

A unifying framework for the conservation of biodiversity in multi-functional European forests

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The maintenance and conservation of forest biodiversity has become a pivotal task of ecologically sustainable forest management. It depends on the appropriate management of forest composition and structure and the clever application of different, complementary instruments with respect to biodiversity and ecosystem functions. Most commonly, segregative approaches such as setting aside old-growth refuges, rare forest types, and biodiversity hotspots as protected areas are the preferred conservation instruments due to the high local impact and effectiveness. However, considering the high proportion of multi-functional forests in Europe, the conservation and restoration of forest biodiversity in managed forests make a crucial contribution to the persistence of viable populations of forest-dwelling species since the large majority of the forest area will continue to be managed for various ecosystem functions and services. Some of these services, like timber production, CO₂-sequestration, and recreation, can conflict with forest biodiversity conservation. Therefore, the integration of structural attributes such as oldgrowth stand relicts, patches of open and light forest, ecotones, disturbance gaps, habitat trees, and standing and downed deadwood into managed forests is essential for an ecological, multi-functional forest management. In this chapter, we review the main approaches and instruments of forest biodiversity conservation, discuss their potential and limitation, and analyse to what extent an integrative approach supports the conservation and restoration of native biota in multi-functional forest landscapes. This chapter presents a unifying conceptual framework for the application of a broad set of conservation instruments in an integrated forest management.

< Fig. B 1.1. "Nature forest reserve – nature conservation area – Attention! Danger from deadwood and dry branches". A variety of signposts indicate the trade-off when provisioning different forest goods and services in a Central European forest (Photo: Andreas Rigling).

Introduction

The provisioning of multiple ecosystem functions and services such as timber production, protection against natural hazards, biodiversity conservation, water purification, CO₂ sequestration and recreation is the central objective of modern sustainable forestry (Chapin et al. 2009; Messier et al. 2014). Although the global community agrees on these general services (Isbell et al. 2017; IPBES 2019),

multifunctional management involves trade-offs and there is a debate about the strength of each function and the appropriate methods for the provision of these services (Byrnes et al. 2014; van der Plas et al. 2017). Not least, timber production and biodiversity conservation shows some inevitable incompatibilities (Paillet et al. 2010; Bouget et al. 2012; Newbold et al. 2015; Nagel et al. 2017), for instance with regard to tree species composition, amounts of old-growth forests and natural deadwood, and structural stand heterogeneity related to natural disturbances. After a long period of deforestation in the Middle Ages in Western, Central and Eastern Europe (Bradshaw 2004: Bradshaw and Hannon, 2004; Pausas et al. 2008), forests were heavily exploited in the pre-industrial and early industrial periods (Kaplan et al. 2009) as a resource for timber, wood, fuel, charcoal, litter, fruits, seeds, fodder, and game, largely shaping the structure and composition of today's forest landscapes (Peterken 1996). As a consequence, pristine forests have become very rare and only 0.4-0.7% of Europe's forest area is left to develop naturally (Parviainen 2005; Bücking 2007; Sabatini et al. 2018). By the end of the seventeenth century, the pressure on forest resources resulted in an increasing shortage of timber and a strong need for restoration of the protective function of forest to stop the progressive erosion of the soil, in particular in mountain regions. Therefore, governmental organisations restricted the exploitation of forest resources in Central Europe by new legislations and built up a state-regulated forestry in the eighteenth century. These new systems aimed for re-stocking the former forest area and to build-up sustainable timber resources. The frequently devastated and degraded forest landscapes resembled often open, park-like stands with few old relict trees (Kirby and Watkins 2015). Litter raking and other intensive biomass extraction additionally caused nutrient export from most forest soils.

The forest history in the boreal parts of Europe is slightly different. Here the large-scale use of forests commenced in the early nineteenth century as the forest resources in central Europe diminished and attention was turned to the large tracts of unexploited forests in the north. A timber frontier moved from southwestern Fennoscandia towards northeast and by the early decades of the twentieth century resulted in a significant reduction in standing timber volumes and stands with low

growth rate (Kuuluvainen et al. 2012; Lundmark et al. 2013). Subsequently, forestry has been conducted in Fennoscandia, and since the last decades also in the Baltic, through more intensive clear-cutting forestry including harvesting, ditching, soil scarification, and commonly regeneration with trees from plant breeding programmes. Although highly successful in restoring timber volume and high growth rates, the resulting forests have lost significant aspects of the natural conditions present in the early nineteenth century (Kuuluvainen 2009).

In order to avert a shortage of wood in central Europe, from the middle of the nineteenth century onwards, the deforested areas were often re-stocked with Norway spruce or Scots pine in the government programmes. fast-growing tree species are better able to cope with the ecological conditions on clearcut areas than beech or fir, and rapidly restored overharvested areas. Accordingly, management concepts with a focus on productive and vital stands with regular high yields became widespread in Central Europe (Otto 1993). Depending on landscape properties and forest history, this has favoured two main forestry systems: (1) the clear-cutting or group shelterwood systems resulting in even-aged and mostly single-species stands which are widespread in large parts of Central-eastern and Northern Europe, and (2) irregular shelterwood and single tree/group selection systems (e.g. "Femelschlag" and "Plenterwald/Jardinage") resulting in uneven-aged or irregular, multi-species stands, typically found in mountainous regions in Switzerland, France, Germany, and Slovenia (Heyder 1986; Schütz 1993; Bauhus and Pyttel 2015). The latter group is often associated with close-to-nature forestry or continuous cover forest ("Dauerwald") management as the prevailing silvicultural philosophy.

Even though the two systems differ greatly in biological, ecological, and technical principles, both are directed to optimise regular timber yields of desired species in targeted dimensions (Jacobsen 2001). These diameters correspond to production cycles of about 80–140 years (oaks to 160–180 years) that deviate in many structural and compositional characteristics from natural forests as complex, multi-scaled hierarchical ecosystems with a succession cycle of several hundreds of years in temperate and boreal regions (Franklin et al. 2002; Puettmann

et al. 2009; Angelstam and Kuuluvainen 2004; Lilja et al. 2006). Uneven-aged as well as even-aged management with regular harvesting interventions impedes the development of characteristic structures of mature natural forests (Franklin et al. 1981; Kuuluvainen 2002b) and excludes the species-rich, old-growth communities (Siitonen 2001; Honnay et al. 2004; Winter and Möller 2008; Palo et al. 2013). In addition, the early seral, pre-forest phase of succession is under-represented (Hilmers et al. 2018) because pre-regeneration and planting accelerate stand development and hamper the establishment of species-rich pioneer plant and animal communities (Swanson 2011; Winter et al. 2015). However, from the forest management perspective, concerns have also been raised about the future of monocultures because of their susceptibility to insect calamities, and about the sensitivity to natural disturbances of even-aged stands (Jactel et al. 2009; Seidl et al. 2011). Examples include the large storm events in the early and late 1990s in Central Europe and in 2005 in Scandinavia and the strong bark beetle outbreaks in both regions in recent years. Moreover, even-aged forests with little between-stand variability are expected to contribute less to multi-functionality than heterogeneous forests because their species communities are less diverse and show higher functional similarity (Blüthgen et al. 2016; van der Plas et al. 2017; Craven et al. 2018). However, recent work (Redon et al. 2014: Schall et al. 2017) has shown that gamma diversity of forest-dwelling species can be higher in landscapes comprised of combinations of even-aged stands at different development stages.

These findings in combination with a better understanding of the effects of forest management on biodiversity (Lindenmayer et al. 2006; Paillet et al. 2010; Newbold et al. 2015; Kaufmann et al. 2018) and ecosystem functions (Gamfeldt et al. 2013; van der Plas et al. 2016; Ratcliffe et al. 2017) caused a momentum for new, biodiversity-friendly and sustainable forest management practices in the last 10 to 20 years (Felton et al. 2010; Bollmann and Braunisch 2013: Fedrowitz et al. MacDicken et al. 2015). The new practices integrate the requests and needs of various stakeholders while at the same time considering the diversity and heterogeneity of mature stands with their structures, functions, and species. However, current policies for more 'bioeconomy' in the European Union (Winkel 2017) support an intensified use of renewable resources such as wood and wood residues from forests. This development can significantly impede the recent progress for more biodiversity-friendly, sustainable forestry systems if no accompanying measures are taken for the preservation of biodiversity as basis for forest goods and services (Bauhus *et al.* 2017).

Most initiatives for biodiversity-friendly forest management systems are based on the concept of graded forest-use intensities across the landscape (Bollmann and Braunisch 2013), or the concepts of land sharing and land sparing and their effectiveness for different forest functions (Edwards et al. 2014: Kremen 2015: Balmford et al. 2019). In general, there are three forest management approaches that combine these concepts in different ways and strive to supply the demand for timber and other forest products while minimising the negative impacts on forest biodiversity (Table B 1.1). The first and integrative approach supports the concept of multifunctional forest management by aiming at satisfying the environmental, social, and economic functions on the same forest land, often implying moderate timber yields (Lindenmayer et al. 2012). In the second and segregative approach, one part of the landscape is dedicated to high yield timber production, the other is free of harvesting and completely dedicated to conservation (Paguette and Messier 2010). The third approach, called TRIAD, divides the forest into three separate zones of complementary functions, namely intensive timber production (high yield), multiple use forestry (moderate yield), and biodiversity conservation (no yield) (Seymour and Hunter 1999). All three approaches have advantages and disadvantages and the usefulness and applicability of one or the other approach depends on the natural and cultural legacy of a forest landscape and national policy rules (Table B 1.1). While the TRIAD system has gained popularity in some areas of North America (Côté et al. 2010; Tittler et al. 2012), segregative approaches can be found in regions with subsistence agriculture, plantation or clearcut forestry (Scharlemann et al. 2010; Hansen et al. 2013; Keenan et al. 2015; Morales-Hidalgo et al. 2015). The integrative approach is traditionally considered in various selection harvest systems in old cultural, multifunctional landscapes with high ownership densities (Bauhus et al. 2013), such as Mediterranean, temperate, and montane Europe. In Central Europe, integrative approaches are currently largely directed towards retention of habitat trees and deadwood (Gustafsson et al. 2020a). Such measures are also essential in boreal north Europe as are leaving buffer zones along watercourses and around wetlands, and retention of forest patches (Gustafsson et al. 2020b), partly through the introduction of forest certification (Gustafsson et al. 2020a). In Europe, the share of forest area available for wood supply amounts to 79 % (Forest Europe 2015), 52 % is primarily designated for production (Köhl et al. 2015), and 9 % are classified as plantations. Europe's long history of deforestation and area-wide cultivation with multi-purpose forest systems such as wood pastures and coppice silviculture

(Kirby and Watkins 2015), and the consequent shortage of pristine forests (Sabatini *et al.* 2018) as well as recent periods of intensive forest use with changing preferences for certain tree species (i.e. oak, spruce) may be the main reasons for the popularity of the integrative approach.

Forest biodiversity conservation: current practices and future requirements

Preserving habitats from human influence by separating natural forests and biodiversity hotspots from detrimental processes is the traditional conser-

Table B 1.1. Comparison of different management systems and their strengths, weaknesses, and appropriateness for forest biodiversity conservation.

	Integrative management system	Segregative management system	TRIAD-system
Strengths	An area-wide representation of minimal habitat quality for general forest biodiversity; regular distribution of key habitat features; gradual ecological differences between forests; often natural regeneration and self-thinning processes; flexibility to respond to unforeseen developments	Spatially explicit production and conservation zones; spatially concentrated harvesting activities within forest landscape; reduced extent of road system; supports natural processes in relatively large conservation zones	Clearly defined zonation system; superior ecosystem service per zone; concentrated harvesting activities within forest landscape; significant amounts of area are devoted to forest biodiversity; supports natural and dynamic forest development in a significant share of the landscape
Weaknesses	Multiple management directions per forest – can be ineffective and create conflicts between stakeholders; can impair the conservation of specialist forest species due to the rarity of old-growth forests; extended forest road system; regular management interventions; emphasis on managing small areas as multi-species, uneven-aged stands may lead to static forest land-scapes; can discriminate light-demanding species	Patchy and often isolated distribution of forest biodiversity zones; mostly embedded in a matrix of production or non-forest; fixed spatio-temporal zoning with superior functions; sharp ecological differences between zones; regeneration in production zone through planting and sowing; can increase resource vulnerability to disturbance or pathogens in production zone	Requires relatively large and continuous forest landscapes with large properties; distinct habitat quality differences between zones; fixed spatio-temporal zoning; regeneration in production zone often through planting and sowing; partial isolation of biodiversity zones
Appropriateness	Regions with a long tradition of area-wide forest use and an extensive road network; regions with a patchy distribution of forest in an intensively used matrix and a clear under-representation of primeval forests; regions with high ownership density and stakeholder participation	Regions with a significant amount of remote, primeval and old-growth forests, and an above-average proportion of endemism; regions with distinct zones of production forestry; regions with low proportion of forest area under management plan and high demands for wood fuel	Regions with large forest landscapes, low human population densities and different development standards of the forest road network; allows addressing bioeconomic and conservation objectives in spatial explicit, neighbouring zones; need for large forest properties (public or companies) and limited stakeholder participation

vation approach and is still considered the "cornerstone" of national and regional conservation strategies (Margules and Pressey 2000; Gustafsson and Perhans 2010; Watson et al. 2014). Forest areas designated primarily for biodiversity conservation account for 13% of the world's forest (FAO 2010), and 16% (5% in Europe, incl. Russian Fed.) are legally protected areas (Morales-Hidalgo et al. 2015). Some larger intact forest landscapes still occur in Europe, e.g. in the Carpathians, the Dianaric mountains, in the "green belts" along the Finnish-Russian border and on the eastern slopes of the Scandinavian Mountain range (Potapov et al. 2017; Sabatini et al. 2018, Jonsson et al. 2019). However, these remnants of pristine forests are exceptions and even a significantly enlarged reserve network is considered to be insufficient to preserve biodiversity (Bengtsson et al. 2003; Sabatini et al. 2020). The large majority of the forest area will continue to be used and an embedded network of a limited number of spatially segregated reserves is unlikely to support viable populations of all native, forest-dwelling species (Fahrig 2020). Therefore, many countries combine set-aside measures for the last remaining pieces of natural and old-growth forests (Parviainen et al. 2000; MCPFE 2003) with an integrative approach on the managed forest area. Such a dual approach corresponds to the Aichi targets #7 (reduce pressure on biodiversity by sustainable use) and #11 (improve status of biodiversity by safequarding ecosystems) of the Convention on Biological Diversity (CBD 2011). There is a strong need for innovative systems dealing with the promotion of biodiversity in managed forests. Integrative measures strive to increase the structural diversity and resource availability by retaining and creating important, permanent or semi-permanent habitat elements such as habitat trees, deadwood and forest gaps at the single forest stand scale (Bauhus et al. 2009; Puettmann et al. 2009; Bollmann and Braunisch 2013; Emberger et al. 2013; Messier et al. 2014). Case studies on integrative management approaches have shown that restoration measures can significantly improve habitat quality and biodiversity at the stand and forest scale within a decade time period (e.g. Doerfler et al. 2017; Roth et al. 2019). Although there is still an ongoing debate regarding the appropriateness and effectiveness of integrative measures (e.g. Gustafsson et al. 2012), in particular the quantities and threshold needed for optimal conservation, it is unlikely that they will be

enough to restore the integrity of European forest and biodiversity (e.g. Bollmann and Braunisch 2013). A structural retention approach in managed forests in combination with the currently small area share of forest reserves is unlikely to represent the entire spectrum of ecological conditions of natural forest ecosystems (Sabatini et al. 2020). Natural disturbance agents such as wind, fire, snow, and water are important ecological drivers of natural forests and have strongly influenced the co-evolution of forest biodiversity (Bengtsson et al. 2000; Franklin et al. 2002; Kuuluvainen 2002a). Wind, fire, and water create stands with large amounts of deadwood (i.e. resource pulse) and associated saproxylic species community (Seibold et al. 2016). These structurally heterogeneous stands provide favourable microclimatic conditions in their early seral stage for the natural establishment of a rich herb and shrub layer with the associated insect community (Winter et al. 2015). Hence, the integration of disturbed stands and early seral stages in forest and biodiversity management is an important element of future conservation strategies. The permanent or temporary delineation of disturbed areas as post-disturbance patches will support forest restructuring and adaptation processes and thereby complement traditional integrative conservation measures (Bollmann and Braunisch 2013). The integration of naturally disturbed stands in forest management will gain in importance under climate change conditions and offers the opportunity to adapt conservation objectives situationally and to accelerate adaptations. The post-disturbance patches should be segregated from management in the first phase of forest succession (15–25 years) and can be later integrated in the area-wide forest management. The combination of integrative and segeregative measures with disturbed forest patches for a pre-defined period in a forest enterprise results in mosaic-like forests with structurally rich stands in different successional stages (Krumm et al. 2013). This is considered favourable for biodiversity conservation as mosaic forest landscapes have been shown to support a high diversity of species and taxa at the regional scale (i.e. multi-taxa gamma-diversity; Schall et al. 2017; Fahrig et al. 2019).

In this book chapter, we present a conceptual framework and the instruments for the conservation of species-rich forest communities. We refer to ecological forest management that intends to keep forests within their natural range of composition, struc-

ture and function and hereby provides habitats for viable populations of native forest species. We briefly present the limiting factors with respect to maintaining viable populations and put a special emphasis on comparing the main instruments for the conservation of biodiversity in the frame of an ecologically sustainable forest management. Influenced by forest ownership, biophysical conditions and socio-economic demands, forest management can create structurally and compositionally heterogeneous forests that provide a multitude of niches for the conservation of forest-dwelling species from stand to landscape scales. We further stress that, although operational management mainly takes place within single stands, landscape structure, composition and connectivity must be included in strategic planning of prioritised conservation approaches to build functional green infrastructures (European Commission 2013).

Limiting factors to forest biodiversity

Forest ecosystems comprise thousands of interacting species that are affected by a variety of abiotic and biotic factors (Noss 1990; Landres et al. 1999). Typical forest-dwelling taxa such as fungi, lichens, beetles, and snails depend on long-term successional processes that are significantly influenced by the life-history of trees and the spatio-temporal dynamics of forest stands (Speight 1989; Siitonen and Saaristo 2000; Lassauce et al. 2011; Dymytrova et al. 2013). Large, senescent trees with their microhabitats and deadwood are characteristic of oldgrowth, primary forests, and are the main resources of saproxylic organisms that contribute about 20-30% of forest species richness (Siitonen 2001; Larrieu et al. 2018; Stokland et al. 2012). Even-aged production stands with rotation cycles of about 80-140 years, as being common in several parts of Europe, are structurally homogeneous and differ considerably from natural forests. Only 0.7% of European forests remain pristine – with key areas in Finland, Sweden, the Carpathians, and the Balkans (Sabatini et al. 2018). Hence, there is an urgent need to strictly protect the last remnants of pristine forests and segregate them from demands of other forest functions, a call clearly expressed in the recent EU Biodiversity strategy (European Commission 2020; Sabatini et al. 2020). These forests are characterised by habitat continuity, shaped by long-term

successional processes, and modulated by periodic natural disturbances (White and Pickett 1985; Attiwill 1994; Korpel 1995). Large old-growth and pristine forests can contain structurally complex stands with notable amounts of deadwood and large giant trees with plenty of microhabitats, and thus, a high variety of saproxylic species (e.g. Stokland et al. 2012). In particular, "Urwald relict" species have been shown to be strongly dependent on habitat continuity (Martikainen et al. 2000; Müller et al. 2005; Moning et al. 2009; but see also Ohlson et al. 1997). Delineating formerly managed forests as forest reserves is a possibility to trigger natural processes and the development of old-growth characteristics within multi-purpose forest landscapes (Vandekerkhove et al. 2009; Motta et al. 2015; Paillet et al. 2015). In summary, native forest biodiversity depends on several factors that should be considered in conservation strategies for production forest landscapes: (a) structure, (b) resources, (c) composition, and (d) processes (Jonsson and Siitonen 2013). These factors vary with the tree, stand, forest, and landscape scales.

- (a) **Structures**: forest structures like old trees, tree microhabitats, multi-layered stands, standing and lying deadwood, and pits and mounds are more abundant in long-term unmanaged forest (Winter et al. 2005; Larrieu et al. 2012) and have been shown to be positively related to saproxylic species richness (Angelstam et al. 2003; Jonsson et al. 2005; Lachat et al. 2012; see also Rolstad et al. 2004) but also to mammals and birds (Harmon et al. 1986; Angelstam et al. 2003; Nagel et al. 2017; Mikusiński et al. 2019).
- (b) Resources: abiotic or biotic factors like water, light, nutrients, food, breeding sites, and their spatial abundance and distribution – that are related to area and connectivity – influence species communities of forest ecosystems. Shortage in any of these factors may negatively impact on species presence and abundance (Kimmins 2004).
- (c) Tree species composition: trees, dead or alive, are the most abundant organisms regarding biomass and structure. Thus, the co-occurrence and trophic relationship between tree species and herbivores, granivores, and frugivores varies with tree species composition. Tree species richness and functional diversity have been shown to be key drivers of forest-associated biodiversity and trophic interactions at the



Fig. B 1.2. The restoration of former coppice with standard forests is an effective measure for the conservation of threatened, light-demanding forest species such as the scarce heath (Coenonympha hero) in this project area (Photo: Kurt Bollmann).

Table B 1.2. Important structural and compositional factors of high-diversity forest stands.

Site factors	Soil conditions and local climate are essential factors for plant and tree species composition	
Light and microclimate	Large variation in light and temperature promotes diversity of herbs, forbs, shrubs, trees, and insects of forest stands	
Stand structure	Large vertical and horizontal variation in stand structure creates many ecological niches and promotes species diversity	
Old and dead trees of various decaying stages	Many species from the diverse groups of saproxylic insects, bryophytes, lichens, and fungi are habitat specific with regard to type of wood and decaying stage	
Tree microhabitats	Coarsely fissured bark, branch and rot holes, fruit-bearing shrubs, lianas, and trees can serve as key structures which improve habitat quality for lichens, bats, small mammals, and insects	
Continuity and maturity	The continuous development and the maturity of a forest ecosystem often increase ecological niches and the complexity of food-networks. Some fungi are dependent on late decaying stages of deadwood, others on years of undisturbed litter for the development of their mycelia	
Disturbances	Disturbances such as browsing, pathogens, windthrows, wildfire and snow breaks increase the number of dead trees and usually creates gaps and other irregularities, and hereby promotes early-successional species, some of which may be uncommon	
Early successional habitats	Early successional habitats originating from clearings and natural disturbances are rich in pioneer and light-demanding species, but underrepresented in many forestry systems due to planting and salvage logging activities	
Edgeline effects	Transition zones between clearings and natural gaps (e.g. disturbance gaps, mires) and closed forests create an edgeline effect with highly different temperature and light conditions at small scales. Such ecotones have often a positive effect on species diversity, but can threaten typical forest species through competition by open habitat or edge species in fragmented forest landscapes	
Mosaic of different vegetation types	Spatial heterogeneity in vegetation types (patchiness) increases the diversity of ecological niches for forest dwelling species. The asynchronous development of such patches creates a successional mosaic cycle	
Size and connectivity of habitats	Size and degree of spatial isolation of forest stands (fragmentation) affect the probability of local extinctions and recolonisation of species	

- stand level (Ampoorter et al. 2020; Staab et al. 2015). Some tree species like oak (Quercus spp.), hornbeam (Carpinus spp.), and poplar/aspen (Populus spp.) are known to provide habitat for several hundreds of forest organisms (e.g. Kennedy and Southwood 1984).
- (d) Processes and disturbances: two types of processes are crucial in forests; disturbance and succession (Holling 1987; Mori 2011). They are closely linked and influence the availability and quality of habitat resources and their spatio-temporal occurrence (Kuuluvainen 2002b). They support a mosaic-cyclic-succession (Bengtsson et al. 2000) and are increasingly considered as being important for natural adaptation and transition processes under climate change (Dietz et al. 2020; Millar et al. 2007).

Factors that increase the structural and compositional heterogeneity of forests stands are an important pre-requisite for high diversity in forest land-scapes. They include abiotic site factors, the

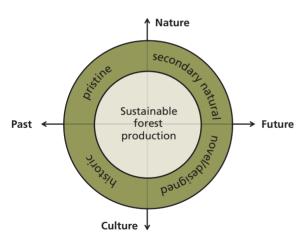


Fig. B1.3. Anthropogenic impact on forest biodiversity is conceptually related to two dimensions Naturalness (from nature to culture) and Time (from past to future) with two reference condition: past/historic and future/novel. Sustainable forest production covers the central part (light brown) of the concept and makes the basic contribution to biodiversity conservation by integrating retention measures (i.e. integrative forestry). Segregative measures aiming at preserving, restoring, designing and re-wilding areas of high conservation values make a complementary contribution (green) to the effects of integrative forestry. They should be applied in areas where they can achieve the best effect for biodiversity conservation within one of the four reference sectors (secondary natural, novel/designed, historic, and pristine).

occurrence of old and decaying trees, microhabitat structures, the abundance and distribution of disturbances and ecotones, and the size and connectivity of various habitat patches (Table B 1.2). Modern forest management integrates the spatial occurrence and distribution of these factors into biodiversity conservation planning under consideration of the regional environmental properties and policy rules.

Conceptual framework and conservation instruments

Conservation actions in human-dominated, multi-purpose landscapes can be arranged along two dimensions with four reference conditions. The first dimension covers the gradient between nature and culture (naturalness), and the second dimension represents the temporal axis ranging from the past to the future (time) (fig. B 1.3). Reference conditions for the past correspond to pristine forests or to historic forest types of high conservation value (e.g. coppice with standards (fig. B 1.2), forest pastures, chestnut orchards). Today's remnants of historic forest management systems benefit forest species that are promoted by light and temperature and are associated with a mosaic of open and stocked habitats (e.g. Lassauce et al. 2012; Mullerova et al. 2015; Miklin et al. 2018). One means to restore natural processes is to withdraw forests from use and let them develop freely within the borders of a strict forest reserve. However, such secondary natural forests need centuries to develop typical habitat characteristics of primary forest (Lilja et al. 2006; Paillet et al. 2015; Paillet et al. 2017; Braunisch et al. 2019). A second reference condition for the future are to design forests towards a desired ecosystem service such as timber production, CO₂-sequestration, or recreation. Proactive approaches for the promotion of biodiversity under novel forms of production forestry have not been sufficiently evaluated so far. However, "Nature by design" (Higgs 2003) has already become a form of biodiversity promotion in human-dominated landscapes (e.g. Koh and Gardner 2010) and is an option to be considered in regions with large areas of plantation forests (Brockerhoff et al. 2008; Bernes et al. 2015).

A conceptual framework that distinguishes between these axes and reference conditions incor-

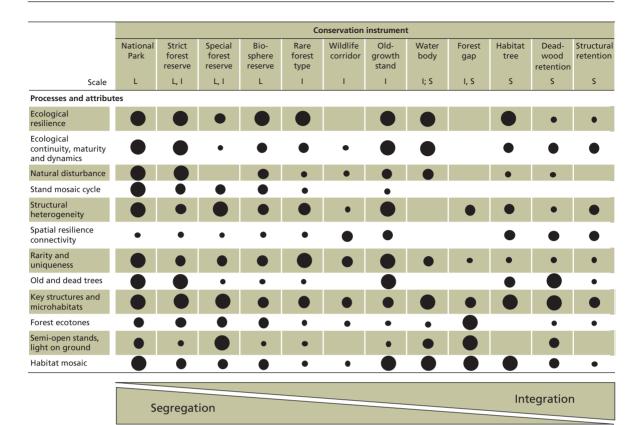


Fig. B 1.4. Conservation instruments to consider important processes and attributes of forest biodiversity. The effective application of the instruments depends on the appropriate scale (L[arge] = regional or forest scale; I[ntermediate] = stand scale; S[mall] = tree scale), and therefore are better suited for integrative or segregative approaches. The supposed conservation impact of the different instruments is indicated with bullets (● = high; • = moderate; · = low). Strict forest reserve: conservation area left to natural development without interventions, Special forest reserve: area with conservation measures through active management, Biosphere reserve: protected landscape with three zones of graded land-use intensities (preservation, sustainable use, socio-economic development).

porates past and future temporal dimensions and offers both the opportunity to preserve remnants of natural and cultural legacies and the opportunity to restore and create forests with biodiversity-friendly forest management practices next to self-organising habitats (e.g. secondary natural forests, wilderness areas).

There are different instruments of the conceptual framework that can be used in a given forest enterprise (fig. B 1.4). The effective use and appropriateness of the instruments depend on the particular situation with regard to the natural species pool, the biophysical conditions, ownership structure and economic demands.

A clever, systematic, and area-specific combination of different conservation instruments

In a systematic conservation approach, integrative and segregative conservation instruments are combined and applied along the dimensions time and naturalness in the conceptual framework (fig. B 1.3). Sustainable production forestry sets the ecological baseline by providing a minimum habitat quality for generalist forest species on the overall forest area (Bollmann *et al.* 2009). The application of different conservation instruments, some of them more suitable for an integrative approach, others for a segregative approach, make an addi-



Fig. B 1.5. Standing and downed deadwood provide habitat for 20–30 % of total forest species (Photo: Kurt Bollmann).

tional contribution to the conservation of a representative forest biota (fig. B 1.4). Tree species diverse forests in combination with the conservation of important structures such as old trees with microhabitats, rocky outcrops, aquatic elements, gaps, and structured forest edges can be an integral part of an area-wide sustainable forest production. The same applies to crucial resources such as standing and downed deadwood (fig. B 1.5) that constitute a limiting factor in most managed forests (reviewed by Jonsson et al. 2005; Stokland et al. 2012: Müller and Bütler 2010: Lassauce et al. 2011). The potential for the integration of rare forest types and biotopes into managed forests depends on the size of the objects, and segregation is the appropriate approach for larger areas of high conservation value (e.g. national park, strict forest reserve, rare forest type, historic conservation forest, wildlife corridor) that require a separate and permanent protection and management.

A biodiversity conservation strategy that combines the advantages of integrative and segregative instruments improves habitat quality across managed forests and landscapes due to the areawide retention of important habitat features at the tree (e.g. 'methuselah' trees) (fig. B 1.6) and stand (e.g. old-growth or early seral) scale and the preservation of entire forests or stands of high conservation concern (e.g. forest reserve, rare forest type) (Doerfler et al. 2018). According to new findings (Fahrig 2020), such an approach is considered to be effective because it puts more emphasis to the conservation of small key structures and patches than on larger reserves which will continue to be the rarer conservation elements in managed forest landscapes. As a consequence, conservation efforts may vary across the forest enterprise in relation to site specificity, rarity and uniqueness of the different habitats or stands. Thus, the strategy can be adapted flexibly to regional forest and conservation



Fig. B 1.6. Retaining old trees is a widespread conservation measure of integrative forestry (Photo: Kurt Bollmann).

planning or to the occurrence of natural disturbances (fig. B 1.7). It is applicable under different ecological, societal, and economic conditions and can be adapted to various ownership situations. A conservation strategy that combines integrative and segregative measures and increasingly considers disturbance agents and processes in the forest management places a special emphasis on biodiversity conservation on the entire forest landscape while simultaneously supporting adaptive processes. Such a combined forest management approach increases overall habitat suitability, functionality, and connectivity. If carefully designed, and taking landscape connectivity into account, it will significantly improve the possibility to establish a functional green infrastructure (e.g. Arts et al. 2017; Mergner 2018; Angelstam et al. 2020).

Conclusions

Maintaining and restoring representative autochthonous forest biota, from genes to entire species communities, requires a comprehensive hierarchical concept that combines segregative (reserves) and integrative (off-reserve) conservation instruments at different spatial scales from single trees to forest landscapes. Such a dual concept tries to optimise the advantages and disadvantages of a pure segregative or integrative forest management. Optimally, it retains and conserves important and rare habitat elements across the entire forest landscape and complements it with a network of reserves and post-disturbance patches. The reserves can develop into secondary, old-growth forests, thus providing habitat for viable populations of rare forest species in a multi-purpose landscape. They serve as biodiversity refuges and functionally link the biodiversity trends in the reserves with species communities in the production forests and post-disturbance patches.

Such a unifying framework provides a flexible ap-proach for foresters and conservationists to take measures in favour of the regional conservation objectives. A broad spectrum of instruments that can take advantage of a large variety of ecological, societal, and economic properties seems to be especially helpful when it comes to applying them in different cultural and political situations (see Synthesis chapter). The measures should be planned at the regional scale according to the four reference

conditions of the conceptual framework (fig. B 1.3) and consider the natural history and cultural legacy of the landscape, as well as the future needs of the different stakeholders.

References

Ampoorter, E.; Barbaro, L.; Jactel, H.; Baeten, L.; Boberg, J.; Carnol, M.; et al., 2020: Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. Oikos 129: 133–146.

https://doi.org/10.1111/oik.06290

Angelstam, P.K.; Butler, R.; Lazdinis, M.; Mikusinski, G.; Roberge, J.M., 2003: Habitat thresholds for focal species at multiple scales and forest biodiversity conservation dead wood as an example. Annales Zoologici Fennici 40: 473–482.

Angelstam, P.; Kuuluvainen, T., 2004: Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecological Bulletins 51: 117–136.

Angelstam, P.; Manton, M.; Green, M.; Jonsson, B.G.; Mikusinski, G.; Svensson, J.; Sabatini, F.; 2020: Sweden does not meet agreed national and international forest biodiversity targets: a call for adaptive landscape planning. Landscape and Urban Planning 202: 103838.

https://doi.org/10.1016/j.landurbplan.2020.103838

Arts, B.; Buizer, M.; Horlings, L.; Ingram, V.; Van Oosten, C.; Opdam, P., 2017: Landscape approaches: a state-ofthe-art review. Annual Review of Environment and Resources 42: 439–463.

https://doi.org/10.1146/annurev-environ-102016-060932 Attiwill, P.M., 1994: The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247–300. https://doi.org/10.1016/0378-1127(94)90114-7

Balmford, B.; Green, R.E.; Onial, M.; Phalan, B.; Balmford, A., 2019: How imperfect can land sparing be before land sharing is more favourable for wild species? Journal of Applied Ecology 56: 73–84.

https://doi.org/10.1111/1365-2664.13282

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

https://doi.org/10.1016/j.foreco.2009.01.053

Bauhus, J.; Puettmann, K.J.; Kühne, C., 2013: Close-to-nature forest management in Europe: Compatible with managing forests as complex adaptive ecosystems? In: Messier, K.; Puettmann, K.J.; Coates, K.D. (eds), Managing forests as complex adaptive systems: Building resilience to the challenge of global change. Routledge, London. 187–213.

Bauhus J.; Kouki, J.; Paillet, Y.; Asbeck, T.; Marchetti, M., 2017: How does the forest-based bioeconomy impact forest biodiversity? In: Winkel, G. (ed.) Towards a sustainable European forest-based bioeconomy – assessment and the way forward. What Science Can Tell Us 8, European Forest Institute. 67–76.



Fig. B 1.7. Natural disturbance agents such as wind have strongly influenced the evolution of forest biodiversity. Therefore, the integration of disturbed stands in forest management supports adaptive ecological processes and the promotion of a rich biodiversity that depends on a favourable microclimate and/or large deadwood amounts (Photo: Kurt Bollmann).

Bauhus, J.; Pyttel, P., 2015: Managed forests. In: Peh, K. S.-H.; Corlett, T.R.; Bergeron, Y. (eds) Routledge Handbook of Forest Ecology. Routledge, Oxon.

Bengtsson, J.; Angelstam, P.; Elmqvist, T.; Emanuelsson, U.; Folke, C.; Ihse, M.; Moberg, F.; Nystrom, M., 2003: Reserves, resilience and dynamic landscapes. Ambio 32: 389–396. https://doi.org/10.1579/0044-7447-32.6.389

Bengtsson, J.; Nilsson, S.G.; Franc, A.; Menozzi, P., 2000: Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132: 39–50.

https://doi.org/10.1016/S0378-1127(00)00378-9

Bernes, C.; Jonsson, B.G.; Junninen, K.; Löhmus, A.; Macdonald, E.; Müller, J.; Sandström, J., 2015: What is the impact of active management on biodiversity in boreal and temperate forests set aside for conservation or restoration? A systematic map. Environmental Evidence 4: 25. https://doi.org/10.1186/s13750-015-0050-7

Blüthgen, N.; Simons, N.K.; Jung, K.; Prati, D.; Renner, S.C.; Boch, S.; Fischer, M.; Holzel, N.; Klaus, V.H.; Kleinebecker, T.; Tschapka, M.; Weisser, W.W.; Gossner, M.M., 2016: Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. Nature Communications 7: 10697.

https://doi.org/10.1038/ncomms10697

Bollmann, K.; Bergamini, A.; Senn-Irlet, B.; Nobis, M.; Duelli, P.; Scheidegger, C., 2009: Konzepte, Instrumente und Herausforderungen bei der Förderung der Biodiversität im Wald [Concepts, instruments and challenges for the conservation of biodiversity in the forest]. Schweizerische Zeitschrift für Forstwesen 160: 53–67. https://doi.org/10.3188/szf.2009.0053

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

Bouget, C.; Lassauce, A.; Jonsell, M., 2012: Effects of fuel-wood harvesting on biodiversity – a review focused on the situation in Europe. Canadian Journal of Forest Research 42: 1421–1432.

https://doi.org/10.1139/x2012-078

- Bradshaw, R.H.W., 2004: Past anthropogenic influence on European forests and some possible genetic consequences. Forest Ecology and Management 197: 203– 212. https://doi.org/10.1016/j.foreco.2004.05.025.
- Bradshaw, R.H.W.; Hannon, G.E., 2004: The Holocene structure of north-west European temperate forest induced from palaeoecological data. In: Honnay, O.; Verheyen, K.; Bossuyt, B. (eds), Forest biodiversity: Lessons from history for conservation. IUFRO, Louvain, Belgium. 11–25.
- Braunisch, V.; Roder, S.; Coppes, J.; Froidevaux, J.S.P.; Arlettaz, R.; Bollmann, K., 2019: Structural complexity in managed and strictly protected mountain forests: Effects on the habitat suitability for indicator bird species. Forest Ecology and Management 448: 139–149. https://doi.org/10.1016/j.foreco.2019.06.007
- Brockerhoff, E.G.; Jactel, H.; Parrotta, J.A.; Quine, C.P.; Sayer, J., 2008: Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17: 925–951. https://doi.org/10.1007/s10531-008-9380-x
- Bücking, W., 2007: Naturwaldreservate in Europa [Strict Forest Reserves in Europe]. Forstarchiv 78: 180–187.
- Byrnes, J.E.K.; Gamfeldt, L.; Isbell, F.; Lefcheck, J.S.; Griffin, J.N.; Hector, A.; Cardinale, B.J.; Hooper, D.U.; Dee, L.E.; Duffy, J.E., 2014: Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5: 111–124. https://doi.org/10.1111/2041-210X.12143
- CBD, 2011: Strategic Plan for Biodiversity 2011–2020, including Aichi Biodiversity Targets. Convention on Biological Diversity (CBD), Montreal, Quebec, Canada. https://www.cbd.int/sp/
- Chapin, F.S.; Kofinas, G.P.; Folke, C., 2009: Principles of Ecosystem Stewardship: Resilience-based natural resource management in a changing world. Springer, New York. https://doi.org/10.1007/978-0-387-73033-2
- Côté, P.; Tittler, R.; Messier, C.; Kneeshaw, D.D.; Fall, A.; Fortin, M.J., 2010: Comparing different forest zoning options for landscape-scale management of the boreal forest: Possible benefits of the TRIAD. Forest Ecology and Management 259: 418–427.
 - https://doi.org/10.1016/j.foreco.2009.10.038
- Craven, D.; Eisenhauer, N.; Pearse, W.D.; Hautier, Y.; Isbell, F.; Roscher, C.; et al., 2018: Multiple facets of biodiversity drive the diversity-stability relationship. Nature Ecology & Evolution 2: 1579–1587.
 - https://doi.org/10.1038/s41559-018-0647-7
- Dietz, L.; Collet, C.; Dupouey, J.L.; Lacombe, E.; Laurent, L.; Gegout, J.C., 2020: Windstorm-induced canopy openings accelerate temperate forest adaptation to global warming. Global Ecology and Biogeography. https://doi.org/10.1111/geb.13177
- Doerfler, I.; Gossner, M.M.; Müller, J.; Seibold, S.; Weisser, W.W., 2018: Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. Biological Conservation 228: 70–78.
 - https://doi.org/10.1016/j.biocon.2018.10.013

- Doerfler, I.; Müller, J.; Gossner, M.M.; Hofner, B.; Weisser, W.W., 2017: Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management 400: 607–620.
 - https://doi.org/10.1016/j.foreco.2017.06.013
- Dymytrova, L.; Nadyeina, O.; Naumovych, A.; Keller, C.; Scheidegger, C., 2013: Primeval beech forests of Ukrainian Carpathians are sanctuaries for rare and endangered epiphytic lichens. Herzogia 26: 73–89. https://doi.org/10.13158/heia.26.1.2013.73
- Edwards, D.P.; Gilroy, J.J.; Woodcock, P.; Edwards, F.A.; Larsen, T.H.; Andrews, D.J.R.; et al., 2014: Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Global Change Biology 20: 183–191. https://doi.org/10.1111/gcb.12353
- Emberger, C.; Larrieu, L.; Gonin, P., 2013: Dix facteurs clés pour la diversité des espèces en forêt. Comprendre l'Indice de Biodiversité Potentielle (IBP). Institut pour le développement forestier, Paris, 56 p.
- European Commission, 2013. Green Infrastructure (GI) Enhancing Europe's natural capital. European Commission: Environment, Brussels.
- European Commission, 2020: EU Biodiversity strategy for 2030 Bringing nature back into our lives. European Commission COM(2020) 380.
- Fahrig, L., 2020: Why do several small patches hold more species than few large patches? Global Ecology and Biogeography 29: 615–628.
 - https://doi.org/10.1111/geb.13059
- Fahrig, L.; Arroyo-Rodriguez, V.; Bennett, J.R.; Boucher-Lalonde, V.; Cazetta, E.; Currie, D.J.; *et al.*, 2019: Is habitat fragmentation bad for biodiversity? Biological Conservation 230: 179–186.
 - https://doi.org/10.1016/j.biocon.2018.12.026
- FAO, 2010: Global Forest Resources Assessment 2010: Main Report. Food and Agriculture Organization of the United Nations, Rome.
- Fedrowitz, K.; Koricheva, J.; Baker, S.C.; Lindenmayer, D.B.; Palik, B.; Rosenvald, R.; Beese, W.; Franklin, J.F.; Kouki, J.; Macdonald, E.; Messier, C.; Sverdrup-Thygeson, A.; Gustafsson, L., 2014: Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51: 1669–1679.
 - https://doi.org/10.1111/1365-2664.12289
- Felton, A.; Lindbladh, M.; Brunet, J.; Fritz, O., 2010: Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260: 939–947.
 - https://doi.org/10.1016/j.foreco.2010.06.011
- Forest Europe, 2015: State of Europe's Forests 2015. Ministerial Conference on the Protection of Forest in Europe, Madrid. 314 p.
- Franklin, J.F.; Cromack, K.; Denison, W.; McKee, A.; Maser, C.; Sedell, J.; Swanson, F.; Juday, G., 1981: Ecological characteristics of old-growth Douglas-fir forests. General Technical Report, 48.
 - https://doi.org/10.2737/PNW-GTR-118

- Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Lindenmayer, D.B.; Harmon, M.E.; Keeton, W.S.; Shaw, D.C.; Bible, K.; Chen, J.Q., 2002: Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155: 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8
- Gamfeldt, L.; Snall, T.; Bagchi, R.; Jonsson, M.; Gustafsson, L.; Kjellander, P.; Ruiz-Jaen, M.C.; Froberg, M.; Stendahl, J.; Philipson, C.D.; Mikusiński, G.; Andersson, E.; Westerlund, B.; Andren, H.; Moberg, F.; Moen, J.; Bengtsson, J., 2013: Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4: 1–8. https://doi.org/10.1038/ncomms2328
- Gustafsson, L.; Baker, S.C.; Bauhus, J.; Beese, W.J.; Brodie, A.; Kouki, J.; Lindenmayer, D.B.; Lohmus, A.; Pastur, G.M.; Messier, C.; Neyland, M.; Palik, B.; Sverdrup-Thygeson, A.; Volney, W.J.A.; Wayne, A.; Franklin, J.F., 2012: Retention forestry to maintain multifunctional forests: A world perspective. BioScience 62: 633–645. https://doi.org/10.1525/bio.2012.62.7.6
- Gustafsson, L.; Bauhus, J.; Asbeck, T.; Augustynczik, A. L. D.; Basile, M.; Frey, J.; Gutzat, F.; Hanewinkel, M.; Helbach, J.; Jonker, M.; Knuff, A., Messier, C.; Penner, J.; Pyttel, P.; Reif, A.; Storch, F.; Winiger, N.; Winkel, G.; Yousefpour, R.; Storch, I., 2020a: Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. Ambio, 49: 85–97. https://doi.org/10.1007/s13280-019-01190-1
- Gustafsson, L.; Hannerz, M.; Koivula, M.; Shorohova, E.; Vanha-Majamaa, I.; Weslien, J.; 2020b. Research on retention forestry in Northern Europe. Ecological Processes, 9: 1–13.

https://doi.org/10.1186/s13717-019-0208-2

- Gustafsson, L.; Perhans, K., 2010: Biodiversity conservation in Swedish forests: Ways forward for a 30-year-old multi-scaled approach. Ambio 39: 546–554. https://doi.org/10.1007/s13280-010-0071-y
- Hansen, M.C.; Potapov, P.V.; Moore, R.; Hancher, M.; Turubanova, S.A.; Tyukavina, A.; Thau, D.; Stehman, S.V.; Goetz, S.J.; Loveland, T.R.; Kommareddy, A.; Egorov, A.; Chini, L.; Justice, C.O.; Townshend, J.R.G., 2013: High-resolution global maps of 21st-century forest cover change. Science 342: 850–853.
 - https://doi.org/10.1126/science.1244693
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; Lienkaemper, G.W.; Cromack, K.; Cummins, K.W., 1986: Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.
 - https://doi.org/10.1016/S0065-2504(08)60121-X
- Heyder, J.C., 1986: Waldbau im Wandel. Sauerländer, Frankfurt am Main.
- Higgs, E.S., 2003: Nature by design: people, natural process, and ecological design. MIT Press, Cambridge.
- Hilmers, T.; Friess, N.; Bässler, C.; Heurich, M.; Brandl, R.; Pretzsch, H.; Seidl, R.; Müller, J., 2018: Biodiversity along

- temperate forest succession. Journal of Applied Ecology 55: 2756–2766. https://doi.org/10.1111/1365-2664.13238
- Holling, C.S., 1987: Simplifying the complex the paradigms of ecological function and structure. European Journal of Operational Research 30: 139–146. https://doi.org/10.1016/0377-2217(87)90091-9
- Honnay, O.; Verheyen, K.; Bossuyt, B.; Hermy, M. (eds), 2004: Forest biodiversity: lessons from history for conservation. CABI Publishing, Oxfordshire.
- IPBES, 2019: Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E.S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo (eds). IPBES secretariat, Bonn, Germany.
- Isbell, F.; Gonzalez, A.; Loreau, M.; Cowles, J.; Diaz, S.; Hector, A.; Mace, G.M.; Wardle, D.A.; O'Connor, M.I.; Duffy, J.E.; Turnbull, L.A.; Thompson, P.L.; Larigauderie, A., 2017: Linking the influence and dependence of people on biodiversity across scales. Nature 546: 65–72. https://doi.org/10.1038/nature22899
- Jacobsen, M.K., 2001: History and principles of close to nature forest management: A Central European perspective. Naconex 3: 56–58.
- Jactel, H.; Nicoll, B.C.; Branco, M.; Ramon Gonzalez-Olabarria, J.; Grodzki, W.; Langstrom, B.; Moreira, F.; Netherer, S.; Orazio, C.; Piou, D.; Santos, H.; Schelhaas, M.J.; Tojic, K.; Vodde, F., 2009: The influences of forest stand management on biotic and abiotic risks of damage. Annals of Forest Science 66. https://doi.org/10.1051/forest/2009054
- Jonsson, B.G.; Kruys, N.; Ranius, T., 2005: Ecology of species living on dead wood Lessons for dead wood management. Silva Fennica 39: 289–309. https://doi.org/10.14214/sf.390
- Jonsson, B.G.; Siitonen, J., 2013: Managing for target species. In: Kraus, D.; Krumm, F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg. 134–143.
- Jonsson, B.G.; Svensson, J.; Mikusinski, G.; Manton, M.; Angelstam, P., 2019: European Union's last intact forest landscape is at a value chain crossroad between multiple use and intensified wood production. Forests 10: 564. https://doi.org/10.3390/f10070564
- Kaplan, J.O.; Krumhardt, K.M.; Zimmermann, N., 2009: The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28: 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028
- Kaufmann, S.; Hauck, M.; Leuschner, C., 2018: Effects of natural forest dynamics on vascular plant, bryophyte, and lichen diversity in primeval Fagus sylvatica forests and comparison with production forests. Journal of Ecology 106: 2421–2434.
 - https://doi.org/10.1111/1365-2745.12981
- Keenan, R.J.; Reams, G.A.; Achard, F.; de Freitas, J.V.; Grainger, A.; Lindquist, E., 2015: Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352: 9–20. https://doi.org/10.1016/j.foreco.2015.06.014

- Kennedy, C.E.J.; Southwood, T.R.E., 1984: The number of species of insects associated with British trees – a re-analysis. Journal of Animal Ecology 53: 455–478. https://doi.org/10.2307/4528
- Kimmins, J.P., 2004: Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry. Prentice Hall, New Jersey.
- Kirby, K.J.; Watkins, C., 2015: Europe's changing woods and forests: from wildwood to managed landscapes. CABI, Oxfordshire.
- Koh, L.P.; Gardner, T.A., 2010: Conservation in human-modified landscapes. In: Sodhi, N.S.; Ehrlich, P.R. (eds), Conservation biology for all. Oxford University Press, Oxford, UK.
- Köhl, M.; Lasco, R.; Cifuentes, M.; Jonsson, O.; Korhonen, K.T.; Mundhenk, P.; Navar, J.D.; Stinson, G., 2015: Changes in forest production, biomass and carbon: Results from the 2015 UN FAO Global Forest Resource Assessment. Forest Ecology and Management 352: 21–34. https://doi.org/10.1016/j.foreco.2015.05.036
- Korpel', S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer, Stuttgart.
- Kremen, C., 2015: Reframing the land-sparing/land-sharing debate for biodiversity conservation. In: Power, A.G.; Ostfeld, R.S. (eds), The Year in Ecology and Conservation Biology. 52–76.

https://doi.org/10.1111/nyas.12845

- Krumm, F.; Schuck, A.; Kraus, D., 2013: Integrative management approaches: a synthesis. In: Kraus, D.; Krumm, F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg. 269–276.
- Kuuluvainen, T., 2002a: Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36: 5–11. https://doi.org/10.14214/sf.547
- Kuuluvainen, T., 2002b: Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36: 97–125. https://doi.org/10.14214/sf.552
- Kuuluvainen, T., 2009: Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: The complexity challenge. Ambio 38: 309–315. https://doi.org/10.1579/08-A-490.1
- Kuuluvainen, T.; Tahvonen, O.; Aakala, T., 2012: Evenaged and uneven-aged forest management in boreal Fennoscandia: A review. Ambio 41: 720–737. https://doi.org/10.1007/s13280-012-0289-y
- Lachat, T.; Wermelinger, B.; Gossner, M.M.; Bussler, H.; Isacsson, G.; Müller, J., 2012: Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecological Indicators 23: 323–331. https://doi.org/10.1016/j.ecolind.2012.04.013
- Landres, P.B.; Morgan, P.; Swanson, F.J., 1999: Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188. https://doi.org/10.1890/1051-0761(1999)009[1179:OOT UON]2.0.CO;2

- Larrieu, L.; Cabanettes, A.; Delarue, A., 2012: Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. European Journal of Forest Research 131: 773–786.
 - https://doi.org/10.1007/s10342-011-0551-z
- Larrieu, L.; Paillet, Y.; Winter, S.; Bütler, R.; Kraus, D.; Krumm, F.; Lachat, T.; Michel, A.K.; Regnery, B.; Vandekerkhove, K., 2018: Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators 84: 194–207.

https://doi.org/10.1016/j.ecolind.2017.08.051

- Lassauce, A.; Anselle, P.; Lieutier, F.; Bouget, C., 2012: Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. Forest Ecology and Management 266: 273–285.
 - https://doi.org/10.1016/j.foreco.2011.11.016
- Lassauce, A.; Paillet, Y.; Jactel, H.; Bouget, C., 2011: Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11: 1027–1039.

https://doi.org/10.1016/j.ecolind.2011.02.004

- Lilja, S.; Wallenius, T.; Kuuluvainen, T., 2006: Structure and development of old *Picea abies* forests in northern boreal Fennoscandia. Écoscience 13: 181–192. https://doi.org/10.2980/i1195-6860-13-2-181.1
- Lindenmayer, D.B.; Franklin, J.F.; Fischer, J., 2006: General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131: 433–445.

https://doi.org/10.1016/j.biocon.2006.02.019

- Lindenmayer, D.B.; Franklin, J.F.; Lohmus, A.; Baker, S.C.; Bauhus, J.; Beese, W.; Brodie, A.; Kiehl, B.; Kouki, J.; Pastur, G.M.; Messier, C.; Neyland, M.; Palik, B.; Sverdrup-Thygeson, A.; Volney, J.; Wayne, A.; Gustafsson, L., 2012: A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conservation Letters 5: 421–431.
 - https://doi.org/10.1111/j.1755-263X.2012.00257.x
- Lundmark, H.; Josefsson, T.; Östlund, L., 2013: The history of clear-cutting in northern Sweden Driving forces and myths in boreal silviculture. Forest Ecology and Management 307: 112–122.

https://doi.org/10.1016/j.foreco.2013.07.003

- MacDicken, K.G.; Sola, P.; Hall, J.E.; Sabogal, C.; Tadoum, M.; de Wasseige, C., 2015: Global progress toward sustainable forest management. Forest Ecology and Management 352: 47–56.
 - https://doi.org/10.1016/j.foreco.2015.02.005
- Margules, C.R.; Pressey, R.L., 2000: Systematic conservation planning. Nature 405: 243–253. https://doi.org/10.1038/35012251
- Martikainen, P.; Siitonen, J.; Punttila, P.; Kaila, L.; Rauh, J., 2000: Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Fin-

- land. Biological Conservation 94: 199–209. https://doi.org/10.1016/S0006-3207(99)00175-5
- MCPFE, 2003. The MCPFE report on sustainable forest management in Europe. Liaison Unit Vienna UNEFCE/FAO, Vienna. 114 p.
- Mergner, U., 2018: Das Trittsteinkonzept: Naturschutzintegrative Waldbewirtschaftung schützt die Vielfalt der Waldarten. Euerbergverlag, Rauhenebrach-Fabrikschleichach.
- Messier, C.; Puettmann, K.J.; Coates, K.D., 2014: Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, London.
- Miklin, J.; Sebek, P.; Hauck, D.; Konvicka, O.; Cizek, L., 2018: Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles. Diversity and Distributions 24: 208–218. https://doi.org/10.1111/ddi.12670
- Mikusiński, G.; Roberge, J.-M.; Fuller, R.J., 2019: Ecology and conservation of forest birds. Cambridge University Press. https://doi.org/10.1017/9781139680363
- Millar, C.I.; Stephenson, N.L.; Stephens, S.L, 2007: Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17: 2145–2151. https://doi.org/10.1890/06-1715.1
- Moning, C.; Werth, S.; Dziock, F.; Bassler, C.; Bradtka, J.; Hothorn, T.; Muller, J., 2009: Lichen diversity in temperate montane forests is influenced by forest structure more than climate. Forest Ecology and Management 258: 745–751. https://doi.org/10.1016/j.foreco.2009.05.015
- Morales-Hidalgo, D.; Oswalt, S.N.; Somanathan, E., 2015: Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. Forest Ecology and Management 352: 68–77. https://doi.org/10.1016/j.foreco.2015.06.011
- Mori, A.S., 2011: Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48: 280–292. https://doi.org/10.1111/j.1365-2664.2010.01956.x
- Motta, R.; Garbarino, M.; Berretti, R.; Meloni, F.; Nosenzo, A.; Vacchiano, G., 2015: Development of old-growth characteristics in uneven-aged forests of the Italian Alps. European Journal of Forest Research 134: 19–31. https://doi.org/10.1007/s10342-014-0830-6
- Müller, J.; Bussler, H.; Bense, U.; Brustel, H.; Flechtner, G.; Fowles, A.; Kahlen, M.; Möller, G.; Mühle, H.; Schmidl, J.; Zabransky, P., 2005: Urwald relict species Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2: 106–113.
- Müller, J.; Bütler, R., 2010: A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129: 981–992.
 - https://doi.org/10.1007/s10342-010-0400-5
- Mullerova, J.; Hedl, R.; Szabo, P., 2015: Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management 343: 88–100. https://doi.org/10.1016/j.foreco.2015.02.003

- Nagel, T.A.; Firm, D.; Pisek, R.; Mihelic, T.; Hladnik, D.; de Groot, M.; Rozenbergar, D., 2017: Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. Biological Conservation 216: 101–107.https://doi.org/10.1016/j. biocon.2017.10.008
- Newbold, T.; Hudson, L.N.; Hill, S.L.L.; Contu, S.; Lysenko, I.; Senior, R.A.; et al., 2015: Global effects of land use on local terrestrial biodiversity. Nature 520: 45–50. https://doi.org/10.1038/nature14324
- Noss, R.F., 1990: Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4: 355– 364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x
- Ohlson, M.; Soderstrom, L.; Hornberg, G.; Zackrisson, O.; Hermansson, J., 1997: Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 81: 221–231.
 - https://doi.org/10.1016/S0006-3207(97)00001-3
- Otto, H.-J., 1993: Waldbau in Europa seine Schwächen und Vorzüge in historischer Perspektive. Forst und Holz 49: 235–237.
- Paillet, Y.; Archaux, F.; Boulanger, V.; Debaive, N.; Fuhr, M.; Gilg, O.; Gosselin, F.; Guilbert, E., 2017: Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and Management 389: 176–186. https://doi.org/10.1016/j.foreco.2016.12.014
- Paillet, Y.; Berges, L.; Hjalten, J.; Odor, P.; Avon, C.; Bernhardt-Romermann, M.; et al., 2010: Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. Conservation Biology 24: 101–112.
 - https://doi.org/10.1111/j.1523-1739.2009.01399.x
- Paillet, Y.; Pernot, C.; Boulanger, V.; Debaive, N.; Fuhr, M.; Gilg, O.; Gosselin, F., 2015: Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. Forest Ecology and Management 346: 51–64. https://doi.org/10.1016/j.foreco.2015.02.037
- Palo, A.; Ivask, M.; Liira, J., 2013: Biodiversity composition reflects the history of ancient semi-natural woodland and forest habitats-Compilation of an indicator complex for restoration practice. Ecological Indicators 34: 336–344. https://doi.org/10.1016/j.ecolind.2013.05.020
- Paquette, A.; Messier, C., 2010: The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment 8: 27–34. https://doi.org/10.1890/080116
- Parviainen, J., 2005: Virgin and natural forests in the temperate zone of Europe. Forest, Snow and Landscape Research 79: 9–18.
- Parviainen, J.; Bucking, W.; Vandekerkhove, K.; Schuck, A.; Paivinen, R., 2000: Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). Forestry 73: 107–118.
 - https://doi.org/10.1093/forestry/73.2.107
- Pausas, J.C.; Llovet, J.; Rodrigo, A.; Vallejo, R., 2008: Are wildfires a disaster in the Mediterranean basin? A

- review. International Journal of Wildland Fire 17: 713–723. https://doi.org/10.1071/WF07151
- Peterken, G.F., 1996: Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge.
- Potapov, P.; Hansen, M.C.; Laestadius, L.; Turubanova, S.; Yaroshenko, A.; Thies, C.; Smith, W.; Zhuravleva, I.; Komarova, A.; Minnemeyer, S.; Esipova, E., 2017: The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances 3: 1–13. https://doi.org/10.1126/sciadv.1600821
- Puettmann, K.J.; Coates, K.D.; Messier, C., 2009: A critique of silviculture: Managing for complexity. Island Press, Washington.
- Ratcliffe, S.; Wirth, C.; Jucker, T.; van der Plas, F.; Scherer-Lorenzen, M.; Verheyen, K.; et al., 2017: Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecology Letters. 1414–1426. https://doi.org/10.1111/ele.12849
- Redon, M.; Berges, L.; Cordonnier, T.; Luque, S., 2014: Effects of increasing landscape heterogeneity on local plant species richness: how much is enough? Landscape Ecology 29: 773–787.
 - https://doi.org/10.1007/s10980-014-0027-x
- Rolstad, J.; Saetersdal, M.; Gjerde, I.; Storaunet, K.O., 2004: Wood-decaying fungi in boreal forest: are species richness and abundances influenced by small-scale spatiotemporal distribution of dead wood? Biological Conservation 117: 539–555.
 - https://doi.org/10.1016/j.biocon.2003.09.008
- Roth, N.; Doerfler, I.; Bassler, C.; Blaschke, M.; Bussler, H.; Gossner, M.M.; Heideroth, A.; Thorn, S.; Weisser, W.W.; Muller, J., 2019: Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity. Diversity and Distributions 25: 430–441. https://doi.org/10.1111/ddi.12870
- Sabatini, F.M.; Burrascano, S.; Keeton, W.S.; Levers, C.; Lindner, M.; Potzschner, F.; et al., 2018: Where are Europe's last primary forests? Diversity and Distributions 24: 1426–1439. https://doi.org/10.1111/ddi.12778
- Sabatini, F.M.; Keeton, W.S.; Lindner, M.; Svoboda, M.; Verkerk, P.J.; Bauhus, J.; et al., 2020: Protection gaps and restoration opportunities for primary forests in Europe. Diversity and Distributions.
 - https://doi.org/10.1111/ddi.13158
- Schall, P.; Gossner, M.M.; Heinrichs, S.; Fischer, M.; Boch, S.; Prati, D.; et al., 2017: The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology 55: 267–278.
 - https://doi.org/10.1111/1365-2664.12950
- Scharlemann, J.P.W.; Kapos, V.; Campbell, A.; Lysenko, I.; Burgess, N.D.; Hansen, M.C.; Gibbs, H.K.; Dickson, B.; Miles, L., 2010: Securing tropical forest carbon: the contribution of protected areas to REDD. Oryx 44: 352–357. https://doi.org/10.1017/S0030605310000542
- Schütz, J.P., 1993: Naturnaher Waldbau in der Schweiz. Allgemeine Forstzeitschrift 45: 731–732.

- Seibold, S.; Bassler, C.; Brandl, R.; Buche, B.; Szallies, A.; Thorn, S.; Ulyshen, M.D.; Müller, J., 2016: Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53: 934–943. https://doi.org/10.1111/1365-2664.12607
- Seidl, R.; Schelhaas, M.-J.; Lexer, M.J., 2011: Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology 17: 2842–2852. https://doi.org/10.1111/j.1365-2486.2011.02452.x
- Seymour, R.; Hunter, M.L.J., 1999: Principles of ecological forestry. In: Hunter, M.L.J. (ed.) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge. 22–61.
 - https://doi.org/10.1017/CBO9780511613029.004
- Siitonen, J., 2001: Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forest as example. Ecological Bulletins 49: 11–41.
- Siitonen, J.; Saaristo, L., 2000: Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of oldgrowth boreal forest. Biological Conservation 94: 211– 220. https://doi.org/10.1016/S0006-3207(99)00174-3
- Speight, M.C.D., 1989: Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.
- Staab, M.; Bluthgen, N.; Klein, A.M., 2015: Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. Oikos 124: 827–834. https://doi.org/10.1111/oik.01723
- Stokland, J.N.; Siitonen, J.; Jonsson, B.G., 2012: Biodiversity in dead wood. Cambridge University Press.
- Swanson, M.E.; Franklin, J.F.; Beschta, R.L.; Crisafulli, C.M.; DellaSala, D.A.; Hutto, R.L.; Lindenmayer, D.B.; Swanson, F.J., 2011: The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125. https://doi.org/10.1890/090157
- Thorn, S.; Bassler, C.; Svoboda, M.; Müller, J., 2017: Effects of natural disturbances and salvage logging on biodiversity Lessons from the Bohemian Forest. Forest Ecology and Management 388: 113–119. https://doi.org/10.1016/j.foreco.2016.06.006
- Tittler, R.; Messier, C.; Fall, A., 2012: Concentrating anthropogenic disturbance to balance ecological and economic values: applications to forest management. Ecological Applications 22: 1268–1277. https://doi.org/10.1890/11-1680.1
- van der Plas, F.; Manning, P.; Allan, E.; Scherer-Lorenzen, M.; Verheyen, K.; Wirth, C.; et al., 2016: Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nature Communications 7: 11109.
 - https://doi.org/10.1038/ncomms11109
- van der Plas, F.; Ratcliffe, S.; Ruiz-Benito, P.; Scherer-Lorenzen, M.; Verheyen, K.; Wirth, C.; et al., 2017: Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. Ecology Letters 21: 31–42.
 - https://doi.org/10.1111/ele.12868
- Vandekerkhove, K.; De Keersmaeker, L.; Menke, N.; Meyer, P.; Verschelde, P., 2009: When nature takes over from

- man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. Forest Ecology and Management 258: 425–435. https://doi.org/10.1016/j.foreco.2009.01.055
- Watson, J.E.M.; Dudley, N.; Segan, D.B.; Hockings, M., 2014: The performance and potential of protected areas. Nature 515: 67–73.
 - https://doi.org/10.1038/nature13947
- White, P.S.; Pickett, S.T.A., 1985: Natural disturbance and patch dynamics: an introduction. In: White, P.S.; Pickett, S.T.A. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL. 3–13.
- Winkel, G. (ed.), 2017: Towards a sustainable European forest-based bioeconomy assessment and the way forward. What Science Can Tell Us 8. European Forest Institute, Joensuu.
- Winter, M.B.; Ammer, C.; Baier, R.; Donato, D.C.; Seibold, S.; Müller, J., 2015: Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase. Forest Ecology and Management 338: 32–45.
 - https://doi.org/10.1016/j.foreco.2014.11.019
- Winter, S.; Flade, M.; Schumacher, H.; Kerstan, E.; Möller, G., 2005: The importance of near natural stand structures for the biocoenosis of lowland beech forests. Forest Snow and Landscape Research 79: 127–144.
- Winter, S.; Möller, G.C., 2008: Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255: 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029