability	Not usually defined	Not defined, but focus on shade-tolerant tree species
Description of habitat	Multi-scale: across the forest area, α-, β-, and γ-diversity	Stand-scale: retention habitat vs. non-habitat, α-diversity	Individual tree, tree group (stand), α-diversity
Heterogeneity	Dynamic heterogeneity inspired by NRV of disturbance type, severity, size, and repeatability	Constrained heterogeneity due to fixed disturbance type, severity, size, and repeatability	Constrained heterogeneity due to fixed disturbance type, severity, size, and repeatability
Emphasis when harvesting	What to leave to promote natural structure and dynamics: continuity and connectivity	What to harvest with retention constraint	What to harvest and what to leave
Emphasis when leaving retention	All legacy structures, incl. coarse woody debris and large/old trees	Live retention trees	Leaving retention is an option
Time scale in focus	Long-term continuity; representative range of successional stages	Short term, post-harvest stage "lifeboating"	Long-term continuity of living tree structure
Retention of wood production in the long-term	10–50%[a]	1–15%[b]	-?[c] Leaving retention is an option
Management principle	Mix of land sharing and land sparing	Mostly land sharing	Land sharing
Sustainability goal, ecology vs. economy	Balancing ecological and economic sustainability	Emphasis on economic sustainability, with some considerations of ecological sustainability	Emphasis on economic sustainability. Considerations of ecological sustainability is an option

[a] *Vanha-Majamaa et al. (2007); Hanski (2011), Koivula et al. (2014).*
[b] *Gustafsson et al. (2012); Kuuluvainen et al. (2019).*
[c] *Pommerening and Murphy (2004); Bauhus et al. (2013).*

and its ecological consequences at stand and landscape scales (**Table 1**). In many cases the retention levels are too low and applied too monotonously at the stand and landscape scale to benefit the native species that are threatened by current forest management (Kuuluvainen et al., 2019; Koivula and Vanha-Majamaa, 2020). Nevertheless, retention forestry continues to be the globally dominant avenue for reconciling the economic, ecological and social goals in forest management (Martínez Pastur et al., 2020).

Recently, continuous-cover forest management, with its roots in the classical model of uneven-aged silviculture (Dauerwald in German), has started to gain more attention as an alternative to clear-cutting based low-retention management, and as a tool in landscape-scale forest ecosystem management (Diaci et al., 2011; Puettmann et al., 2015; Peura et al., 2018). Continuous-cover management means management without clear cutting. Harvesting is based on single tree, group selection and irregular shelterwood cuttings, where a significant portion of the trees is retained (Sharma et al., 2016; Felton et al., 2017; Sténs et al., 2019). Summaries of research show that continuous-cover forestry retains species living in mature forests and late-successional stages better than rotation forestry with clear-cuts (Kuuluvainen et al., 2012; Peura, 2019).

Although retention and continuous cover forestry have goals similar to natural disturbance-based management, such as to conserve the structural, functional and compositional diversity of managed forest ecosystems (Mori and Kitagawa, 2014; Peura et al., 2018), there are fundamental differences (**Table 1**). Notably the spatial and temporal scales of planning and management differ. In natural disturbance-based management all forest area is regarded as part of the ecosystem and habitat to be managed, whereas in the retention approach, habitat consists of retention trees, tree groups and patches and the rest of the managed forest is treated as non-habitat matrix, echoing the theory of island biogeography (MacArthur and Wilson, 1967; Gustafsson et al., 2012).

Continuous-cover management, in its basic form, aims at utilizing small-scale natural dynamical processes of stands (for example gap dynamics) for cost-efficient production silviculture (Pommerening and Murphy, 2004). Thus, the spatial uneven-aged structure characteristic for continuous-cover management is a byproduct of the production-oriented silvicultural method and goals, rather than a result of intentional management of habitat or biodiversity. The removal of trees in continuous-cover management is done in the first place to enhance and secure continuous wood production, not to imitate variability of natural gap and habitat sizes. Although closed-forest species may benefit from more sheltered and continuous canopy cover (Kuuluvainen et al., 2012), those species that require, for example, large amounts and specific kinds of dead wood (i.e., conditions created by natural disturbance) suffer. Thus, in continuous-cover management the ecological impact depends by and large on the overall structural variation and amount of retention trees left for habitat (Peura et al., 2018; Gustafsson et al., 2020a).

Natural disturbance-based management is different in that it explicitly considers the variability of forest habitat structures at

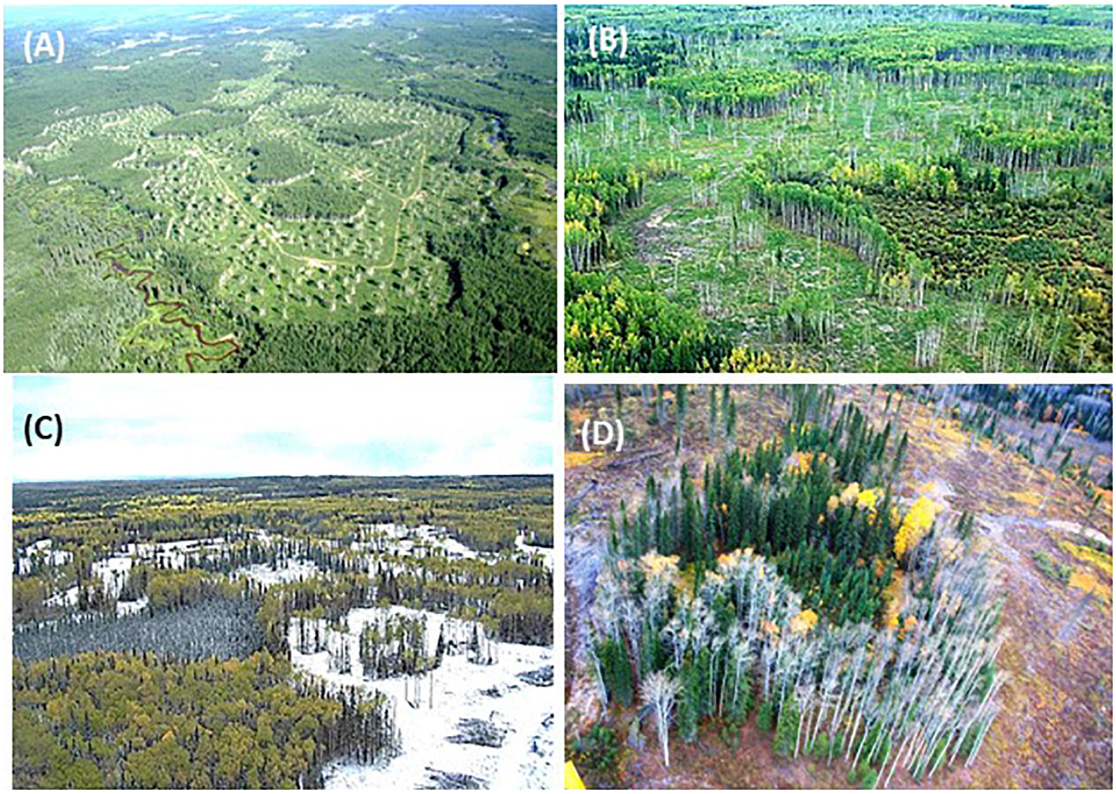

FIGURE 4 | Approaches to natural disturbance-based management in the western Canadian boreal forest. **(A)** Cutover area including a mixture of small and large patch retention; shape of the cut area and pattern of retention are designed to mimic residuals left by wildfire. **(B)** Retention left as a mixture of small patches, large patches, and a buffer next to a peatland. **(C)** Retention left as a mixture of medium-size patches and small patches arranged to improve landscape connectivity. **(D)** Retention patch specifically designed to include a mixture of conifer and hardwoods.

multiple spatial scales from microsites to landscapes, whereas in retention and continuous-cover forestry, the focus is on individual trees, patches and their close surroundings. This affects the ways in which habitat and species diversity are viewed and managed (**Figures 4**, **5**). In retention and continuous-cover forestry the focus is on stand (compartment) structures and their species composition (alpha diversity), whereas natural disturbance-based management also pays attention to the variability among stands and properties of species pools within the landscape (beta diversity), and landscape or regional variability (gamma diversity) (**Table 1**; Kuuluvainen et al., 2019).

The temporal scale in disturbance-based management ranges from years to centuries as inspired by reference disturbance regimes driving the dynamic heterogeneity ecosystems. The long-term view is important when managing systems such as the boreal forest, with naturally long developmental cycles. Special attention must be paid to managing for important legacy structures, such as large old trees, dead wood and the natural range of successional stages with characteristic properties (Kuuluvainen and Gauthier, 2018).

In contrast, in retention and continuous-cover management reference disturbance regimes are normally not defined and the time scale of management is tied to short harvest rotation cycles. Retention typically aims at short-term impacts, such as bringing the species over a successional bottleneck caused by clear cutting ("lifeboating") or managing the visual quality of the landscape. Continuous-cover management aims at maintaining a relatively stable uneven-aged structure with high economic return; it may also provide habitat for species requiring closed-canopy conditions (Bauhus et al., 2013; Peura et al., 2018). This is likely to result in decreased among-stand and within-landscape variability (beta- and alpha-diversity, respectively). The differences between the approaches indicate that, although literature about retention and continuous-cover forestry commonly states that the approach is based on knowledge about natural disturbances, the use and implementation of this knowledge in on-the-ground management remains limited. This is because their disturbance characteristics, fixed type, size, severity, and repetition are tied to the harvesting cycles that differs greatly from those applied in disturbance-based management (Kuuluvainen, 2009; **Table 1**).

There are also differences in practical approaches to management. When harvesting, retention forestry concentrates on what can be harvested with a given retention constraint (Kuuluvainen et al., 2019). In disturbance-based management equal attention is paid on what to harvest and what to leave to promote natural-like habitat structure, dynamics, continuity and connectivity. In leaving retention, disturbance-based management focuses on promoting all legacy structures

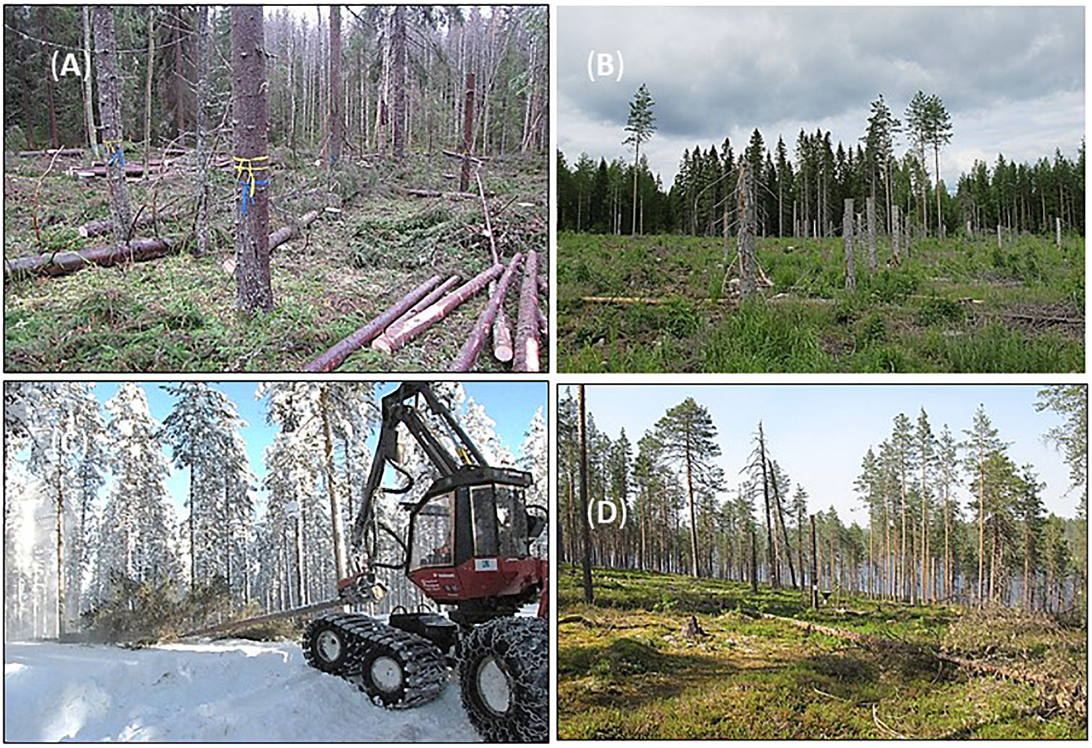

FIGURE 5 | Examples of cutting treatments in the Finnish research and development project "Forest management inspired by natural disturbance dynamics" (DISTDYN, Koivula et al., 2014). **(A)** Selectively felled spruce stand with high amount of retained living and dead trees (Isojärvi research area). **(B)** Clear cut forest with high amount of retention. Note the 2–3 m tall high stumps and their tree tops on the ground (Isojärvi research area). **(C)** Gap felling in pine dominated Ruunaa research area, winter 2010/11. Selection and gap felling can be done using the existing machinery, and the foresters quickly adopt the required new ways of thinking about retention. **(D)** Gap felled pine forest, with intentionally retained legacy elements (e.g., dead or large and old trees. Ruunaa research area, 1.5 years after harvesting). Photos © Matti Koivula **(A–C)** and Timo Kuuluvainen **(D)**.

and their long-term continuity and connectivity, whereas in retention forestry the focus is on leaving live trees (green-tree retention).

In retention forestry, typical retention levels of timber production range between 1 and 15% (Gustafsson et al., 2012; Kuuluvainen et al., 2019), whereas in natural disturbance-based management the levels could vary between 10 and 50% (Vanha-Majamaa et al., 2007; Hanski, 2011; Koivula et al., 2014). In continuous-cover management leaving retention trees is optional (Pommerening and Murphy, 2004; Bauhus et al., 2013).

Finally, the ways space is allocated to different functions and fulfilment of goals differ between the three approaches. Retention and continuous-cover management are by and large based on the land-sparing principle. This means that, for example, retention patches and key biotopes are set aside within the matrix, which is managed using business-as-usual clearcutting. In contrast, natural disturbance-based management is based on land sharing, meaning that all forest area is considered habitat and is managed holistically for different goals. However, natural disturbance-based management can also be used as a land-sparing solution, for example, for forest restoration in newly established conservation areas (Halme et al., 2013). Furthermore, in retention and continuous-cover management the priority is on economic profit, with some considerations of ecological sustainability, whereas the natural disturbance-based management provides a comprehensive approach that strives for a balance between timber production, biodiversity conservation and provisioning of other ecosystem services.

DISCUSSION

Sustainable management of natural resources can, in principle, be spatially arranged by two types of planning, namely land sharing or land sparing. Perhaps the most radical suggestion of the land sparing type is the "half-earth" initiative by Wilson (2015), to protect half of the global ecosystems. Another example of a regionally applicable conservation initiative is the "third-of-third" initiative by Hanski (2011) for combining the approaches of land sparing and land sharing: one-third of the area is managed as multi-objective conservation landscapes containing both agricultural and forestry land areas, within which a third of the area is strictly protected. This kind of zoning is also called the Triad approach (Tittler et al., 2016). Although perhaps controversial to traditional forestry, the area extent of these suggestions reflects the scale and severity of problems caused by wood production aiming at maximum sustained yield, and the urgency to employ radically new and comprehensive approaches to tackle the global biodiversity and sustainability crisis.

With increasing pressures of global change, sustainability in managing forest ecosystems can probably only be achieved with an efficient combination of land sparing and land sharing. At the moment, globally 18% of forests are protected and 3% are plantations, whereas 79% of forests are managed for multiple goals and benefits (FAO, 2020). However, only 10% of the global terrestrial network of protected areas is structurally connected (Ward et al., 2020). Increasing the share of protected forest areas is necessary but has proven to be difficult, given mounting land-use pressures. In these circumstances, sustainable multifunctional management, involving combinations of land sharing and land sparing, is required to halt further degradation of biodiversity.

The ongoing forest crisis has led to a development of land-sharing management practices aimed at finding a balance between sustainable timber production and protection of other ecosystem services (Messier et al., 2013; Franklin et al., 2018). These practices are holistic, with their roots in the historical continuum of ideas of "ecological forestry" (**Figure 1**, Puettmann et al., 2008; D'Amato et al., 2017). These ideas are embodied in widely applied management concepts and approaches, such as close-to-nature silviculture (Bauhus et al., 2013), retention forestry (Gustafsson et al., 2012), and continuous-cover forestry (Pommerening and Murphy, 2004). Nevertheless, these practices typically have their emphasis on timber production, instead of a balanced treatment of economic, ecological and social values.

The framework of natural disturbance-based forest management goes one step further and provides an ecosystem-based approach, combined with land sharing and land sparing, for reconciling the goals of sustainable forestry, including protecting biodiversity, and maintaining resilience and adaptive capacity of forests (**Table 1**; Drever et al., 2006; Messier et al., 2013). Compared to radical land-sparing solutions, the advantage of land-sharing solutions is that they are more easily applied and adapted to varying local socio-ecological conditions (Angelstam and Elbakidze, 2017; Angelstam et al., 2021b,a).

In a way, natural disturbance-based forest management can be seen as a link between land sparing and land sharing. On the one hand, its principles can be applied for restoration of degraded ecosystems to improve the functionality of land sparing. On the other hand, it can be used to improve the functionality of multi-purpose land sharing aiming at sustainable forest management based on both traditional wood-based value chains, and those based on a wider range of goods, services and values (Jonsson et al., 2019; Angelstam et al., 2020b).

Whatever the chosen forest-management approach, humans unavoidably interfere with the forest ecosystem by extracting timber. This alters a large part of the structures and resources upon which a myriad of forest-dwelling organisms and their communities have adapted to and depend on. There is no perfect solution, but natural disturbance-based management attempts to minimize the negative impacts of timber harvesting to ecosystems by identifying and maintaining key forest-habitat structures and dynamics from micro to macro scales, which can be best expected to support natural species communities and ecological processes at multiple scales (**Figures 3–5** and **Table 1**). This holistic principle defines the ecological foundation of natural disturbance-based forest management. In the following we discuss the advantages and potential limitations of this approach from an application and operational point of view.

Strengths and Advantages

It is not possible to precisely mimic all aspects of natural disturbances in forest management. However, we can use the accumulating knowledge of natural disturbances and their ecological effects at multiple scales in two ways. As the first step, it is possible to adopt a holistic approach, with a general aim to minimize the gap between managed and natural habitat structures across multiple scales by imitating natural disturbances in harvesting operations (**Figures 2–5**; Gauthier et al., 2009). This is the "coarse filter" approach (Hunter, 1993). For example, in forest management of the province of Quebec in Canada, this approach is referred to as ecosystem-based development (Government of Quebec, 2018) and it is based on a solid scientific foundation (Gauthier et al., 2009). Near-to-nature forestry is also emphasized in the EU Biodiversity Strategy (European Commission, 2020) and in the forthcoming EU Forest Strategy.

A comprehensive learning-by-doing strategy or active adaptive management can be implemented in the natural disturbance-based management. This can be accompanied by scientific, experimental and reductionist approaches, with questions or hypotheses concerning the ecological functioning of specific disturbance-related structures or processes (Bergeron et al., 2002; Koivula et al., 2014). This process includes generation of educated hypotheses about ecosystem responses to specific types and qualities of disturbances (Koivula et al., 2014). These hypotheses can in turn be tested in experiments that are based on natural disturbance dynamics or in monitoring protocols in different ecological conditions. The results of this research can then be fed back to management to improve the overall efficiency of the system. Overall, the process can be understood as an active adaptive management cycle built on the natural disturbance-based management approach.

Hypotheses of potential benefits, which can be put forward and tested in the adaptive management framework, may include the following (Kuuluvainen and Grenfell, 2012). (a) Biodiversity criteria: natural disturbance-based management supports the original range of ecological processes and specialized species better than conventional even-aged management or low-retention and continuous-cover management (Siitonen, 2012; Nordén et al., 2013). Evidence supporting this hypothesis comes from comparisons among different logging and retention regimes. (b) Resilience criteria: natural disturbance-based management maintains higher adaptive capacity and resilience to environmental disturbances than conventional even-aged management or low-retention and continuous-cover management (Drever et al., 2006). Comparisons of logging regimes indeed suggest that the original taxonomic and functional composition of species is better retained the higher the retention (Kusumoto et al., 2014; Koivula and Vanha-Majamaa, 2020), with retention patches providing sources for recolonization of adjacent cleared patches. (c) Ecosystem-service criteria: natural disturbance-based management maintains a wider range of ecosystem services, such as carbon sequestration, scenery and recreation, as compared with conventional even-aged management or low-retention and continuous-cover management. (d) Operational feasibility criteria: in forestry, emulation can be implemented at the stand level, whereas transforming the structure of landscapes with a normal harvesting rotation is a decades-long process. Experience from Finnish experiments has shown that quite sophisticated logging variations can be performed with existing business-as-usual machinery (**Figure 5**; Koivula et al., 2014).

Limitations and Challenges

A number of challenges have to be faced when implementing natural disturbance-based management in practice. Firstly, the question of availability of reference systems to guide management and facilitate comparisons needs to be addressed (Kuuluvainen, 2009). Ideally, naturally dynamic landscapes are available and can be used as references and to learn from Landres et al. (1999). This knowledge can then be used to manage ecosystem properties at multiple scales. Unfortunately, naturally disturbed landscapes are in scarce supply in many regions because of post-disturbance (salvage) harvesting or suppression of natural disturbances (Leverkus et al., 2018).

Secondly, even if natural reference systems still exist, their natural or historical disturbance regimes may be poorly known (Kneeshaw et al., 2011; Angelstam et al., 2021b). This applies, for example, for regions such as eastern Eurasia (Siberia), Russian Far-East and western Canada. Thirdly, in more southern areas with long-term and extensive human impact, it may simply be impossible or at least difficult to define historical disturbance regimes. These ecosystems may have departed from their natural range of variation a long time ago (Keane et al., 2006). Because of this, in many human-altered regions the natural disturbance-based management approach may not be easily applicable (e.g., Maeshiro et al., 2013), at least not without a lengthy period of ecological restoration (Angelstam et al., 2021b).

In areas where intensive management is recent or natural forest is harvested, we may assume that environmental adaptations of current forest-dwelling species, communities and ecosystems have developed in past natural forest conditions, including the disturbance regimes of these areas as an important environmental filter. Understanding natural forest conditions, and how these have been modified historically, are key references for sustainable management. Luckily, there is an increasing body of research on past and current natural forest structures and dynamics (Kuuluvainen and Aakala, 2011; Johnstone et al., 2016; Berglund and Kuuluvainen, 2021).

Even if knowledge on past forest conditions and species communities is lacking, the situation is not hopeless. This is because certain structural legacies can be assumed to be common among most forest disturbance regimes (Kneeshaw et al., 2011; **Figure 3**). These include, for example, high variability in sizes of canopy openings (gap dynamics), high vertical and horizontal structural variability, high variability in disturbance return intervals, and abundance of coarse woody debris (Kuuluvainen, 2002; Johnstone et al., 2016). These broad guidelines can be implemented into natural disturbance-based management even if we do not know the details of the historical disturbance regime. In addition, the variability of characteristics may be approximated if general characteristics of a given disturbance regime are known. With these we refer to, e.g., crown fire, mixed fire, surface fire, and fire-independent regimes.

Irrespective of whether the past disturbance regimes are known or not, complication is added by the fact that disturbance regimes are dynamic and constantly changing, and possibly not less so in the future with the warming climate (Gauthier et al., 2015). Hence, the reference disturbance regime may become a moving target. Climate change adds to the overall environmental complexity and unpredictability, and novel combinations and ranges of disturbances are likely to emerge. New species assemblages may emerge, constituting new types of ecosystems with new, or at least different, disturbance types and regimes. Such novel ecosystems may challenge the value of historical and current references as targets of management in the future (Keane et al., 2006).

Most importantly, cutting trees alone is not able to emulate the ecological outcomes of some key natural disturbances. This is perhaps most evident when considering the multiple specific impacts of fire on forest ecosystems compared with harvesting. Such fire impacts include quality and heterogeneity of legacies, changed microclimate, rapid release of nutrients and creation of charred wood and soil surfaces. Nevertheless, the outcome of harvesting operations may emulate certain definable impacts of fire, such as covered area, and the spatio-temporal aspects of structural variation of forests (Koivula et al., 2014; Palik and D'Amato, 2019).

Finally, in addition to management disturbances, there will always be natural disturbances. These two, and their interactions, have to be taken into account to avoid overcutting (Frelich et al., 2018). Because natural disturbances are stochastic phenomena, they make long-term planning of harvesting quota difficult and prediction uncertain. Another challenge in natural disturbance-based management is that, compared to the business-as-usual regime, more retention trees and legacy structures need to be left behind (**Table 1**).

CONCLUSION

Given ongoing global declines in the area of forests, and degradation of their ecological quality, we should urgently adopt management approaches that search for a balance between (1) human management designs, commonly based on homogenization of forest structure for commodity production, and (2) self-emerging heterogeneous ecosystem designs, which promote key ecosystem properties, such as biodiversity, resilience and evolutionary adaptive capacity. However, the currently dominating forest management approaches aimed at sustainability, retention forestry and continuous-cover forestry, may risk failure because they are not compatible with current understanding of ecological dynamics underlying biodiversity, ecosystem resilience and adaptive capacity (**Table 1**). Natural disturbance-based management provides a comprehensive and ecologically sound framework for managing forests for human needs, while maintaining ecosystem health in the rapidly changing global environment.

AUTHOR CONTRIBUTIONS

TK presented the research idea, and led and organized writing. PA, LF, KJ, MK, YK, BL, and EM all significantly contributed to writing and analysis. All authors contributed to the article and approved the submitted version.

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