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In forest ecosystems, the area of protected forests is restricted and the large majority of forests have to provide multi-purpose services. Hence, the effectiveness and progress in forest biodiversity conservation heavily depend on an appropriate and complementary use of integrative and segregative conservation instruments

Worldwide, there is an obvious dominance of forestry systems that aim at integrating biodiversity conservation into commodity production. In total, only 11 % of forests are under different protection status. While there is an ongoing debate on the pros and cons of integrative versus segregative approaches for nature preservation, a comprehensive framework for biodiversity conservation in forest ecosystems will rely on both types of instruments and their effective and appropriate use at different spatial scales. In this paper we aim to (1) present segregative and integrative instruments for forest biodiversity conservation, (2) discuss their potential and limitations, and (3) propose a conceptual framework for supporting the comprehensive preservation of autochthonous forest biodiversity in a system of multi-purpose forestry. With a focus on Europe, we do not define overall goals for forest biodiversity conservation instruments in this context. We highlight the generality of the presented concept, which offers practitioners and decision makers the opportunity to assess the trade-offs between different conservation instruments and their implications for other forest functions and to adapt their choice to the specific environmental and socio-economic situations found in Europe.

Forest is the dominant natural vegetation type in Europe, covering a broad bioclimatic gradient from Mediterranean broadleaved evergreen and thermophilic deciduous forests to the deciduous lowland and conifer-dominated mountain forests of Central Europe as well as to the boreal forests in Fennoscandia (EEA 2008). European forests are highly variable with regard to site conditions, management regimes, history of use, and socio-economic value. A long history of landscape and forest use has altered European forests, and apparently almost no pristine forests remain (Welzholz and Johann 2007). During the last 150 years, there has been a distinct trend towards silvicultural systems with permanent stocking of a few target tree species that provide a continuous supply of timber in a balanced age-class distribution,

Box 1. Protected forest area

Forest ecosystems cover approximately 30 % of the world's and 32 % of Europe's land surface (FAO 2010; FOREST EUROPE 2011). These ecosystems provide a multitude of services, such as timber production, the protection of soil and water resources, climate regulation, and the provisioning of habitat for forest species. The vast majority of forestland is designated for multi-purpose use and is outside formally protected areas. Forest reserves of different protection regimes account for only about 11 % of the global forest area; the respective proportion for Europe is 10 % (Parviainen and Schuck 2011), and human intervention is totally banned in only 0.7 % (Bücking 2007). Thus, concepts and instruments that integrate the habitat requirements of forest biota into the management and production of other forest goods and services are mandatory for sustainable forestry that balances human commodity needs with the management of natural resources and ecosystem services (Thompson et al. 2011). Often criticized aspects of current forest management are the uniformity of forest structure and composition, the lack of late seral stages caused by regular harvesting and management for stand stability and productivity in general (Puettmann et al. 2009), and the consequential loss of suitable habitat, e.g. old-growth stands and large and decaying trees, for forest organisms in particular (Lindenmayer et al. 2006).

managed by constant production cycles. Although in some parts of Europe this is termed "close-to-nature management", the resulting forests lack the diversity in composition and structure of forest ecosystems that are driven by natural succession and dynamics (Puettmann et al. 2009; Bauhus et al. 2013). However, old-growth attributes and relicts of pristine forests have an important function in preserving limited resources for the conservation of "relict species" of primeval forests or "ancient forest species" (e.g. Müller et al. 2005; Winter et al. 2005; Hermy and Verheyen 2007; Bollmann and Müller 2012). Thus, strict forest reserves and the retention of old-growth attributes have become important tools for the preservation of forest biodiversity in cultural landscapes (Bauhus et al. 2009). On the other hand, "cultural forests" that were once part of a traditional agro-silvicultural land-use system, including coppice with standards, woodland pastures, and chestnut orchards, are known to provide important habitats for thermo- and photophilic species (e.g. Bürgi 1998; Lassauce et al. 2012). Thus, independently of the discussion whether to preserve or even reconstruct secondary forests originating from past land-use forms, a conceptual framework for the conservation of autochthonous biodiversity in the cultural forest landscape of Europe needs to - at least regionally - consider the contribution of traditional forest practices to structural and compositional diversity (Figure 4).

A comprehensive approach to preserve the authentic diversity of an ecosystem has to consider its structural, compositional, and functional characteristics

In forest ecosystems, structural, compositional and functional characteristics are heavily influenced by site conditions, successional stage, and type and frequency of disturbance and human use (Leibundgut 1978, Noss 1999). Forests generally show a long development time, during which species richness often increases with seral stage (Scherzinger 1996) and ecosystem stability (Pimm 1991). However, the idealized concept of an autogenic ecosystem change characterized by directed forest succession, i.e. starting with the early seral stage of stand rejuvenation and ending with the late seral stage of a climax or mature forest (Leibundgut 1978), has to be complemented with a spatio-temporal stochastic disturbance component interrupting the directional process (Bengtsson et al. 2003; Schulze et al. 2007). Change and disturbance are natural features of forest ecosystems and have strongly influenced natural species communities in Europe. The type of disturbance - including fire, windthrows, floods, avalanches, bark beetle infestations, and browsing by large herbivores - differs among biogeographic regions: Fire is a relevant driver of structural heterogeneity in Taiga forests in Northern Europe (Zackrisson 1977) and Mediterranean forests in Southern Europe (e.g. Pausas et al. 2008). Deciduous forests are mostly disturbed by small-scale windthrows (Splechtna et al. 2005) or snow-break, whereas coniferous forests are typically disturbed by large-scale windthrows (Usbeck et al. 2010) with subsequent bark beetle infections (Müller et al. 2010) as well as by avalanches in mountain areas (Kulakowski et al. 2011).

Box 2. Post-glacial forest development in Europe

Most of the European indigenous forest species have evolved under conditions of post-glacial re-immigration of formerly ice-covered regions (Hewitt 1999). Species richness is considered to have steadily increased until the period of industrialization (Küster 1995). Until then, forest use was characterized by a large variety of co-existing agroforestry activities, including the burning of forest patches to support animal grazing or field crops and collecting firewood and other non-timber products as well as cutting construction wood. During this period, forests close to human settlements were heavily impacted (Hausrath 1982; Bürgi 1998). Intensive clearings and the pluralistic use of forest products caused a transformation of many woodlands into park-like landscapes, with introduced agricultural plants and a general increase of beta-diversity (Korneck et al. 1996), the latter resulting from the spatial heterogeneity of land use types and intensity creating patchy habitat mosaics. With the onset of industrialization, the focus shifted towards wood production, which resulted in a large-scale spatial separation of different land use types. As a consequence, the number of indigenous species and traditional agricultural plant species decreased (Küster 1995).

The underlying principles of forest biodiversity conservation are the maintenance of ecosystem integrity and resilience, structural complexity, and habitat connectivity

Box 3. Biodiversity

Biological diversity encompasses the diversity of ecosystems, species, genes, and interactions thereof. Species diversity, as the most commonly considered aspect, is measured as species richness (i.e. the number of species present in a particular ecosystem) and species evenness (i.e. the relative abundance of different species in a particular ecosystem). Species diversity is related to spatial scale. The total species diversity in a landscape (gamma diversity) depends on alpha diversity (the number of species at a distinct forest stand, forest patch, or forest type) and beta diversity (the degree of variation of alpha measures across different stands, forest patches, or forest types).

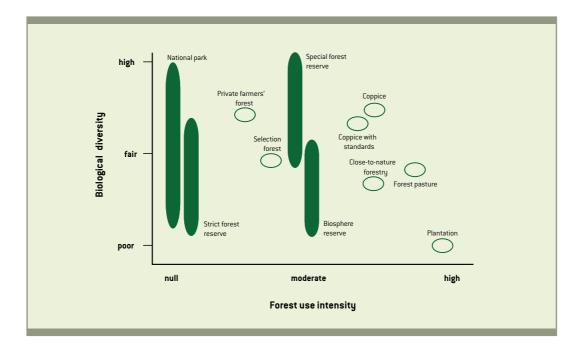


Figure 4. Relationship between forest types under different use intensities or harvesting regimes, respectively, and the biological diversity therein. Green symbols indicate forests primarily assigned to biodiversity conservation; light symbols indicate forests primarily assigned to commodity production. Source: Modified from Schulze et al. (2007).

Biological conservation has placed strong emphasis on the preservation of the last remaining pristine forests. Continuity in the presence of forest habitats over time and a stand mosaic composed of different successional stages are important requirements for the occurrence of a mature forest species community. In particular, taxa such as fungi, insects, mosses, and lichens show a high diversity and abundance in natural forests not subject to wood extraction (Siitonen 2001; Paillet et al. 2010). Interestingly, however, naturalness per se is not the only good predictor for species diversity. Traditional forest use has also created suitable habitat for many species in spite of high intensity (Figure 4). Through nutrient extraction and high harvesting ratios, many historical agroforestry systems created stands with semi-open

canopies, reduced dominance of shade tolerant generalist species (Beech, Norway spruce), and single old-growth habitat trees. Such stands comprise many ecological niches for thermoand photophilic species such as orchids, beetles, butterflies, and their host plants.

Conservation biology mainly follows three underlying principles that guide the preservation of biodiversity in forests. They include the maintenance and restoration of the following:

- -> **Ecosystem integrity** by supporting natural composition, succession, and disturbance;
- Structural complexity by supporting within and among stand heterogeneity in structure and composition, long rotation cycles, and a variety of elements such as old, diseased, and decaying trees;

Three strategic management fields have been defined to support the underlying principles of biodiversity conservation in European cultural landscapes: preservation, retention, and natural dynamics

The cultural landscape of Europe has been transformed over centuries. Three strategic management fields have been defined to support the underlying principles:

- The preservation of rare, representative, and threatened forest types or stands, such as the last remaining pristine and ancient forests, as well as the retention of old or old-growth stands, mature trees, and coarse woody debris (CWD) within managed forest landscapes;
- the restoration of important habitats and structural characteristics by constitutive measures (e.g. creating gaps, controlled burning and browsing, ring barking, uprooting of trees);

The importance and priority of these management fields can differ among regions and countries depending on the site conditions, previous silvicultural practices, the current state of the forest, and minimum standards for forestry. The same applies to the instruments supporting activities in these fields, which can differ according to national legislation and conservation objectives (Table 1). Yet, independently of political and cultural differences, maintaining or restoring the different components of forest biodiversity requires a comprehensive concept that combines segregative (reserves) and integrative (off-reserve) conservation instruments so as to support species within hotspots of their occurrence as well as across the matrix, at different spatial (stand, forest patch, landscape) and hierarchical (genes, species populations, communities, ecosystems) scales.

Table 1. Definition of the integrative (i) and segregative (s) conservation instruments discussed in this paper and used in figures 4–7.

Instrument	Purpose	Category
National park	Designated landscape area according to IUCN protected area management categories in order to preserve unique ecosystems with native species and communities under natural dynamics to enable their long-term viability.	S
Strict forest reserve	Protected forest area aiming for biodiversity conservation by natural dynamics with no or minimal human intervention (MCPFE-classes 1.1 and 1.2) ¹ ; class 1.2 can include control of ungulates, insect outbreaks, and fire.	S
Special forest reserve	Protected area aiming for enhancing forest biodiversity through active habitat restoration ² or management ³ (MCPFE-class 1.3) ¹ , such as prescribed burning, cutting and mowing, controlled grazing and browsing, and rebuilding of coppice with standards.	s, (i)
Biosphere reserve	Established areas designated under UNESCO's Man and the Biosphere (MAB) Programme to promote sustainable development by a zonal concept based on local community efforts and evidence-based conservation.	i
Structural retention	Retention of key structural habitat elements such as habitat trees, snags, lying deadwood, gaps, and riparian stands in commercially used forests.	i
Old-growth stand protection	Protection of old-growth stands with mature and dead trees as habitat patches and stepping stones in commercially used forests.	i
Wildlife corridor	Site traditionally used by wildlife species to move between populations separated by human activities or structures such as highways, urban development, and clearcuts.	i
Ecological process area	Temporally restricted and spatially flexible conservation instrument that integrates natural dynamics and its habitat features after a disturbance event in production forests for some decades. Later, the area is re-integrated and managed again according to the purposes of regional forestry until a consecutive disturbance occurs.	i

¹ Vandekerkhove et al. (2007)

² Measures taken in protected forests that strive to restore a high degree of naturalness more quickly than would occur under natural dynamics alone.

³ Measures taken to maintain or enhance important habitat characteristics and features of rare and threatened biotopes or species in commercially used forests.

A strictly segregative approach allocates a certain ratio of the landscape for nature conservation (e.g. forest reserve), while commodity production is maximized in the remaining landscape. In contrast, a strictly integrative approach aims at combining ecological, economic, and social issues across the total forest area at the same time. Yet, in recent years growing evidence has emerged that large-scale forest biodiversity conservation depends on a combination of both approaches (Bengtsson et al. 2003; Bollmann 2011), especially since the impact of the various tools and the responses to their application are scale-dependent (Figure 6).

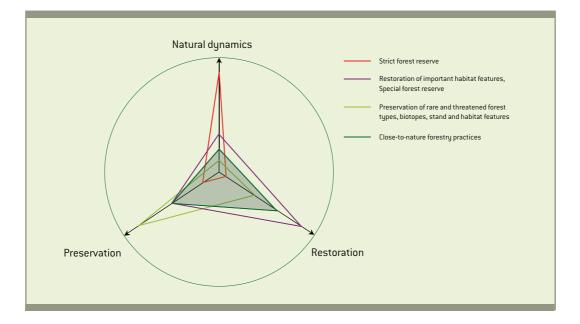


Figure 5. Qualitative model of the impact of different biodiversity conservation tools along the three conservation axes – preservation (lower left arrow), restoration (lower right arrow), and natural dynamics (upper arrow) – in comparison with the basic performance of close-to-nature forestry practices (blue). Source: Modified from Bollmann (2011).

To preserve the multitude of different niches and processes in forest habitats along the gradient of human land use intensity and natural disturbance, various conservation tools are needed

> These tools (Table 1, Figure 6) should be complementary in their function (preservation, natural dynamics, restoration; Figure 5) so as to support the different principles in conservation (integrity, complexity, and connectivity). Instruments to preserve rare and threatened habitats and species were among the first ones applied in forest habitat management in many countries (Table 1). Later, constitutive measures were added to the toolbox and used to restore ancient forests or species habitats or to trigger developments for more naturalness such as the restoration of alluvial forests. In recent times, the designation of strict forest reserves has become a high priority in many countries so as to support natural dynamics and selection processes (FAO 2010). Instruments with a focus on preservation and natural dynamics are usually considered segregative, whereas restoration and retention approaches have a more integrative notion. However, the distinction between segregative and integrative instruments is a matter of scale and national legislation: while the designation of strict forest reserves or national parks count among the segregative tools, small-scale approaches for maintaining natural dynamics, such as retention forestry (Gustafsson et al. 2012) maintaining old and decaying trees within a managed-forest matrix, are considered to be integrative. Since it is difficult to define a scientifically justified spatial threshold for the distinction of segregative and integrative tools, we refer to the categorization as defined in Table 1.

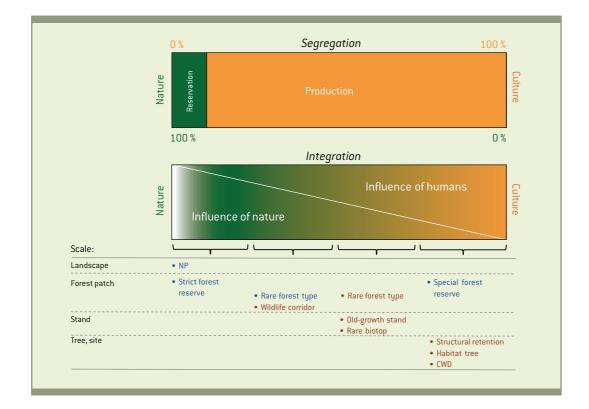


Figure 6. Conceptual differences between segregative and integrative approaches in forestry. In a segregative forestry system, national parks and forest reserves often preserve primeval or heritage forests that are embedded in a matrix of intensively used forests or plantations with low habitat quality. In a purely integrative system, structural retention and restoration measures (brown) are an integral part of sustainable forest practices. They mainly support minimum targets of habitat features and resources, but their impact is mostly restricted to the site and stand scale. In an optimized integrative system, these small-scale conservation measures are combined with segregative tools (blue). They often support ecological process dynamics at the forest patch and landscape scale as targeted by national parks or strict forest reserves. Yet, segregative tools can also be used to actively restore traditional forest habitats for specific conservation purposes (e.g. special forest reserve). Integrative forestry systems such as those in Central Europe often lack remnants of primeval forest at the very left side (white) of the nature-culture gradient (see Winter et al. 2010).

Both segregative and integrative conservation instruments have specific impacts on forest biodiversity but also limitations. Hence, the appropriate use and combination of these instruments depend on the overall goals

Off-reserve instruments include the protection of rare forest habitats and large biotope trees, the establishment of wildlife corridors and patches of CWD, the retention of old-growth attributes, and the active maintenance of structurally rich forest edges as high quality ecotones between forests and the open landscape. Biodiversity responses to the application of these instruments mainly occur at the small and intermediate scale. Accordingly, integrative conservation

elements should be distributed across the entire forest matrix. On the other hand, segregative instruments should be located in areas of high conservation value (see Bollmann and Müller 2012) because they represent a minority of the total forest area. Areas primarily devoted to conservation currently cover 10 % and should increase to 17 % according to international biodiversity targets (Strategic Plan for 2011-2020, Convention on Biological Diversity). The design of segregative instruments is supported by the island theory (MacArthur and Wilson 1967). Thus, national parks, strict forest reserves, and special forest reserves should cover a large extent of area, especially areas delineated to restore natural dynamics and the associated species communities, which should at least cover several hundreds to thousands of hectares (Scherzinger 1996). Such reserves should be large enough to represent a mosaic of various seral stages, reorganize after natural disturbances (Pickett and Thompson 1978, Turner et al. 1998), and, in the optimal case, harbour minimum viable populations of priority species of conservation concern (Margules and Pressey 2000). In contrast to strict forest reserves, which are passively managed, thereby allowing underlying stochastic processes to deviate from initially defined conservation goals (target-open process), special forest reserves are actively managed and hence can be developed more closely along a developmental trajectory or to the ecological needs of one or several target species (target-oriented process).

Primeval forest relict species mainly depend on extended habitat traditions and quite often on the abundance and quality of deadwood (Bässler and Müller 2010). Some of them, such as the polypore fungus *Antrodiella citrinella* for example, are suggested to occur only in habitats with a minimum threshold of large quantities of deadwood of ca. 140 m³ per hectare. Such spatially aggregated quantities can only accumulate in strictly protected areas with natural disturbance as the major driver and can hardly be integrated in an area-wide multi-purpose silviculture management. On the other hand – as they are naturally occurring in a scattered distribution – the preservation of rare biotope types, old-growth stands, and large habitat trees and the retention of CWD mainly takes place at the site and stand scale. These measures can be well integrated in areas primarily devoted to commodity production (Figure 7).

The appropriate application of off-reserve instruments allows for an integration of important habitat features and limiting resources as well as their connectivity in multi-purpose forests, which represent the vast majority of forest area

The crucial questions for practitioners are the following: How much integration is possible in a system of multi-purpose forestry? How much segregation is mandatory to complement the spectrum of habitats available in multi-purpose forests and to increase the range of niches to restore parts of the old-growth species community and to make the overall conservation work in forests effective?

The best choice and effective combination of segregative and integrative instruments will be influenced by national objectives and legislation for forest biodiversity conservation as well as the silvicultural legacy and the initial condition of the environment. In an optimized system, the various instruments complement each other in their impact on the different aspects of

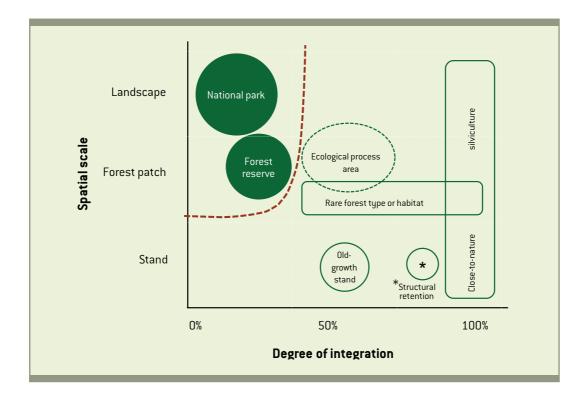


Figure 7. Distribution of integrative (light symbols) and segregative (green) biodiversity conservation instruments along the spatial planning scale of forestry. The brown line represents the virtual border between a segregative and an integrative system. Area-wide integrative approaches have to be complemented with strong segregative instruments when aiming at comprehensively preserving forest biodiversity in a cultural landscape. In the future, advances are required to fill the central gap between integrative and segregative instruments by delineating ecological process areas (dashed green line) that integrate natural dynamics and habitat features in production forest landscapes. In contrast to forest reserves, ecological process areas would be spatially and temporally flexible conservation tools (see text).

biodiversity (genes, species, ecosystems, functions) and at different spatial scales and degrees of forest use intensity (Figure 7). A concept with a dual strategy combining integrative and segregative instruments seems to be the best option to support biodiversity conservation in a cultural landscape, with a system of multi-purpose forestry and variation in forest tenure. Some progress has been achieved in the protection of forests for biodiversity and landscape in Europe (Forest Europe 2011). Between 2000 and 2010, the area of protected forest annually increased by 5,000 km² on average. Thereof, the large majority consist of protected forest with active management, whereas the area of strictly protected forest only marginally increased. Comparable, country-specific numbers for the retention of old-growth attributes and habitat trees are not available. However, the preservation of deadwood as substrate for a large number of forest species has become a management issue in many countries and data for North and Central-West Europe indicate a positive trend in the weighted average volume of standing and lying deadwood (Forest Europe 2011). In the future, more emphasis should be given to the preservation of the last primeval forests in Europe and to the development of an appropriate instrument that integrates natural dynamics and its habitat features at the forest-landscape mosaic outside strictly protected forests. Such an instrument should increase the ecological

memory in the production forest landscape (Bengtsson et al. 2003). We recommend the delineation of ecological process areas as a new conservation tool. Such conservation areas could be envisaged in regions exposed to frequent disturbance events and, in contrast to traditional static conservation tools (e.g. reserves), would be spatially flexible and temporally restricted. Depending on the disturbance history, ecological process areas could encompass different states and functions. In periods of undisturbed, directed succession, the area would be managed according to the guidelines of multi-purpose forestry. Yet, immediately after a disturbance has occurred, the area would be set aside for natural regeneration. Salvage logging and sanitation felling should be omitted or - in cases of large disturbed areas - only partially implemented because such treatments modify rare post-disturbance habitats, remove biological legacies, and impair natural vegetation regeneration (Lindenmayer and Noss 2006). After a pre-defined period of several decades, the area could be re-integrated and managed according to the purposes of regional forestry or forest owners. In general, such an instrument is expected to increase stand heterogeneity and gamma diversity in production forest landscapes and, compared to segregative instruments, has the advantage that the acceptance of land owners should be better due to the temporal limitation of the measures.

The available integrative and segregative conservation instruments represent a flexible and comprehensive toolbox that could serve most biodiversity conservation goals in European forests

Yet, evidence-based and quantitative target values with regard to the amount, size, and configuration of the different instruments required to achieve a particular goal (e.g. Müller and Bütler 2010) are still rare. An important field of research remains how the combination of complementary instruments in a qualitative and spatially optimized way may support ecosystem functions that cannot be supported with one type of instrument alone. Ecological standards of close-to-nature forestry determine the minimum habitat quality of forests and their suitability as a dispersal matrix between hotspots of species occurrence.

There is a need to develop an integrative multi-functional forestry with strong segregative elements that complement integrative tools and are effective enough to preserve the richness of rare and threatened species in forests of high conservation value

> In recent decades, public perception of the functions of European forests has changed, which is reflected in the progressive request of integrating biodiversity conservation with timber production and other functions in multi-purpose forestry. Yet, an exclusively integrative approach is not suitable to provide the large variety of ecological niches and processes needed to preserve a representative forest biodiversity in Europe. Although close-

to-nature forestry provides a minimum habitat quality for the majority of generalist species, an area-wide integrative approach does not comprise niches for many habitat specialists, particularly species that depend on extended habitat tradition (e.g. lichens, fungi, insects), the accumulation of limiting resources (e.g. deadwood; sapro-xylobiont insects, fungi, and birds), natural dynamics and disturbances (e.g. fire-dependent plant and insect species), or particular forms of forest use and their habitat features (thermo- and photophilic species). Thus, there is an obvious need to develop an integrative multi-functional forestry with complementary segregative elements that are effective enough to preserve species richness in forests of high conservation value. A dual strategy that flexibly combines integrative and segregative conservation instruments could serve most biodiversity conservation goals in European forests. Beyond that, managing forest biodiversity by focusing on the underlying conservation principles and applying a dual strategy that combines the advantages of various instruments will enable silviculturalists to adapt the prevailing conservation concepts to their current environmental conditions, previous harvesting types, and future developments.

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