In Focus – Managing Forest in Europe

Integrative approaches as an opportunity for the conservation of forest biodiversity

Daniel Kraus and Frank Krumm (eds.)

Integrative approaches as an opportunity for the conservation of forest biodiversity

Supported by:

Federal Ministry of
Food, Agriculture
and Consumer Protection

based on a decision of the Parliament
of the Federal Republic of Germany

IMPRINT:

Recommended citation: Kraus D., Krumm F. (eds) 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute. 284 pp.
Layout: design.idee GbR, Büro für Gestaltung, Erfurt
Printing: rombach digitale manufaktur, Freiburg

Disclaimer: The present volume is the final report of the Integrate project carried out by the Central European Regional Office of the European Forest Institute – EFICENT. The views expressed in this publication are those of the authors and do not necessarily represent those of the European Forest Institute.

ISBN: 978-952-5980-06-6 printed
ISBN: 978-952-5980-07-3 pdf

Photo credits: Claus Bässler (p. 10), Michele Bozzano (p. 205 right), Heinz Bussler (p. 145 right, 276), Heinrich Holzer (p. 145 left, back cover centre), Heike Kappes (back cover left), Daniel Kraus (cover, p. 5, 15, 16, 83 left and right, 204, 254), Frank Krumm (p. 10, 82), Tomi Muukkonen (p. 144), Juri Nascimbene (back cover right), Albert Reif (p. 205 left).

Integrative approaches as an opportunity for the conservation of forest biodiversity

Contents

Contributing Authors and Drafting Committee

Contributing authors

Per Angelstam, SLU, Skinnskatteberg, Sweden
Jürgen Bauhus, Freiburg University, Germany
Heike Begehold, State Agency for Environment, Health and Consumer Protection of Brandenburg (LUGV), Potsdam, Germany
Simon Birrer, Swiss Ornithological Institute, Sempach, Switzerland
Kurt Bollmann, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Christophe Bouget, Irstea, Nogent-sur-Vernisson, France
Peter Brang, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Veronika Braunisch, FVA, Freiburg, Germany, and University of Bern, Switzerland
Marc Buée, INRA, Nancy, France
Helga Bültmann, Münster, Germany
Rita Bütler, Swiss Federal Research Institute WSL, Lausanne, Switzerland
Marco Conedera, Swiss Federal Research Institute WSL, Bellinzona, Switzerland
Simon Egli, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Marine Elbakidze, SLU, Skinnskatteberg, Sweden
Jörg Ewald, University of Applied Sciences Weihenstephan-Triesdorf, Freising, Germany
Paolo Giordani, University of Genova, Italy
Marion Gosselin, Irstea, Nogent-sur-Vernisson, France
Frederic Gosselin, Irstea, Nogent-sur-Vernisson, France
Lena Gustafson, SLU, Uppsala, Sweden
Isabelle Herrmann, TU Dresden, Tharandt, Germany
Franka Huth, TU Dresden, Tharandt, Germany
Bengt-Gunnar Jonsson, Mid Sweden University, Sundsvall, Sweden
Heike Kappes, Naturalis Biodiversity Center, Leiden, The Netherlands
Jarkko Koskela, Bioversity International, Rome, Italy
Jari Kouki, University of Eastern Finland, Joensuu, Finland.
Daniel Kraus, EFICENT, Freiburg, Germany
Wolf-Ulrich Kriebitzsch, Thünen Institute, Hamburg, Germany
Frank Krumm, EFICENT, Freiburg, Germany
Thibault Lachat, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Laurent Larrieu, INRA & CNPF, Auzeville-Tolosane, France
François Lefèvre, INRA, Avignon, France
Markus Lier, Metla, Joensuu, Finland
Marcus Lindner, EFI, Joensuu, Finland
Asko Lõhmus, University of Tartu, Estonia
Ulrich Mergner, BaySF, Ebrach, Germany
Frits Mohren, Wageningen University, Netherlands
Pierre Mollet, Swiss Ornithological Institute, Sempach, Switzerland
Jörg Müller, Bavarian Forest National Park, Grafenau, Germany
Gert-Jan Nabuurs, Alterra, Wageningen, The Netherlands
Thomas A. Nagel, University of Ljubljana, Slovenia

Juri Nascimbene, University of Trieste, Italy
Cecile Nivet, GIP-ECOFOR, Paris, France
Anne Oxbrough, Edge Hill University, Lancashire, UK
Yoan Paillet, Irstea, Nogent-sur-Vernisson, France
Momchil Panayotov, University of Forestry, Sofia, Bulgaria
Jari Parviainen, Metla, Joensuu, Finland
Gilberto Pasinelli, Swiss Ornithological Institute, Sempach, Switzerland
Martina Peter, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Juha Pykälä, Finnish Environment Institute, Helsinki, Finland
Michael Scherer-Lorenzen, Freiburg University, Germany
Marcus Schmidt, Northwest German Forest Research Station, Göttingen, Germany
Nicola Schoenenberger, Museum of Natural History, Lugano, Switzerland
Andreas Schuck, EFICENT, Freiburg, Germany
Juha Siitonen, Metla, Helsinki, Finland
Anne Sverdrup-Thygeson, Norwegian University of Life Sciences, Ås, Norway
Miroslav Svoboda, Czech University of Life Sciences, Prague, Czech Republic
Hjalmar Thiel, Rosdorf, Germany
Arno Thomaes, INBO, Brussels, Belgium
Kris Vandekerkhove, INBO, Brussels, Belgium
Goddert von Oheimb, Leuphana University of Lüneburg, Germany
Thomas Vrška, University of Brno, Czech Republic
Sven Wagner, TU Dresden, Tharandt, Germany
Beat Wermelinger, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Susanne Winter, TU Dresden, Tharandt, Germany
Anna-Liisa Ylisirniö, University of Lapland, Rovaniemi, Finland
Eric K. Zenner, Pennsylvania State University, USA
Tim Ziesche, LFE Brandenburg, Eberswalde, Germany

Drafting committee

Kurt Bollmann, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
Renate Bürger-Arndt, Göttingen University, Germany
Marco Conedera, Swiss Federal Research Institute WSL, Bellinzona, Switzerland
Thorsten Hinrichs, BMELV, Bonn, Germany
Daniel Kraus, coordinator, EFICENT, Freiburg, Germany
Frank Krumm, coordinator, EFICENT, Freiburg, Germany
Frits Mohren, Wageningen University, Netherlands
Jari Parviainen, Metla, Joensuu, Finland
Andreas Schuck, EFICENT, Freiburg, Germany
Kris Vandekerkhove, INBO, Brussels, Belgium

Reviewers

We would like to thank the following people for carefully reviewing different chapters: Claus Bässler, Jürgen Bauhus, Annemarie Bastrup-Birk, Peter Bebi, Simon Birrer, Kurt Bollmann, Veronika Braunisch, Marco Conedera, Bengt-Gunnar Jonsson, Jari Kouki, Thibault Lachat, Marcus Lindner, Asko Lõhmus, Marco Moretti, Jörg Müller, Gert-Jan Nabuurs, Thomas A. Nagel, Yoan Paillet, Peter Ódor, Gilberto Pasinelli, Christopher Prins, Christian Rixen, Philippe Rosenberg, Andreas Schuck, Veronika Stöckli, Anne Sverdrup-Thygeson, Kris Vandekerkhove, and Beat Wermelinger.

Ostoma ferruginea

Preface

The protection of forests and forest-related biodiversity has received increasing attention both at the national and international level. At the same time, increasing demands are being made on European forests with respect to the products and energy they can and do provide on a renewable, climate-friendly, and domestic basis. Forests provide income for many farmers, forest owners, and the forest industry and offer valuable recreation opportunities and protection from various hazards, especially for urban dwellers, and are thus subject to many questions on the state of their biodiversity and their protection. The positive or negative impacts of forest management practices and the question whether biodiversity in multi-functional forests can be better enhanced by integrative or segregative approaches are subjects of ongoing debate. Trade-offs between different interests and management objectives need to be examined.

Forests are primarily used in their phase of economic maturity. Consequently, forests in late development, degradation, or complete stand breakdown phases are scarce. However, it is often these forest development phases that contain a rich diversity of niches and species. On the other hand, forests that have been managed over centuries, such as those in Europe, often harbour endangered species that would disappear under natural processes. It is therefore important to integrate biodiversity conservation into the management of commercial forests in order to provide suitable habitats for forest-dwelling species over the long term.

Current policy processes such as the negotiations on a European Forest Convention, the EU Forest Strategy and the EU Biodiversity Strategy, the discussions on sustainability criteria for biomass, and the guidance document for forestry in Natura 2000 areas demonstrate that there is the scope and need for further scientific guidance on these questions.

The present publication presents the results of a research project of EFI-EFICENT, initiated by the Federal Ministry of Food, Agriculture and Consumer Protection (BMELV) in 2011. Its task was to look into these questions on a Central European scale, i.e. beyond national borders, and provide answers that are helpful for policy and practice. In my view, it did a marvellous job of organizing cross-border scientific exchange among eminent researchers working on this subject, while also taking into account the experiences of practitioners and drawing the most up-to-date conclusions. I hope that the results of the project will inform and support relevant political processes and will stimulate both future discussions and further scientific work on the integration of biological biodiversity in forest management across sectors.

Matthias Schwoerer

Head of Division
International and European Forest Policy
Federal Ministry of Food, Agriculture and Consumer Protection

Figure 1. Deadwood of large dimensions provides habitats for wood decaying fungi and saproxylic insect species that have become threatened in areas with intensive forest management. Photo by K. Vandekerkhove.

Introduction

Daniel Kraus and Frank Krumm

Biodiversity became a keyword in research, political conferences, and society within a few years after E.O. Wilson popularized the term in the early 1990s. It was first addressed at the global political level in 1992 at the United Nations Conference on Environment and Development (UNCED) in Rio and updated at subsequent Ministerial Conferences on the Protection of Forests in Europe in Helsinki (1994) and Lisbon (1998). Since then maintaining forest biodiversity has been closely related to the sustainable use of forests. Sustainable use and protection of forests are considered equally important for the conservation of biodiversity. The practical implementation of biodiversity as a criterion for sustainable forest management has proved more difficult than expected. Species diversity turned out to be the easiest aspect to implement among the main biodiversity elements (the other two being genetic diversity and diversity of ecosystems) because of the extensive studies that had already been carried out in this field. As a result, species diversity rapidly found its way into forest ecology projects. Species abundance of selected groups was often used as a comparative criterion for the quality and naturalness of habitats. However, this criterion often proved to be of little value, e.g. for indicator species groups such as birds and saproxylic beetles, as semi-natural forests may have a comparable or even higher species abundance than unmanaged or natural forests. Moreover, species abundance was not necessarily the main concern of the Convention on Biological Diversity (CBD): Article 7 explicitly requests signatory states to "identify components of biological diversity important for its conservation and sustainable use", a clearly differentiated qualitative approach.

The Bern Convention and the EU Habitats Directive, as instruments for implementation of the CBD, give clear qualitative directives on the protection and conservation of rare, threatened, or endemic species or taxa for which a special responsibility exists

The Natura 2000 process finally brought some clarity by explicitly listing habitats and species of special community importance. Several strategy papers on the national level on the conservation and sustainable use of biological diversity have focused on integrative approaches (e.g. integration of deadwood into commercially managed forests), but there is not yet a clear idea on the operationalization and monitoring of these goals. Therefore, the new focus is on the measurability of biodiversity through, for example, indicator species or habitat structures that can be influenced and controlled by forest management. Meanwhile, several studies on forest structure and its influence on forest biocenoses have been published. In particular, deadwood aspects have been studied extensively, including interrelations between species such as saproxylic fungi and structural elements or the distribution and connectivity of deadwood.

Habitat continuity, natural and anthropogenic variability of site conditions, and natural dynamics are the essential prerequisites for biodiversity in forests

The concept of diversity of site conditions is primarily related to heterogeneity within a biotope: several studies suggest that local variations of growing and climate conditions, natural disturbances, and various land use practices create a mosaic of niches and consequently a high biodiversity. Interestingly, biodiversity is not necessarily positively correlated with naturalness. Coppice forests with and without standards, silvopastoral forest systems, and other forms of historical forest use practices show a remarkable diversity of species. However, specific richness and specific, taxonomic, or functional diversity (trophic levels, key species, guilds) are only measures for a part of the concept of biodiversity and therefore only consider known species (15% of the living organisms on our planet). Additionally, these limitations are linked to spatio-temporal variations of biodiversity.

The recognition that disturbances play an important role in Central European forest ecosystems has many implications, especially for how forests are managed. Knowledge of natural disturbance regimes and forest dynamics is the foundation for any system of ecologically based forest management (e.g. ecological forestry, close-to-nature silviculture, natural disturbance based silviculture, ecosystem based management).

> *A main premise of ecological forest management is that silviculture based on patterns and processes found in old-growth forests will maintain a variety of non-timber forest functions, especially the provision of important habitat for biodiversity*

In this context, the type of forest management can also be considered as a disturbance of the natural functioning of forests. Central European forests are primarily used in their phase of economic maturity, in which yield and market based criteria are mainly considered. Consequently, forest phases of late development, degradation, or complete stand break down are virtually lacking or exist only sporadically and on a small scale. However, due to their long habitat continuity, it is these forest development phases that hold a rich diversity of rare niches and species. In order to conserve and restore such species communities, forest management concepts have to ensure that structural elements found in late development phases are re-established or re-introduced into managed forests (see Figure 2).

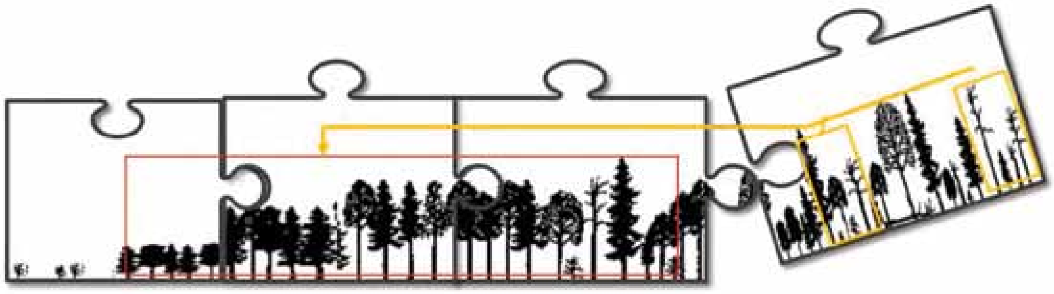


Figure 2. Commercially managed forests often show a significant lack of early and late development phases. Structural elements such as high amounts of deadwood, old trees with microhabitats, and diverse stand structure can be integrated into commercially managed forests to provide habitats for rare and threatened species.

Nevertheless, there is still a knowledge gap on habitat relations of various potential indicator species, and, because of their complexity, there is a clear research need on relevant sets of habitat parameters. Consequently, the main challenge for the implementation of the criterion of biodiversity remains the lag between ecological knowledge and political initiatives. Having detailed knowledge on such complex relations will create a sound basis for the implementation of integrative conservation concepts in forests.

The present publication aims to provide a basis for discussion by informing the ongoing debate on how biodiversity can be best preserved in commercially managed forests of Central Europe and beyond.

Forest management concepts in European forests often do not sufficiently consider measures to integrate biodiversity protection, maintenance, or enhancement into commercial forest management. The degree of integration of conservation measures and instruments is still an issue of ongoing dispute and plays a crucial role in the development of new management concepts. The efficiency of criteria and indicator initiatives for forest biodiversity monitoring must also be discussed in this context. Natural forest development and naturalness as a concept provide a unique opportunity from which to learn and can be used as a reference for the identification of conservation goals in forests. Therefore, it is important to understand management options and their trade-offs in silvicultural systems as well as possible adaptations to multifunctional forestry and retention approaches.

1 Concepts

Chapter 1 aims to provide background information on the relevant principles and concepts for integrative forest management approaches and is structured into six sections:

1.1 To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests

1.2 European initiatives on criteria and indicators for forest biodiversity

1.3 Research in old-growth forests and forest reserves: implications for integrated forest management

1.4 Forest Naturalness as a key to forest biodiversity preservation

1.5 Silvicultural systems and multiple service forestry

1.6 Retention Forestry – an integrated approach in practical use

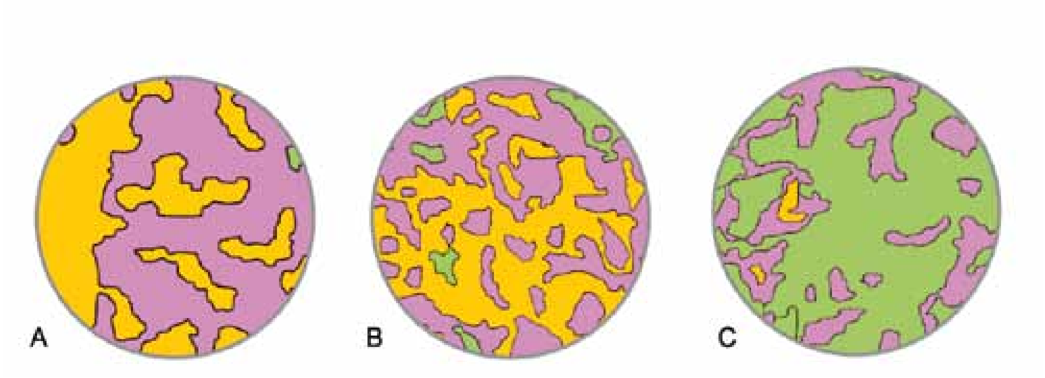


Figure 3. Model forest landscapes with two negatively correlated management goals from left to right: (A) large scale segregation, (B) small scale segregation, (C) large scale integration. Green coloured areas show where the integration of both goals is highest.

1.1 To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests

Kurt Bollmann and Veronika Braunisch

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 but present the underlying ecological principles and discuss the different 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).

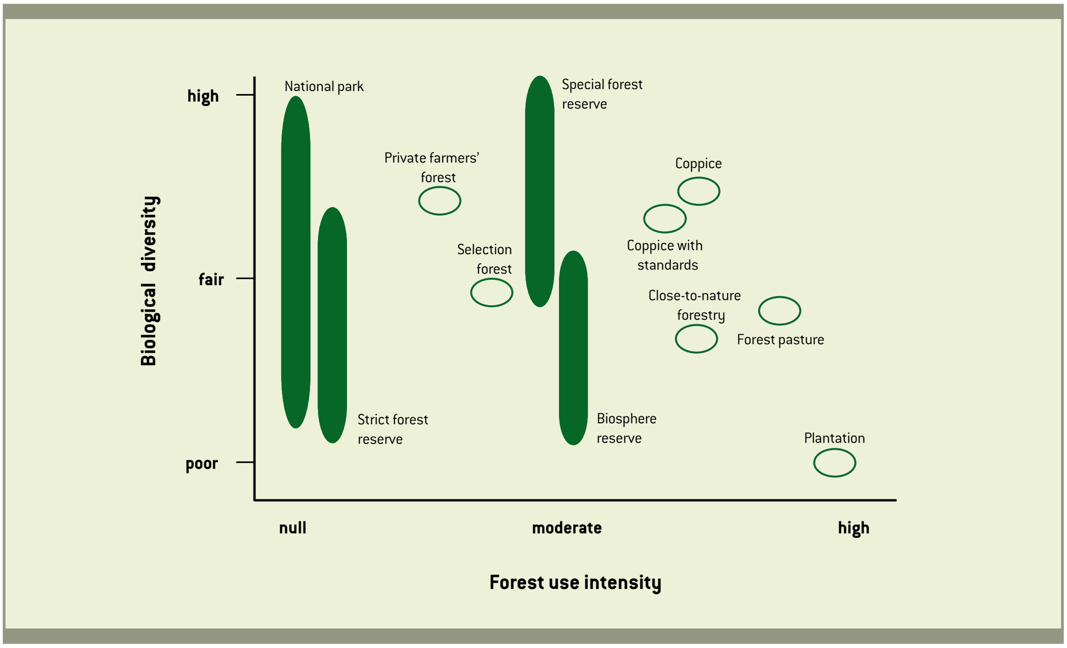


Figure 4. Relationship between forest types under different use intensities or harvesting regimes, respectively, and the biological diversity therein. Green symbols indicate forests primarily assigned to biodiversity conservation; light symbols indicate forests primarily assigned to commodity production. 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 thermo- and 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;
- **Habitat connectivity** by supporting a landscape with interconnected forest patches as well as within-forest connectivity of structural elements so as to allow for sufficient individual or genetic exchange between forest biota.

> *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 support of **natural** (succession) **dynamics** after disturbance events (Figure 5).

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).

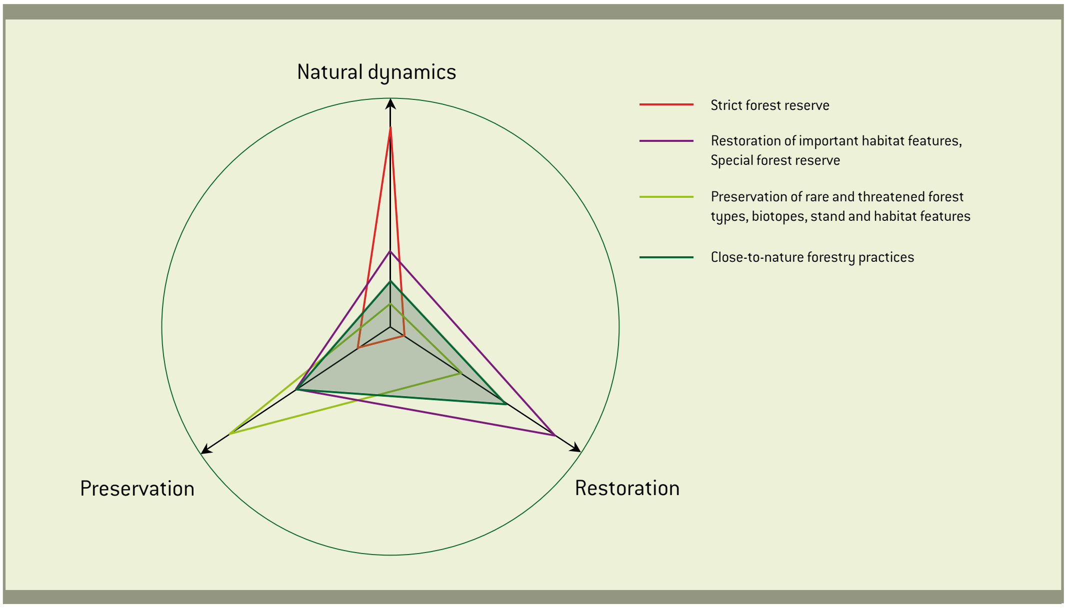


Figure 5. Qualitative model of the impact of different biodiversity conservation tools along the three conservation axes – preservation (lower left arrow), restoration (lower right arrow), and natural dynamics (upper arrow) – in comparison with the basic performance of close-to-nature forestry practices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

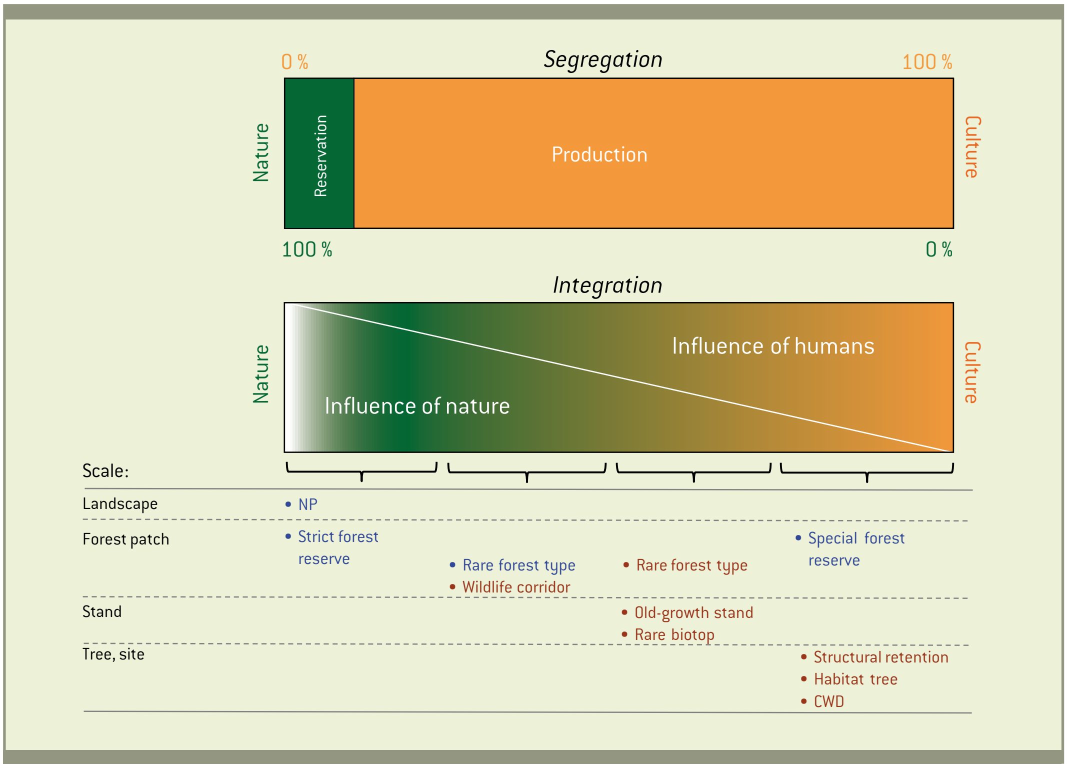


Figure 6. Conceptual differences between segregative and integrative approaches in forestry. In a segregative forestry system, national parks and forest reserves often preserve primeval or heritage forests that are embedded in a matrix of intensively used forests or plantations with low habitat quality. 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 m^3 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

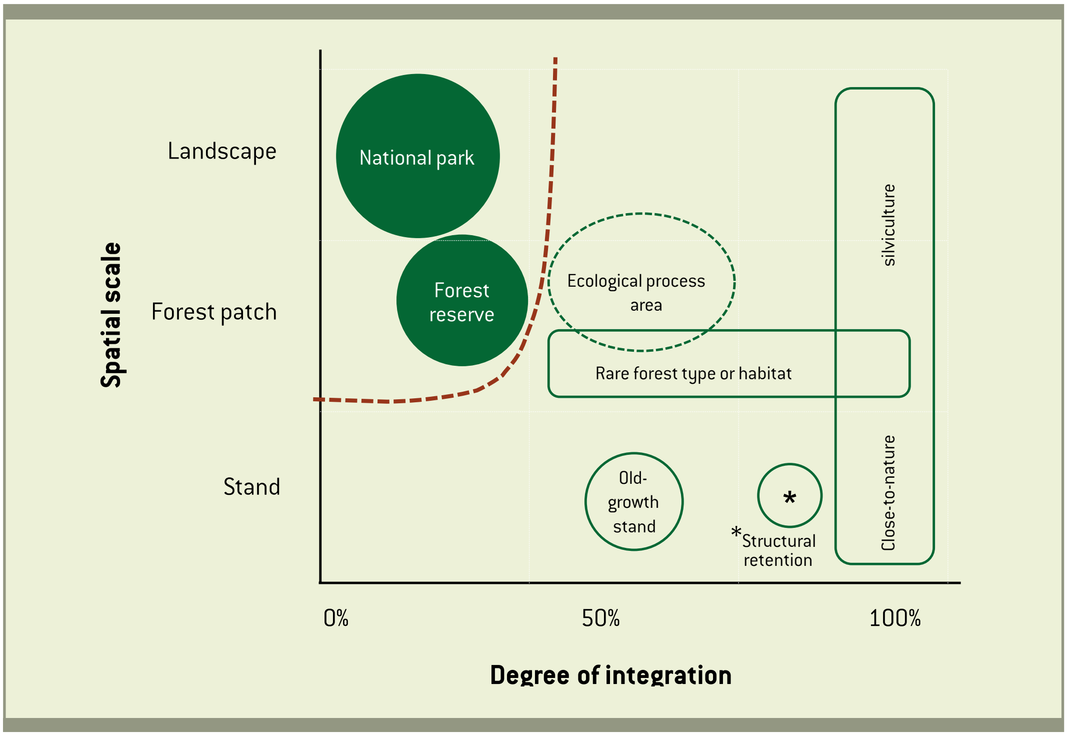


Figure 7. Distribution of integrative (light symbols) and segregative (green) biodiversity conservation instruments along the spatial planning scale of forestry. The brown line represents the virtual border between a segregative and an integrative system. Area-wide integrative approaches have to be complemented 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 km^2 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.

References

Bässler, C. and Müller, J. 2010. *Importance of natural disturbance for recovery of the rare polypore Antrodiella citrinella Niemela & Ryvarden. Fungal Biology 114:129–133.*

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

Bauhus, J., Puettmann, K.J. and Kühne, C. 2013. *Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In: Messier, C., Puettmann, K.J. and Coates, K.D. (eds.). Managing forests as complex adaptive systems: building resilience to the challenge of global change. The Earthscan forest library, Routledge. Pp. 187–213.*

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. and Nystrom, M. 2003. *Reserves, resilience and dynamic landscapes. Ambio 32:389–396.*

Bollmann, K. 2011. *Naturnaher Waldbau und Förderung der biologischen Vielfalt im Wald. Forum für Wissen. Pp. 27–36.*

Bollmann, K. and Müller, J. 2012. *Naturwaldreservate: welche, wo und wofür? Schweizerische Zeitschrift für das Forstwesen 163:187–198.*

Bücking, W. 2007. *Naturwaldreservate in Europa. Forstarchiv 78:180–187.*

Bürgi, M. 1998. *Habitat alterations caused by long-term changes in forest use in Switzerland. In: Kirby, K.J. and Watkins, C. (eds.). The ecological history of European forests. CAB International, UK, Oxford. Pp. 203–211*

EEA. 2008. *European forests – ecosystem conditions and sustainable use. European Environmental Agency, Copenhagen.*

FAO. 2010. *Global forest resources assessment 2010: Main report. Rome.*

FOREST EUROPE, UNECE and FAO. 2011. *State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe.*

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. and Franklin, J.F. 2012. *Retention forestry to maintain multifunctional forests: A world perspective. Bioscience 62:633–645.*

Hausrath, H. 1982. *Geschichte des Deutschen Waldbaus: Von seinen Anfängen bis 1850. Hochschulverlag, Freiburg.*

Hermy, M. and Verheyen, K. 2007. *Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecological Research 22:361–371.*

Hewitt, G. M. 1999. *Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society 68:87–112.*

Korneck, D., Schnittler, M., Klingenstein, F., Ludwig, G., Takla, M., Bohn, U. and May, R.M. 1996. *Warum verarmt unsere Flora? Auswertungen der Roten Liste der Farn- und Blütenpflanzen Deutschlands. Schriftenreihe für Vegetationskunde 29:299–444.*

Kulakowski, D., Bebi, P. and Rixen, C. 2011. *The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120:216–225.*

Küster, H. 1995. *Geschichte der Landschaft Mitteleuropas Beck, München.*

Lassauce, A., Anselle, P., Lieutier, F. and 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.*

Leibundgut, H. 1978. *Über die Dynamik europäischer Urwälder. Allgemeine Forst Zeitschrift für Waldwirtschaft und Umweltvorsorge [AFZ/DerWald] 33:686–690.*

Lindenmayer, D.B., Franklin, J.F. and Fischer, J. 2006. *General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131:433–445.*

Lindenmayer, D.B. and Noss, R.F. 2006. *Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20:949–958.*

MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography. Princeton University Press, Princeton, N.Y.*

Margules, C.R. and Pressey, R.L. 2000. *Systematic conservation planning. Nature 405:243–253.*

Müller, J., Bussler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J. and Zabransky, P. 2005. *Urwald relict species – Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2:106–113.*

Müller, J. and 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.*

Müller, J., Noss, R.F., Bussler, H. and Brandl, R. 2010. *Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation 143:2559–2569.*

Noss, R. F. 1999. *Assessing and monitoring forest biodiversity: A suggested framework and indicators. Forest Ecology and Management 115:135–146.*

Paillet, Y., Berges, L., Hjalten, J., Odor, P., Avon, C., Bernhardt-Romermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, B., Uotila, A., Valladares, F., Vellak, K. and Virtanen, R. 2010. *Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. Conservation Biology 24:101–112.*

Parviainen, J. and Schuck, A. 2011. *Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems. In: FOREST EUROPE, UNECE and FAO: State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. Pp. 65–97.*

Pausas, J.C., Llovet, J., Rodrigo, A. and Vallejo, R. 2008. *Are wildfires a disaster in the Mediterranean basin? – A review. International Journal of Wildland Fire 17:713–723.*

Pickett, S.T.A. and Thompson, J.N. 1978. *Patch dynamics and design of nature reserves. Biological Conservation 13:27–37.*

Pimm, S. L. 1991. *The balance of nature? Chicago University Press, Chicago. Pp. 448.*

Puettmann, K.J., Coates, K.D. and Messier, C. 2009. *A critique of silviculture: Managing for complexity. Island Press, Washington.*

Scherzinger, W. 1996. *Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung. Ulmer, Stuttgart.*

Schulze, E.-D., Hessenmoeller, D., Knohl, A., Luyssaert, S., Boerner, A. and Grace, J. 2007. *Temperate and boreal old-growth forests: how do their growth dynamics and biodiversity differ from young stands and managed forests? In: Wirth, C., Gleixner, G. and Heimann, M. (eds.). Old-growth forests: function, fate and value. Springer, Berlin, Heidelberg. Pp. 343–366.*

Siitonen, J. 2001. *Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forest as example. Ecological Bulletin 49:11–41.*

Splechtna, B.E., Gratzer, G. and Black, B.A. 2005. *Disturbance history of a European old-growth mixed-species forest – A spatial dendro-ecological analysis. Journal of Vegetation Science 16:511–522.*

Thompson, I.D., Okabe, K., Tylianakis, J.M., Kumar, P., Brockerhoff, E.G., Schellhorn, N.A., Parrotta, J.A. and Nasi, R. 2011. *Forest biodiversity and the delivery of ecosystem goods and services: Translating science into policy. Bioscience 61:972–981.*

Turner, M.G., Baker, W.L., Peterson, C.J. and Peet, R.K. 1998. *Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.*

Usbeck, T., Wohlgemuth, T., Dobbertin, M., Pfister, C., Burgi, A. and Rebetez, M. 2010. *Increasing storm damage to forests in Switzerland from 1858 to 2007. Agricultural and Forest Meteorology 150:47–55.*

Vandekerkhove, K., Parviainen, J., Frank, G., Bücking, W. and Little, D. 2007. *Classification systems used for the reporting on protected forest areas (PFAs). In: Frank, G., Parviainen, J., Vandekerkhove, K., Latham, J., Schuck, A. and Little, D. (eds.). Protected forest areas in Europe – analysis and harmonisation (PROFOR): Results, conclusions and recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, Austria. Pp. 95–102.*

Welzholz, J.C. and Johann, E. 2007. *History of protected forest areas in Europe. In: Frank, G., Parviainen, J., Vandekerkhove, K., Latham, J., Schuck, A. and Little, D. (eds.). Protected forest areas in Europe – analysis and harmonisation (PROFOR): Results, conclusions and recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, Austria. Pp. 17–40.*

Winter, S., Fischer, H.S. and Fischer, A. 2010. *Relative quantitative reference approach for naturalness assessments of forests. Forest Ecology and Management 259:1624–1632.*

Winter, S., Flade, M., Schumacher, H., Kerstan, E. and 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.*

Zackrisson, O. 1977. *Influence of forest fires on north Swedish boreal forest. Oikos 29:22–32.*

1.2 The use of European criteria and indicator systems for measuring changes in forest biodiversity

*Markus Lier, Jari Parviainen, Cecile Nivet, Marion Gosselin,
Frederic Gosselin and Yoan Paillet*

The direct and indirect benefits of conservation and enhancement of forest biodiversity, in addition to economic, social, and other environmental objectives, have been widely recognized as an essential element of sustainably managed forests. Biodiversity within forest ecosystems has been addressed since the early 1990s by several forest-related policy processes worldwide, including initiatives such as the pan-European FOREST EUROPE (former MCPFE) process in Helsinki in 1993, the EU Streamlining European Biodiversity Indicators 2010 (SEBI) project in 2005, and the EU 2020 biodiversity strategy, all as a response to the objectives set out in the Convention on Biological Diversity adopted in 1992 in Rio (FOREST EUROPE 2011, EC 2011).

> *The challenge is to reconcile established instruments for assessing and measuring the development of forest biodiversity in order to produce balanced, politically relevant, scientifically sound, and practically feasible information*

However, the implementation of these international commitments varies due to different factors: natural growing conditions, forest cover, forest ownership structure, traditions, and population density. Currently, common instruments for the conservation, maintenance, and appropriate enhancement of forest biodiversity are the protection of the most valuable forest ecosystems through the establishment of protected areas and integrated biodiversity-oriented management, including the protection of rare and vulnerable ecosystems in multifunctional forests (Parviainen 2003).

The question lies in how much forest-related national and international policies and strategies have influenced the development of forest biodiversity in a country and how those developments can be measured. The challenge is to reconcile established instruments for assessing and measuring the development of forest biodiversity in order to produce balanced, politically relevant, scientifically sound, and practically feasible information. Currently, the use of criteria and indicators enables a country to measure forest biodiversity by describing it in terms of measurable attributes and to steer the effects of practical silvicultural management and forest policy. But can criteria and indicator systems measure changes in biodiversity, and if so, how have they been used? This article focuses on the pan-European FOREST EUROPE criteria and indicators of sustainable forest management (SFM) and the EU Streamlining European Biodiversity Indicators (SEBI) process and how they have been used to integrate biodiversity aspects into forest-related policies in Finland and France.

The development of criteria and indicators and other harmonized methods for biodiversity assessment in forest ecosystems has already been addressed by several European initiatives since the early 1990s, such as FOREST EUROPE in 1993 and 2003, followed by SEBI 2010.

> *The pan-European FOREST EUROPE criteria and indicators, based on the concept of sustainable forest management, encompass a broader concept of sustainability, including ecological, economic, and social aspects*

The pan-European forerunner in developing criteria and indicators is the FOREST EUROPE process, based on the concept of sustainable forest management. FOREST EUROPE encompasses a broader concept of sustainability, including ecological, economic, and social aspects.

Currently, the FOREST EUROPE C&I set has been used by 46 European countries to report on SFM, including forest biodiversity. The FOREST EUROPE indicators are divided into two categories: 1) qualitative indicators on general policies and specific policy instruments and 2) 35 quantitative indicators. Quantitative indicators are distributed in six criteria (forest resources, health and vitality of forests, productive functions, biological diversity, protective functions, and socio-economic functions) and represent numerically measurable parameters or other statistical data mainly based on a country's national forest inventory or other statistical sources (Parviainen and Västilä 2011).

The FOREST EUROPE criterion 4 includes nine forest biodiversity quantitative indicators related to trees and stand structure in order to describe maintenance, conservation, and appropriate enhancement of biological diversity in forest ecosystems (Table 2). Additional indicators relevant to forest biodiversity (e.g. 1.1 forest area, 1.2 growing stock, 3.1 increment and fellings) are included in other FOREST EUROPE criteria. Information on the state-of-the-art of Europe's forests, including the biological diversity in forest ecosystems, has been published by FOREST EUROPE in 2003, 2007, and 2011.

The FOREST EUROPE indicators, including the forest biodiversity indicators, were developed on the basis of practical and operational reasons (incl. the existing monitoring methodology and measurable data) and their scientific value. These indicators can measure and describe trends in biodiversity conservation with accumulated and repeated data series, allowing the use of time series. However, the relevance of some indicators (e.g. landscape patterns (4.7)), identification of critical threshold values for indicators (e.g. minimum amount of deadwood left in the forest), and the development of new combined indicators to describe forest biodiversity have been – and still are – debated among specialists and decision makers.

Table 2. FOREST EUROPE indicators within criterion 4: Maintenance, conservation, and appropriate enhancement of biological diversity in forest ecosystems.

Indicator		Description
4.1	**Tree species composition**	Area of forest and other wooded land, classified by the number of tree species occurring and by forest type
4.2	**Regeneration**	Area of regeneration within even-aged stands and uneven-aged stands, classified by regeneration type
4.3	**Naturalness**	Area of forest and other wooded land, classified by “undisturbed by man”, by “semi-natural”, or by “plantations”, each by forest type
4.4	**Introduced tree species**	Area of forest and other wooded land dominated by introduced tree species
4.5	**Deadwood**	Volume of standing deadwood and of lying deadwood on forest and other wooded land classified by forest type
4.6	**Genetic resources**	Area managed for conservation and utilization of forest tree genetic resources (in situ and ex situ gene conservation) and area managed for seed production
4.7	**Landscape pattern**	Landscape-level spatial pattern of forest cover
4.8	**Threatened forest species**	Number of threatened forest species, classified according to IUCN Red List categories in relation to total number of forest species
4.9	**Protected forests**	Area of forest and other wooded land protected to conserve biodiversity, landscapes, and specific natural elements, according to the FOREST EUROPE Assessment Guidelines

> *The Streamlining European Biodiversity Indicators (SEBI) informs progress towards the EU 2020 targets of halting biodiversity loss for major European habitat types, including forests*

In 2005 an approach was proposed by the European Environment Agency (EEA) called Streamlining European Biodiversity Indicators (SEBI). It was aimed at assessing the goals of the Convention on Biological Diversity and was built around its focal areas and addresses key policy questions for decision makers. SEBI 2010 consists of a pan-European set of 26 specific biodiversity indicators (Table 3) to initially assess and inform progress towards the EU 2020 targets of halting biodiversity loss for major European habitat types (forest, mountain, grassland, freshwater, arctic, coastal and marine, agricultural, and urban). Each indicator is related to a key policy question in order to aid in its interpretation.

The SEBI 2010 indicator set includes three specific indicators that indirectly or directly address forest biodiversity: forest growing stock, increment and fellings, and the occurrence of deadwood. Other forest specific indicators are included into the general biodiversity indicators but only partially cover forest biodiversity, such as nationally designated protected areas, including forest protection areas (see Table 3). The European Environmental Agency (EEA) has published a report on the status of biodiversity in Europe in 2010 (SEBI 2010).

Table 3. The 26 SEBI indicators grouped according to Convention on Biological Diversity focal area and their relation to forest indicators and key policy questions.

N°	CBD Focal area	Proposed indicators SEBI 2010	Forest related indicator	Key policy question
1	Status and trends of the components of biological diversity	Abundance and distribution of selected species	Yes	Have declines in common species in Europe been halted?
2		Red list index for European species	Yes	Has the risk of extinction for European birds changed?
3		Species of European interest	Yes	What is the conservation status of species of Community interest?
4		Ecosystem Coverage	Yes	Which changes are occurring in the distribution of Europe's ecosystems and habitats?
5		Habitat of European interest	Yes	What is the conservation status of habitats of Community interest?
6		Livestock genetic diversity	No	Are fewer livestock breeds being used in Europe?
7		Nationally designated protected area	Yes	What is the progress with the national designation of protected areas as a tool for biodiversity conservation[1]?
8		Sites designated under the EU Habitat and Birds directive	Yes	Have countries proposed sufficient sites under the Habitats and Birds Directives?
9	Threats to biodiversity	Critical load exceedance for nitrogen	Yes	What are the trends in nitrogen emissions and where in Europe does atmospheric nitrogen deposition threaten biodiversity?
10		Invasive alien species in Europe	Yes	Is the number of alien species in Europe increasing or decreasing? Which invasive alien species should be targeted by management actions?

Table 3. continued.

N°	CBD Focal area	Proposed indicators SEBI 2010	Forest related indicator	Key policy question
11		Occurrence of temperature-sensitive species	Yes	What are the negative (and positive) impacts of climate change on biodiversity?
12	Ecosystem integrity and ecosystem goods and services	Marine Trophic Index of European seas	No	What is the impact of existing fisheries and maritime policies on the health of fish stocks in European seas?
13		Fragmentation of Natural and semi-natural areas	Yes	Are European natural/ semi-natural lands becoming more fragmented? Are forest landscapes becoming more fragmented?
14		Fragmentation of river systems	No	How fragmented are rivers in Europe, and how does this affect the fish species living in them?
15		Nutrients in transitional, coastal and marine waters	No	What is the status of transitional, marine, and coastal waters in Europe?
16		Freshwater quality	No	What is the status of freshwater quality in Europe?
17	Sustainable use	<u>Forest</u>: growing stock, increment, and felling	Yes	Is forestry in Europe sustainable in terms of the balance between increment of growing stock and fellings?
18		<u>Forest:</u> deadwood	Yes	How much deadwood is present in European forests?
19		Agriculture: nitrogen balance	No	How big is agriculture's pressure on the environment? Is the nitrogen surplus reduced?
20		Agriculture: area under management practices potentially supporting biodiversity	No	To what extent is European agriculture geared towards prevention of biodiversity loss?
21		Fisheries: European commercial fish stocks	No	What is the status of European commercial fish stocks, and what can be done to prevent stocks from collapsing?
22		Aquaculture: effluent water quality from finfish farms	No	How is aquaculture and its potential pressure on the environment developing?

Table 3. continued.

N°	CBD Focal area	Proposed indicators SEBI 2010	Forest related indicator	Key policy question
23		Ecological Footprint of European countries	No	What impact does the overall resource demand and use of European societies have on biodiversity and ecosystems outside Europe?
24	Status of access and benefits sharing	Patent applications based on genetic resources	No	What percentage of European patents is biodiversity-related?
25	Status of resource transfers and use	Financing Biodiversity Management	No	To what extent are public funds being committed to conservation of biodiversity?
26	Public opinion	Public Awareness	No	What is the level of public awareness about biodiversity in Europe and what actions do Europeans take to preserve biodiversity?

If a country has included in its legislation the sites designated under the EU Birds and Habitats Directives, the Natura 2000 sites of this country are included in the figure.

Dedicated to biodiversity, SEBI aims at assessing the state and dynamics of biodiversity, whatever the type of habitat, whereas the FOREST EUROPE indicators are dedicated to forests and aim at assessing the sustainability of forest management practices. As a consequence, FOREST EUROPE indicators are partially dedicated to biodiversity (Criterion 4): FOREST EUROPE encompasses a broader concept of sustainability, and includes in addition to the ecological aspects, economic and social aspects, in which stakeholders are included. Despite these differences, several indicators overlap between SEBI and FOREST EUROPE, not only in criterion 4 but also in other quantitative (1 to 6) and qualitative (A and B) criteria (Table 4).

It can be noted that the forest cover varies considerably between European countries, from 10% in the Netherlands up to 76 % in Finland. These differences have a huge influence on the approach to assessing the biodiversity of forests in a country. In countries with low forest cover, the influence of habitat types other than forest is strong on the overall biodiversity characteristics and species, while in countries where forest habitats predominate, the influence of other habitats is minor.

Feedback can be provided to policy makers through the use of the DPSIR conceptual framework for assessing the effectiveness of biodiversity conservation policies

Table 4. Comparison between SEBI indicators and FOREST EUROPE indicators, all criteria included.

SEBI indicators partially or totally related to forest ecosystem	Related FOREST EUROPE indicators	
	Related criterion	Related indicator
1-Abundance and distribution of selected species (birds only)	No related indicator[1]	
2-Red list index for European species	Criterion 4	4.8 Threatened forest species
3-Species of European interest	No related indicator[1]	
4-Ecosystem Coverage	Criterion 1	1.1 Forest area
5-Habitat of European interest	No related indicator[1]	
7-Nationally designated protected area[2]	Criterion 4	4.9 Protected forest[3] - MCPFE Class 1 (biodiversity) and Class 2 (landscape)
8-Sites designated under the EU Habitat and Birds directives (Natura 2000 network)		4.9 Natura 2000 forest areas (only provided for EU-27 countries)
9-Critical load exceedance for nitrogen	Criterion 2	2.1 Deposition of air pollutants (Nitrogen, sulphur dioxide,…)
10-Invasive alien species in Europe	Criterion 4	4.4 Introduced tree species (partially related)
11- Impact of climatic change on bird populations	No related indicator	
13-Fragmentation of natural and semi-natural areas	Criterion 4	4.7 Landscape Pattern
17-Forest: growing stock, increment and felling	Criterion 1	1.2 Growing stock
	Criterion 3	3.1 Increment and fellings
18-Forest: deadwood	Criterion 4	4.5 Deadwood
23-Ecological Footprint of European countries	No related indicator	
24- Patent applications based on genetic resources	No related indicator	
25- Financing Biodiversity Management	Part A (qualitative)	A.4 Financial instruments/economic policy
26- Public Awareness	Part B (qualitative)	B.11 Public awareness and participation

---

[1] No explicit link was found in FOREST EUROPE with the Directive on the Conservation of natural habitats and of wild fauna and flora.

[2] A "nationally designated area" is an area designated by a national designation instrument based on national legislation. If a country has included in its legislation sites designated under the EU Birds and Habitats Directives, the Natura 2000 sites of this country are included.

[3] EU-27 countries were asked to fill out a separate form on Natura 2000 forest areas in order to examine the overlap between Natura 2000 protected forest areas and areas fitting MCPFE classes.

In order to assess the effectiveness of biodiversity conservation policies and provide feedback to policy makers, the European Environment Agency (EEA) has adopted a conceptual framework (DPSIR framework).

According to the DPSIR framework, there is a chain of assumed causal links: "driving forces" (economic sectors, human activities) exert "pressures" (emissions, waste, etc.) on the "states" of an ecosystem (physical, chemical, and biological) that have “impacts” on human well-being, and eventually lead to political “responses” (prioritization, target setting, etc.). The process is then reiterated.

However, the causal chain between all indicators in the SEBI process is not fully explicit, and for forests, SEBI remains unbalanced in relation to the DPSIR system as the two forest-specific indicators are considered as “pressure” indicators (European Environment Agency 2012, Table 4.1, p. 25). Also the relevance of the indicator “growing stock, increment and felling” as an indicator of forest biodiversity can be questioned since its link with biodiversity is neither explicit nor unequivocal. In addition, one indicator can have several roles and can be a pressure, impact, or even response indicator.

The question remains: Can criteria and indicator systems measure changes in biodiversity, and if so, how have they been used? This is illustrated in case studies in Finland and France.

The Finnish example shows how a change in forest management policy has influenced the state of biodiversity, as assessed through repeated monitoring of red-listed species (FOREST EUROPE indicator on threatened forest species)

The forest management policy has brought measurable positive changes for biodiversity to commercial forests in Finland since the early 1990s. The main methods for safeguarding biological diversity in commercial forests are the protection of valuable habitats and biotopes, favouring mixed tree stands, and increasing the amount of decayed wood. Biodiversity-oriented forest management that takes into account the forest’s natural development cycle has been a statutory requirement (new forest law was adopted in 1997) in Finland for 15 years. At the same time, the production of information about biodiversity and related research, discussion, and consultation have been a key area, with broad participation by forest owners and other actors and interest groups in forest management (Parviainen and Västilä 2011).

The application of the FOREST EUROPE indicators of sustainable forest management in Finland has produced a time series spanning more than 15 years. Although changes in forests are slow, the indicators have enabled certain trends to be distinguished and comparisons to be made, especially concerning the impacts of forest policy on forests and forest management (Parviainen and Västilä 2011). A national evaluation of threatened species has been conducted four times by the Ministry of the Environment: in 1983–85, 1987–91, 1997–2000, and 2007–2010. The last two evaluations are based on the IUCN criteria by the International Union for Conservation of Nature. The evaluations produce information about the number of threatened species, the causes of decline, risks, and proposals for improving their protection (FOREST EUROPE indicator 4.8: Threatened forest species). The rate of decline of certain forest species has slowed in Finland, or in some cases even stopped since the 1990s, although it has not been possible to halt the decline in forest species overall. The evaluation of threatened species (incl.

vertebrates, invertebrates, vascular plants, cryptogams, and fungi and lichens) conducted in 2000 and 2010 showed that the decline slowed or stopped for 81 forest species but continued for 108 species. Retention trees at felling sites have been particularly important for curbing species decline (Parviainen and Västilä 2011).

Unlike in other European countries, strict forest protection is emphasised in Finland. Under various protection programmes and decisions, the area of protected forests has been tripled over the past 35 years. The total area of protected forests is currently 2.2 million hectares, or 9.6% of all forestland. The total area of protected forests and forests under restricted use is almost 3 million hectares, or 13.0% of all forestland. The percentage of strictly protected forests in Finland (5.2% of forestland) is the highest in Europe. In southern Finland, where the percentage of strictly protected forests varies between 1.0% and 3.6%, biological diversity and protection is promoted through the Forest Biodiversity Programme for Southern Finland (METSO). The METSO programme involves developing silvicultural methods, as well as voluntary measures by private forest owners to protect biodiversity, and restoration management of protected areas in state ownership.

This example shows how a policy response to biodiversity decline (e.g. the plan created in 1997 for increasing the area of strictly protected forest area, the new biodiversity orientated forest law in 1997, and the programme to increase the areas of protected forests by voluntary means supported with financial compensation in private forestland since 2003 (METSO)) has had an effect on the state of biodiversity, and how it has been monitored according to a systematic and repeated data collection method and indicator.

The France case study illustrates the remaining difficulties of criteria and indicators in reaching their goals, and provides solutions to improve biodiversity monitoring and forest policy assessment

In France, the translation of FOREST EUROPE indicators for biodiversity criteria comprises the initial set of nine pan-European indicators and some additional indicators specific to France (e.g. proportion of the main tree species in basal area, area of overmature regular stands). They have been published every five years since 1995. Fifteen years after the first publication, an assessment of the effectiveness of this reporting system as a communication, monitoring, and management tool appears interesting. As a communication tool, the French national biodiversity indicators for sustainable forest management offer synthetic and accessible information. They provide basic contextual elements to describe forest biodiversity. However, the picture they provide is too incomplete and unstructured to be used as a forest biodiversity-monitoring tool.

There are two main reasons for this: First, some important parts of biodiversity are not addressed due to a lack of data. For example, neither a forest saproxylic species monitoring system nor a national saproxylic red-list for France are currently available, although saproxylic species are particularly at stake since they represent 25% of the forest species and many of them are predicted to decline. Second, despite the fact that genetics constitutes a crucial driver of biodiversity dynamics, and functional diversity ensures ecosystem function and related services, these biodiversity organization levels are almost not addressed in comparison to the taxonomic diversity level, thus giving an incomplete view of biodiversity. In addition, structural indicators (proxies built on structural stand data supposed to be linked with biodiversity, as species habitat characteristics) are far more abundant in this system than all the indicators mentioned above.

As a monitoring tool, the set of national biodiversity indicators could be used to assess the efficacy of forest biodiversity conservation policies

For example, biodiversity orientated initiatives in public forests promote an increase in the area of strict forest reserves and conservation of deadwood in managed forests. The question is whether the current indicators can assess the effectiveness of these policies. For such an objective, the DPSIR framework or the PSR (Pressure – State – Response) is appropriate and enables the monitoring of, at the same time, a response indicator (a policy dedicated to manage a pressure on biodiversity, e.g. to promote deadwood conservation), its effects on the pressure indicator concerned (e.g. volume of deadwood), and its effects on the part of biodiversity in focus (e.g. richness and abundance of saproxylic communities). However, the current FOREST EUROPE criteria and indicators are neither PSR nor DPSIR structured. In order to use them as an evaluation or management tool, it would be useful (at least for the more at stake parts of biodiversity concerned by conservation policy) to complete each response indicator at least by a state and a pressure indicator (PSR system being the simplest one in a first step). For the next publication of French sustainable forest management indicators (due in 2015), working groups have been set up to allow indicators to evolve within the framework of European and international reporting. This will bring about constant improvement as well as increasing visibility of the national reporting. The working groups have decided to structure the national reporting according to a list of key policy questions addressed to the forest sector in the context of sustainable use of forest resources. In this way the French national part of FOREST EUROPE will be linked with the SEBI structure.

Current forest biodiversity indicator sets have allowed the sharing of common figures for a given criterion, but the linkage of common policy goals with biodiversity indicators is still lacking in several countries

The current forest biodiversity indicators sets have allowed, within the forest sector and other forest related sectors, the sharing of common figures for a given criterion, but the linkage of common policy goals with biodiversity indicators is still lacking in several countries.

According to the two country examples above it can be stated that there exists a much-improved situation as regards the assessment of changes in biodiversity in forests. Still, due to the complexity of forest biodiversity, much more work needs to be done to develop the current forest biodiversity indicator sets for the practical use in European countries. Obstacles for the detailed monitoring of biodiversity include, for example, the definition of forest biodiversity in an operational way and the financing of the operational work. The collection of data on threatened species is time-consuming and expensive, especially under conditions of high biological diversity and large forest areas.

> *The next step should include a more structured approach in order to use indicators to monitor the effects of policies and forest management on biodiversity and assess the efficacy of biodiversity-orientated measures*

There are ongoing initiatives by UNECE and FOREST EUROPE to improve the assessment of the status of forests by the current pan-European indicators. This system is based on three types of parameters and on defining threshold values (warning levels) of the key parameters. The assessment needs interactive consultation between the evaluators, data collectors, and responsible country correspondents. An option is also to apply the DPSIR framework developed by EEA for biodiversity indicators. DPSIR is, however, still quite a conceptual methodology and needs to be refined for practical and operational use. Its use in forestry would be problematic since some indicators, such as pressure, impact, and response, often have overlapping roles, the relation between forest growth and fellings being an example.

It is also important to monitor and assess biodiversity in such a way that the biodiversity functions of the forest can be compared, in an evidence based way, with the other functions of the forest so that operational and policy decisions can be taken in a balanced way. This implies that monitoring biodiversity in forests should be done in a framework that also includes production, recreation, protection, and other functions.

References

European Commission 2011. *EU biodiversity strategy to 2020. http://ec.europa.eu/environment/nature/biodiversity/comm2006/2020.htm Last accessed on 9.12.2011*

European Environment Agency 2012. *Streamlining European biodiversity indicators 2020: Building a future on lessons learnt from the SEBI 2010 process. EEA Technical report No 11/2012, 50 p.*

FOREST EUROPE, UNECE and FAO 2011. *State of Europe's Forests 2011. Status and Trends on Sustainable Forest Management in Europe.*

Parviainen, J. 2003. *Introduction: maintain forest biodiversity-intentions and reality. Journal of Environmental Management 67:3–4.*

Parviainen, J. and Västilä, S. 2011. *State of Finland´s Forests 2011. Based on the Criteria and Indicators of Sustainable Forest Management. Ministry on Agriculture and Forestry and Finnish Forest Research Institute. 99 p.*

SEBI 2010. *Assessing Biodiversity in Europe – the 2010 report. EEA European Environment Agency. 64 p.*

1.3

Research in old-growth forests and forest reserves: implications for integrated forest management

Thomas A. Nagel, Eric K. Zenner and Peter Brang

For thousands of years, Europe's forests have been influenced by a variety of land use practices to support society's changing needs for forest products and services. Centuries of cutting, burning, and grazing have culminated in contemporary forests that are dramatically different from the primary forests that once covered much of the continent. In Central Europe in particular, more than 10% of today's forests are comprised of Norway spruce plantations (Forest Europe 2011), which are much less diverse in structure and composition than the broadleaved dominated stands that once occurred there. Some forests that have not been substantially altered compositionally, such as those currently dominated by European beech, are nonetheless structurally quite different from their antecedents. Many Central European beech forests, for example, are managed with shelterwood silvicultural systems, which give rise to more or less even-aged forest patches. In contrast, the few remnants of old-growth (see Box 4 for a definition) beech forests that still occur in Europe typically have complex uneven-aged structures shaped by natural disturbances, ranging from relatively stable mortality of single old canopy trees to intermediate severity damage from periodic storms. Such old-growth forests contain substantial amounts of accumulated deadwood and large canopy trees of exceptional age that develop diverse microhabitats such as hollows and stem cracks (Commarmot et al. 2013). All these structural features provide unique habitats for numerous species of animals and fungi that have evolved in forest conditions regulated by natural processes, and they apply not only to beech forests, but also to old-growth forests of other forest types in Central Europe (Korpel 1995).

Restoring some old–growth features in managed forests provides habitat for old-growth dependent species

An important goal of contemporary forest management in Europe is to balance the sustainable production of timber with the conservation of biological diversity. Stands previously managed only for timber are therefore increasingly managed to become more similar to the structural and compositional patterns found in old-growth forests (often referred to as "reference conditions"). The idea is that restoring some of the features typical of old-growth forests will again provide habitat for species that evolved under such conditions (Seymour et al. 2002). In practical forest management, this means re-establishing a more natural tree species composition, often by reducing the share of Norway spruce monocultures, enabling natural regeneration in canopy openings that are similar in size to those created by natural processes, allowing some trees to die or leaving some of the harvesting residues in the forest to increase the amount of deadwood, and maintaining habitat and veteran trees.

Managing for old-growth resemblance, however, is predicated on the presence of old-growth forests where natural patterns and processes can be studied and quantified as reference conditions (see Box 4 for definitions of “old growth”). Because old-growth forests have developed under natural processes with little to no direct anthropogenic disturbances, they provide unique opportunities to study a variety of natural processes, such as natural disturbance regimes and forest dynamics, tree demography, and carbon cycling (Foster et al. 1996). Moreover, old-growth forests enable the investigation of structural characteristics, such as deadwood quantity and quality, horizontal and vertical heterogeneity, and microhabitats associated with veteran trees. Finally, because old-growth ecosystems are home to unique assemblages of organisms, they act as living laboratories for many ecological studies.

Box 4. Old-growth forests: definitions

There are many definitions and terms (e.g. virgin, primary, ancient forest) used for old-growth forests. These definitions are often related to natural processes or structural characteristics associated with late stages of stand development (Wirth et al. 2009, Frelich and Reich 2003, Oliver and Larson 1996). Here, we provide two definitions that may be useful in the context of this chapter:

Old-growth

- Definition based on natural processes: Forests that were initiated under a regime of natural disturbance and have developed with minimal human influence. Certainly, old-growth forests, like all forests, are subject to indirect human impact, such as climate change, air pollution, and altered population densities of ungulates. However, under this definition, stands in the process of recovery from severe natural disturbance would still be considered part of an old-growth ecosystem because they arose from natural processes and their development would not be guided by human interventions (e.g. through thinnings). Often, the terms “primary”, “virgin” or “natural heritage” forests are used in this context (Figure 8a).
- Definition based on structure: Forests in a late stage of stand development, characterized by the presence of old trees near their maximum longevity, large amounts of standing and lying deadwood, and heterogeneous stand structure, including both horizontal and vertical heterogeneity (Figure 8b).

It is important to note that these old-growth definitions hold for any forest type, although disturbance regimes and structural features vary greatly among different old-growth ecosystems. For example, old-growth is often associated with large ancient trees and abundant deadwood, which may be typical characteristics of productive sites with ample precipitation. However, ancient stands can also develop on dry, less productive sites that may not be easily recognized as old-growth, such as thermophilic steep-slope forests (Figure 8c).

The two definitions outlined in Box 4 have important implications for an integrative forest management that aims at both timber production and maintenance of biodiversity. At the tree and stand scale, a management goal may be to emulate, to a degree that is feasible, structural features typical of late-successional old-growth, such as standing and lying deadwood, veteran trees, and small-scale uneven-aged structure. At the landscape scale, it is important that management not only focus on mature forest development stages, but also on early successional stages, which are part of the natural dynamics in forests that experience occasional high severity disturbances. This may be achieved simply by leaving managed forests that have been damaged by natural disturbances to natural development (i.e. leave damaged timber on the site and refrain from salvage logging).

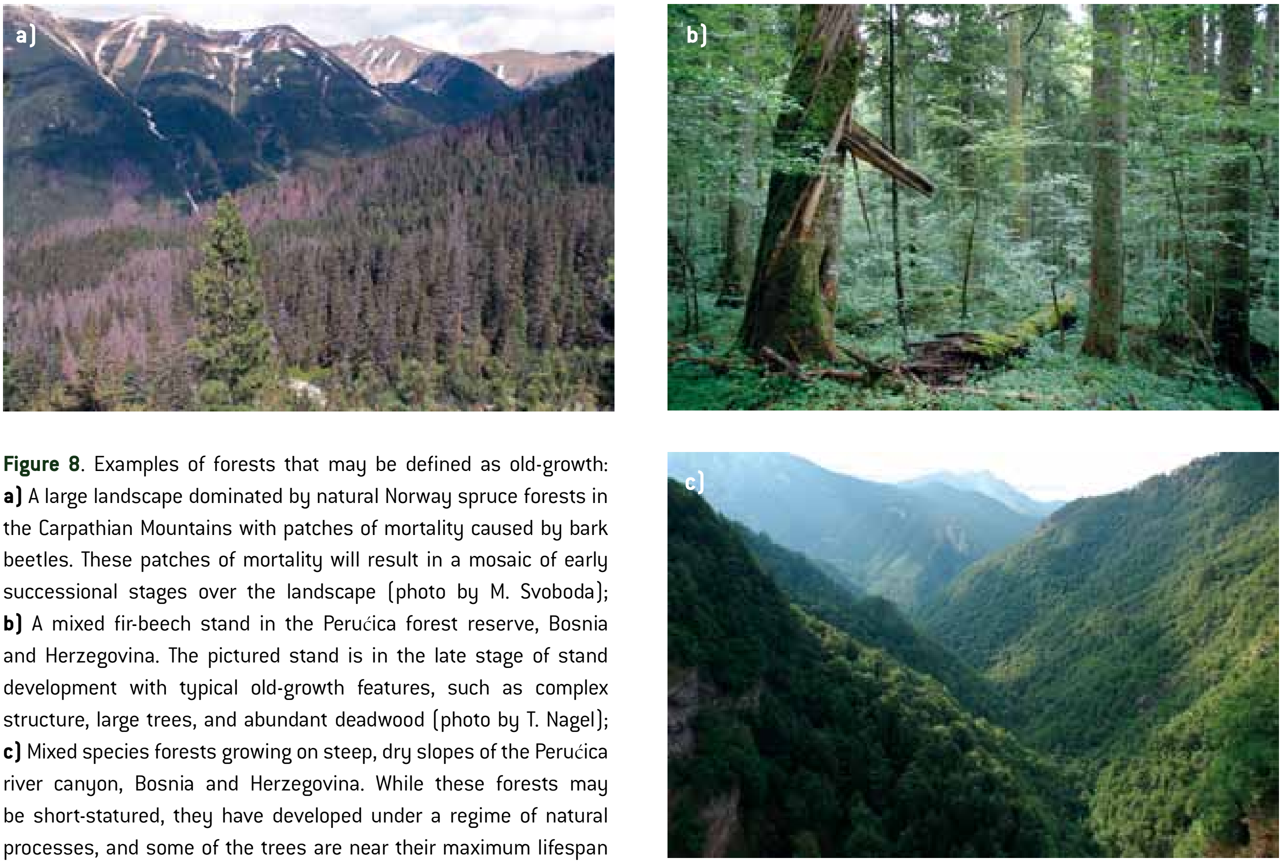


Figure 8. Examples of forests that may be defined as old-growth: **a)** A large landscape dominated by natural Norway spruce forests in the Carpathian Mountains with patches of mortality caused by bark beetles. These patches of mortality will result in a mosaic of early successional stages over the landscape (photo by M. Svoboda); **b)** A mixed fir-beech stand in the Perućica forest reserve, Bosnia and Herzegovina. The pictured stand is in the late stage of stand development with typical old-growth features, such as complex structure, large trees, and abundant deadwood (photo by T. Nagel); **c)** Mixed species forests growing on steep, dry slopes of the Perućica river canyon, Bosnia and Herzegovina. While these forests may be short-statured, they have developed under a regime of natural processes, and some of the trees are near their maximum lifespan (photo by T. Nagel).

Old-growth forests are living laboratories for ecological studies

While old-growth forests are important for providing information on reference conditions for forest management, secondary forests (i.e. forests in recovery from past management activities) that have been protected as forest reserves are equally important because they can serve as controls to disentangle and quantify the effects of management (Frelich et al. 2005, Frelich and Reich 2003, Brang et al. 2011). In fact, secondary forest reserves are often better controls than old-growth because they likely share similar histories of anthropogenic disturbance and environmental conditions. These forest reserves may also hold surprises as to which successional pathways they will follow in the absence of management, providing opportunities to improve our understanding of successional theory and our ability to predict future structural and compositional conditions (Heiri et al. 2012). For instance, interspersed trees of light-demanding species with weak competitive ability were shown to disappear within a few decades in Swiss beech forest reserves after cessation of management (Heiri et al. 2009). In addition to serving as controls, secondary forests set aside from management also have an important direct conservation function themselves because they are the sites where future old-growth will develop. Such sites provide conditions that are currently very scarce in Europe and are particularly valuable if they are of large extent and can thus capture a wide range of natural disturbances and the habitats created by them.

Research in forest reserves helps to understand the effects of management on forest structure and biodiversity

In addition to providing reference conditions and controls for forest management, there are a number of other important insights that can be gained from studies in old-growth forests and secondary forest reserves (Foster et al. 1996) (Figure 9). Because they are not, or no longer, confounded by management practices, these forests provide unique opportunities to study the influence of long-term environmental change, particularly climate change and air pollution as well as long-term effects of harvesting on productivity, carbon cycling, and biodiversity. For example, monitoring of permanent plots that tracks the growth and mortality of individual trees over several decades has detected changes in background rates of tree mortality due to climate change (van Mantgem et al. 2009). Likewise, old-growth forests often contain a significant number of ancient trees that can be used to reconstruct climates several centuries past.

Old-growth forests can also play an enormous role in the education and training of forestry professionals. Experience shows that visits to old-growth forests are highly inspiring to forest practitioners because they often create enduring first impressions – which is by far more convincing than textbook wisdom – of late development phases and associated phenomena such as giant trees and large amounts of deadwood. For the general public, old-growth forests play a similar role; they can go a long way toward convincing the public that a forest is not necessarily even-aged, park-like, clean and devoid of snags and downed wood, a view that many Europeans, especially older people in rural regions, continue to embrace.

Old-growth forests provide inspiration for foresters and the public

It is important to note, however, that any forest where timber production is a management goal, even if management is carried out with practices that attempt to emulate some of the patterns and processes identified in old-growth stands, will always differ from old-growth reference conditions. Optimal rotations for timber production that are much shorter than the lifespan of the trees preclude the development of mature and late-successional development stages, timber extraction limits inputs of deadwood in the form of large snags and logs, and harvesting patterns often lead to structurally simple stands. Ultimately, this means that forest reserves that both preserve existing old-growth and ensure the development of future old-growth are an essential part of integrative forest management. Otherwise habitat specialists such as some bird or saproxylic beetle species that require large deadwood volumes will disappear or remain absent from the whole region.

One consequence of increasing the amount of forestland set aside in reserves is an increased pressure to produce timber in managed forests. Where and how this timber is produced is central to the theme of this book. In some parts of the forest area, timber production may remain the primary management objective, whereas in other areas, ecosystem services such as recreation, protection of biodiversity, or carbon sequestration may be the primary management objectives with timber production as a more ancillary benefit.

If a goal of forest management is preservation of biodiversity, both integrative and segregative approaches are needed

Finally, it is important to emphasize that while foresters have been aware of old-growth patterns and processes for a long time, the practical implementation of these concepts in integrative forest management remains a significant challenge (Brang 2005). Clearly, emulating certain structural features typical of natural forests is crucial for maintaining forest biodiversity, but the degree and extent of this emulation for maintaining forest biodiversity is not sufficiently known. For example, quantitative thresholds for the amount of deadwood in different size and decay classes for conservation of different groups of biota have only been established recently (e.g. Gossner et al. 2013). It is also well known that some lichens require habitat continuity for many decades or even centuries, and thus very old trees (Scheidegger et al. 2000). Other structural characteristics, however, are not so clearly linked to biodiversity. One example may include the diameter structure of a stand, which is important information for silviculturists interested in sustainable timber yields of appropriately sized trees; however, it is less clear that diameter structure is important for beetles, fungi, and woodpeckers as long as large habitat trees and deadwood are present. Unravelling the complex relationship between forest structure and biodiversity thus requires further research in both old-growth and managed forests in Europe.

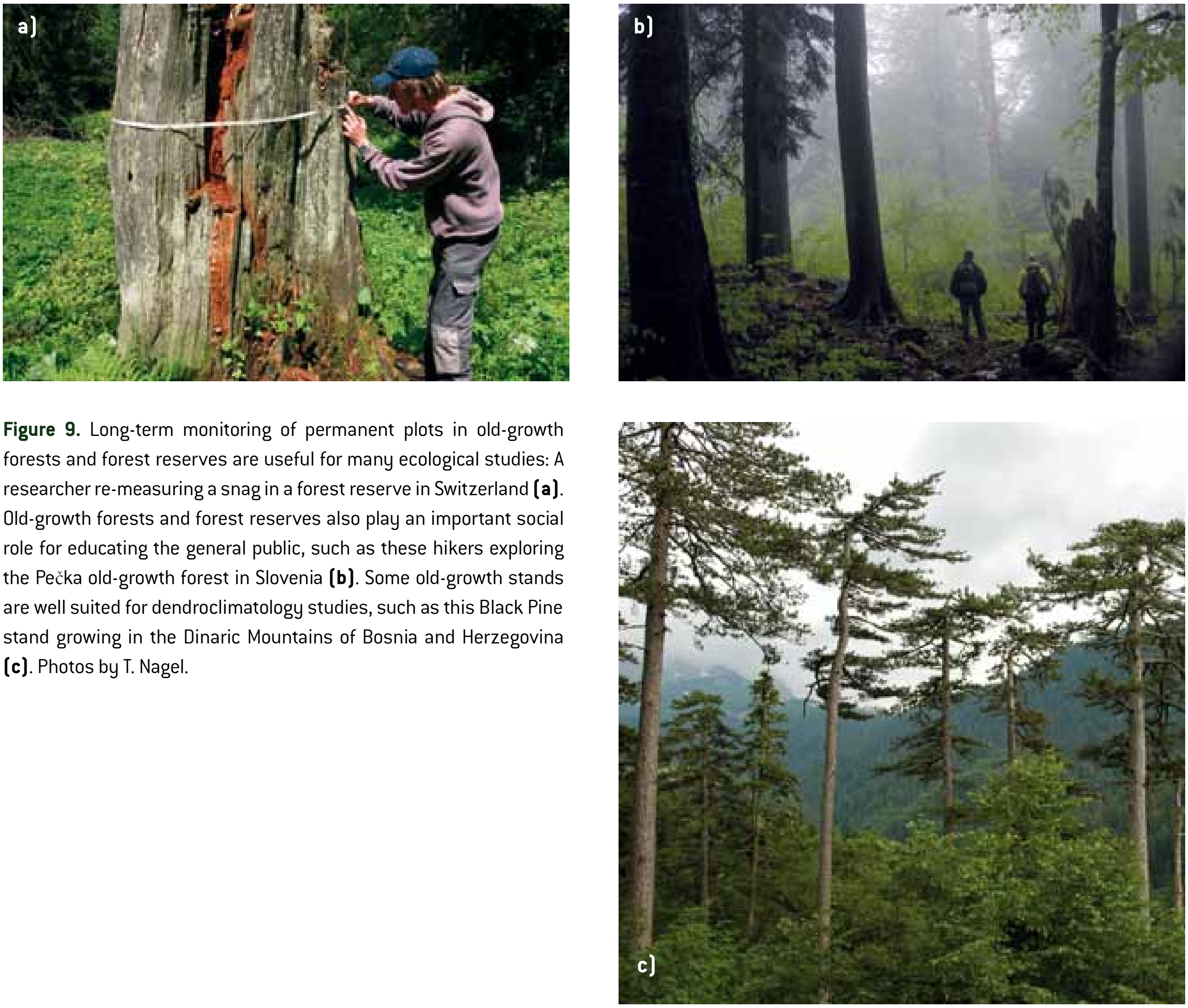


Figure 9. Long-term monitoring of permanent plots in old-growth forests and forest reserves are useful for many ecological studies: A researcher re-measuring a snag in a forest reserve in Switzerland **(a)**. Old-growth forests and forest reserves also play an important social role for educating the general public, such as these hikers exploring the Pečka old-growth forest in Slovenia **(b)**. Some old-growth stands are well suited for dendroclimatology studies, such as this Black Pine stand growing in the Dinaric Mountains of Bosnia and Herzegovina **(c)**. Photos by T. Nagel.

References

Brang, P. 2005. *Virgin forests as a knowledge source for central European silviculture: reality or myth? Forest Snow and Landscape Research 79:19–32.*

Brang, P., Heiri, C. and Bugmann, H. 2011. *Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Eidg. Forschungsanstalt WSL, Birmensdorf; ETH Zürich, Zürich. Haupt Verlag, Bern, Stuttgart, Wien. 272 p.*

Commarmot, B., Brändli, U.-B., Hamor, F. and Lavnyy, V. (eds.) 2013. *Inventory of the largest virgin beech forest of Europe. A Swiss-Ukrainian scientific adventure. Swiss Federal Institute of Forest, Snow and Landscape Research, Birmensdorf, National Forestry University, L'viv, Carpathian Biosphere Reserve, Rakhiv. 69 p.*

FOREST EUROPE, UNECE and FAO 2011. *State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe.*

Foster, D. R., Orwig, D. A., and McLachlan, J. S. 1996. *Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends in Ecology & Evolution 11:419–424.*

Frelich, L. E., Cornett, M.W., and White, M.A. 2005. *Controls and reference conditions in forestry: The role of old-growth and retrospective studies. Journal of Forestry 103:339–344.*

Frelich, L. E. and Reich, P.B. 2003. *Perspectives on development of definitions and values related to old-growth forests. Environmental Reviews 11:9–22.*

Gossner, M.M, Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W. and Muller, J. 2013. *Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27:605–614.*

Heiri, C., Wolf, A., Rohrer, L., and Bugmann, H. 2009. *Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. Ecological Applications 19:1920–1934.*

Heiri, C., Wolf, A., Rohrer, L., Brang, P., and Bugmann, H. 2012. *Successional pathways in Swiss mountain forest reserves. European Journal of Forest Research 131:503–518.*

Keeton, W. S. 2006. *Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. Forest Ecology and Management 235:129–142.*

Korpel, S. 1995. *Die Urwälder der Westkarpaten. Gustav Fischer, Stuttgart, Jena, New York. 310 p.*

Oliver, C.D. and Larson, B.C. 1996. *Forest stand dynamics. John Wiley and Sons, New York.*

Scheidegger, C., Stofer, S., Dietrich, M., Groner, U., Keller, C. and Roth, I. 2000. *Estimating regional extinction probabilities and reduction in populations of rare epiphytic lichen-forming fungi. Forest, Snow and Landscape Research 75:415–433.*

Seymour, R. S., White, A. S., and deMaynadier, P. G. 2002. *Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management 155:357-367.*

van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fule, P. Z., Harmon, M. E., Larson, A. J., Smith, J. M., Taylor, A. H., and Veblen, T. T. 2009. *Widespread increase of tree mortality rates in the western United States. Science 323:521–524.*

Wirth, C., Gleixner, G., and Heimann, M. 2009. *Old-growth forests – Function, Fate and Value. Spinger-Verlag Berlin Heidelberg.*

1.4 Forest Naturalness as a key to forest biodiversity preservation

Susanne Winter, Tomáš Vrška and Heike Begehold

Forest management is currently and globally dedicated and adapted to the service of wood production with management decisions mainly based on economic aspects. Even in protected areas with ongoing forest use, economic considerations chiefly dominate forest management decisions. However, sustainable management approaches promote or at least attempt to combine economic, social, and ecological outcomes, and in strict forest reserves such as wilderness areas, nature conservation approaches determine the forest management. The proportion of near-natural and natural forested areas is very low in Europe (Table 5). In Germany, for example, harvesting is currently and continuously strictly abandoned in less than 4% of forests, of which only a minor proportion are near-natural forests. More than 95% of Germany's forests are managed on an economic basis.

Table 5. Proportion of near-natural and natural forested areas in Europe (Branquart and Latham 2007).

European region	Proportion of near-natural and natural forested areas (%)
Western Europe Belgium, Denmark, France, Netherlands, United Kingdom	0.1
Southern Europe Cyprus, Greece, Italy, Portugal, Spain	1.3
Central Europe Austria, Bulgaria, Czech Republic, Lithuania, Macedonia, Romania, Slovenia, Switzerland	2.5
Northern Europe Finland, Norway, Sweden	8.3
Europe excluding Russia	<5

Global forest biodiversity co-evolved with forest habitats in a primeval state or a highly natural state. Gibson et al. (2012) examined 138 studies conducted in the tropics and showed that forest use negatively affects biodiversity, selective cutting systems being no exception – although they had a lesser effect. For Europe, Paillet et al. (2010) analysed as many scientific papers as were available (49) and again showed that forest biodiversity is negatively affected by forest use. Here again selective cutting had a lesser impact. Further studies revealed that the impact of the first cutting of a primeval forest (e.g. missing species, lower population densities of target species) is still present even decades later (Burgess 1971, Paillet et al. 2010, Wilson and Johns 1982, Wilson and Wilson 1975) and that the impact of land use pressure on biodiversity might be greatly underestimated (Dullinger et al. 2013). Preserving biodiversity is a global objective documented in numerous conventions (CBD 1992, European Habitats Directive 1992, countries' nature conservation laws) and political declarations (MCPFE 2003, BUNR 2007), thus it is officially and unequivocally stated that countries agree globally on biodiversity conservation. At the same time, this objective is not considered or implemented in economic planning and profit calculation at most levels of organization (from the private sector to the state level).

Concepts of naturalness and its assessments emerged as a consequence of unbalanced forest management

One weakness of integrated forest management approaches that aim at integrating conservation into silviculture and wood production is that we can fully report the direct financial outcome of forest cuttings but only rudimentarily report the biodiversity status of a forest site. Consequently, for balanced forest use, we need an additional concept – one that must reliably report and demonstrate forest integrity in a way that the state of forest biodiversity is expressed with the same emphasis and certainty as economic aspects. Naturalness is defined as the similarity of a current ecosystem state to its natural state (Winter 2012). In a fully natural state (100%), there is no long-lasting human impact on the ecosystem. Therefore, the large and continuous impact of civilization is not taken into account. Remmert (1978) wondered if natural forests actually still exist. All of the world's forests face indirect human influences and therefore naturalness has decreased. Nevertheless, a naturalness gradient from tree-dominated areas such as plantations and simplified forests up to the status of the most natural forest possible under current conditions is still a pronounced gradient and is clearly linked with forest biodiversity formation (Winter et al. 2010; Figure 10).

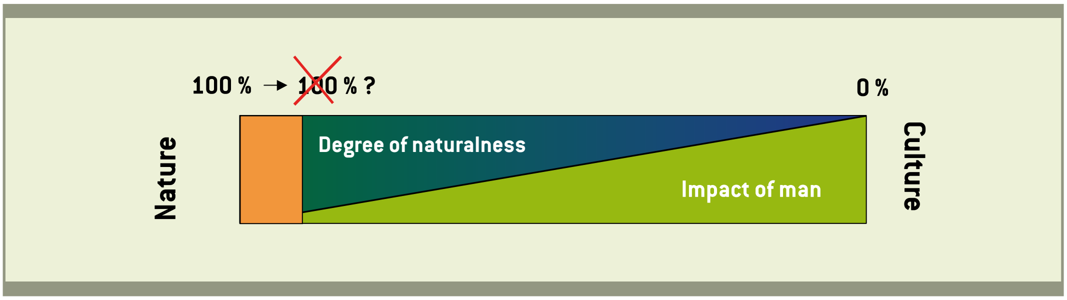


Figure 10. Theory of the naturalness gradient (modified from Winter et al. 2010).

A scientifically sound and diagnostically conclusive naturalness assessment reports biodiversity conservation as reliably as a financial statement reports economic output

A primary key to the preservation of global biodiversity is a high level of naturalness (Winter 2012). Until now, few diagnostically conclusive naturalness assessments have been applied for evaluating conservation schemes such as protected areas established under IUCN categories where nature restoration is the main management objective (e.g. National Parks). Direct biodiversity reporting requires too many records when considering the essential taxonomic forest groups and is not feasible at larger landscape or country levels. Surrogate forest monitoring that takes into account many different habitat requirements at different scales is therefore necessary. The Relative Quantitative Reference Approach for Naturalness Assessments (RANA, Winter et al. 2010) is a proposed methodology that was developed and tested in the Bavarian Forest National Park in southeastern Germany. RANA is based on the current knowledge of the main drivers that are strongly connected with biodiversity (for an example, see Box 5, Michel and Winter 2009, Winter et al. 2010), thus higher naturalness guarantees higher forest biodiversity and its conservation. For assessing forest naturalness with RANA a reference system is necessary. References are forests that are suitable for comparison and in the most natural state possible in the region studied (for an example, see Box 5).

To calculate the naturalness of a forest area, the mean difference (%) to the reference state defines the loss of naturalness. For assessing naturalness at a landscape scale, and for different land use classes, the calculation is area-weighted for each indicator considered. This general approach reveals the general trends of forest biodiversity and provides a tool for regions where no primeval forests remain.

Without a commonly accepted naturalness definition and a naturalness assessment approach, there can be no effective means of monitoring forest biodiversity trends

RANA has to consider indicators at different biodiversity scales. Additionally, an advantage of the proposed RANA concept is that indicators can be 1) measured in different units and 2) at different scales, and 3) absolute, 4) relative, 5) dynamic, and 6) invariant indicators can be used and joined for the naturalness assessment (for details see Winter et al. 2010, Rademacher and Winter 2003). The naturalness assessment for the whole area of the Bavarian Forest National Park included several of these naturalness indicators. The results show values for single drivers varying between 13% and 84% naturalness compared with the reference state (Figure 11 shows selected drivers) that referred to different reference systems:

- The modelled potential natural vegetation of the whole National Park.
- Old nature reserves that were already under nature protection before the National Park was established.
- A long-term unmanaged forest reserve (Boubin) in Sumava in the Czech Republic close to the Bavarian Forest National Park.
- Indicators that do not need a reference site (For example, the completeness for the lying deadwood is measured by the share of stumps that include the lying stem. The reference value is 100%. Stumps without lying stems indicate removed deadwood.

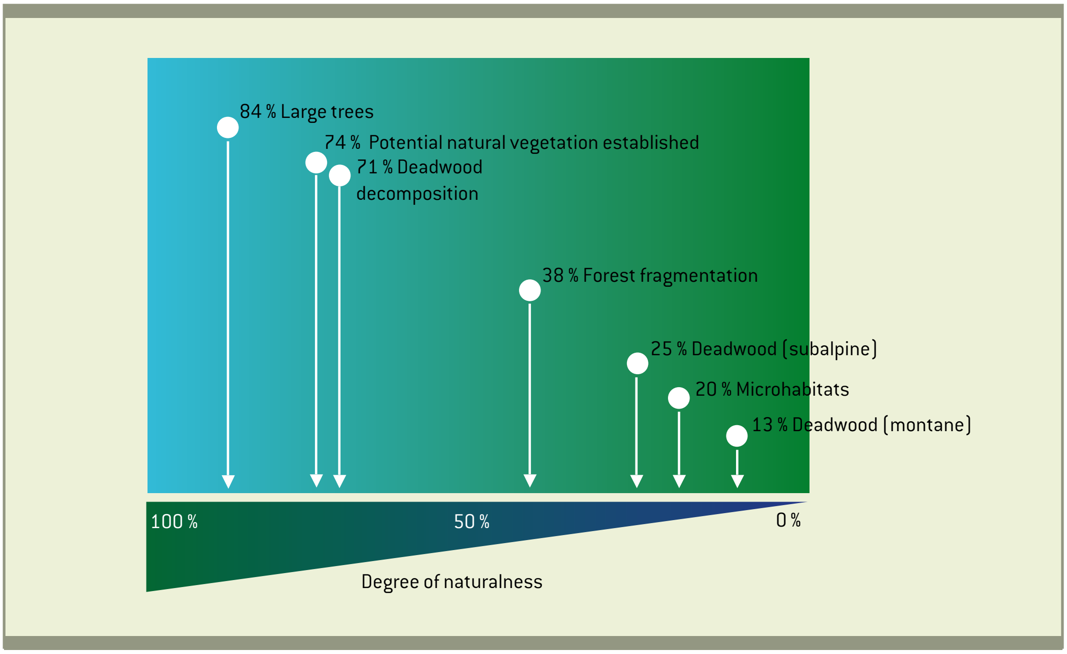


Figure 11. Single main naturalness drivers and RANA results of the naturalness assessment in the Bavarian Forest National Park. Source: Modified from Winter et al. (2010).

After one decade of practice, naturalness-promoting forest management effects are already detectable and measurable by naturalness assessment

The main underlying assumption for proposing naturalness assessments and monitoring is the detectability of naturalness changes by monitoring, when using naturalness-promoting forest management. Naturalness-promoting management considers a responsible handling of the forests' biodiversity according to the current scientific knowledge on how to preserve this biodiversity. For example, preservation and interconnection of large trees and old forest stands, natural patchiness of forest development phases, layer complexity, deadwood amount and dimensions, conservation of microhabitats, natural regeneration, and tree species composition are considered by naturalness-promoting forest management. We tested the feasibility of forest development phase records for changes within ten years. Forest development phases are an important naturalness indicator that should be able to indicate naturalness-promoting management. After just a 10-year-period of naturalness-promoting management, forests showed a larger diversity of these phases (see Box 5). Naturalness-promoting management allowed the forest to partially grow into later phases, and initiated the forest to be more diverse in younger phases. Naturalness-promoting management finally should result in some proportions of all forest development phases combined with different stand densities and additional structured gaps promoting e.g. light demanding species.

The revealed changes in the forest development phases within a 10-year-period designate this biodiversity driver as a feasible indicator for naturalness assessments. Similar feasibility tests have to be performed for other drivers such as layer complexity and in other forest habitats in the future.

High forest naturalness in common forests under use is the only possibility to preserve biodiversity at a high level

A high level of naturalness in harvested forests is undoubtedly necessary because humanity still needs almost all forested areas of the earth for its welfare (Table 5 and Box 6 for Europe, Chape et al. 2007 for the world). The available area in protected sites is too small for forest biodiversity preservation (IUCN 1980, Bauhus et al. 2009). Areas needed for forest biodiversity protection substantially overlap with harvested forest areas, thus approaches for integrating biodiversity maintenance and forest use are necessary worldwide.

“The danger is that forest degradation will neither be apparent nor adequately recognized, and the loss of biodiversity will increasingly be accepted by forest managers and other decision makers” (Winter 2012). We urge policy makers and governments to promote scientifically sound naturalness assessments for biodiversity monitoring within integrated management approaches. Ecologically and economically balanced management should be output-driven. Output-driven in the context of naturalness-promoting management means a clear decrease in threatened forest communities and forest species. Successful forestry does not harm forest biodiversity more than its capacity to recover, and this pertains to the entire biodiversity at different scales.

The concept of naturalness as presented goes much further than other approaches using the term “naturalness”. RANA is a multi-criteria ecosystem assessment approach combining essential biodiversity indicators instead of using “naturalness” as a simple indicator along with other single and separated indicators at the same level. Such an overly simplistic “naturalness” indicator has been proposed by the Ministerial Conference on the Protection of Forests in Europe (MCPFE 2002) and categorizes “naturalness” in only three categories:

1) undisturbed by man, 2) semi-natural, and 3) plantations. In another work “naturalness” is linked primarily to forest isolation from human impact (FAO 2002). The presented naturalness assessment approach RANA is a complex net of reliable biodiversity indicators comprised in a concept that is designed to report biodiversity changes even of different forest management types at different scales.

> *Under the current dominance of economically-based forest management, the integrated management process is successful when naturalness assessment scores increase*

Box 5. Naturalness-promoting management provides more diversity and a more natural forest development.

It is well known that forest diversity is generally connected with forest development phases (fdp), which make up the forest life cycle (Figure 12). However, data on the short-term effects of naturalness-promoting management have not been available.
A project conducted in northeastern Germany focused on changes in forest development phases over a decade (Research and Development Project 2012). Forest development phases were studied in eight beech forest stands (according to Tabaku 2000, modified by

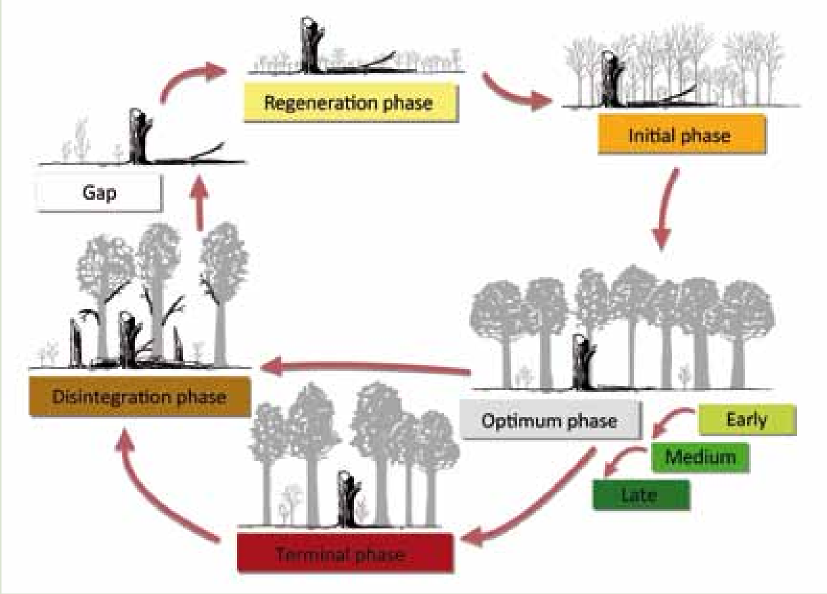


Figure 12. Forest life cycle broken down into forest development phases. Source: Begehold & Winter, in prep.

Winter 2005) in 2012/2013 and ten years prior. For both records, stands in conventionally managed forests (defined as management without an integrated biodiversity focus) are predominated by the medium optimal phase; late phases (late optimum, terminal, and disintegration phase) remain almost absent, while the number of different fdp and fdp patches per hectare is lower than in naturalness-promoting managed, recently unmanaged (approx. 25 years), and reference sites unmanaged for more than 120 years (Winter 2005, Begehold & Winter in preparation). Stands under naturalness-promoting management show an increase in late fdp of the forest life cycle and a more balanced distribution across the present fdp.

The development of individual fdp patches (n=1,434) was followed and compared between the two records of the last decade. The development of the most common fdp in managed stands, the medium optimum phase (n=206), is illustrated in Figure 13.

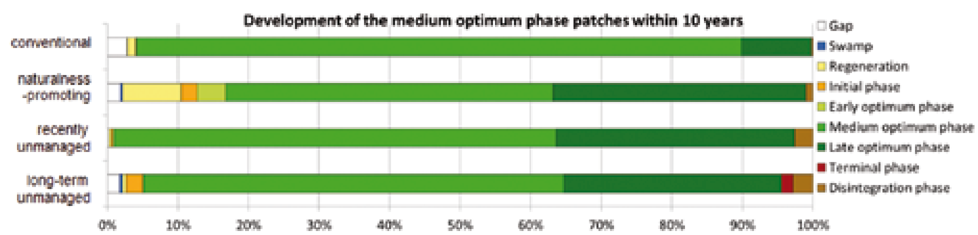


Figure 13. Diversification of medium optimum phase patches (n=206) after 10 years of different management (conventional and naturalness-promoting) and compared to unmanaged stands (25 and more than 60 years out of management). Ten years ago, the medium optimum phase was present in 100% of the 206 presented patches (139.5 ha). Source: Begehold & Winter, in prep.

Differences between the management approaches have already become apparent after a decade of naturalness-promoting management (Figure 13 and 14). Naturalness-promoting management chiefly allows the development of a fdp into a subsequent fdp from the medium optimum phase patches (n = 31, 62.4 ha), about 50% changed into another phase within a decade, with 35% growing to the late optimum phase. In the conventionally managed forests, only 10% of the patches changed to a subsequent fdp, although the share of trees close to the fdp threshold of 60 cm diameter at breast height differentiating the medium and late optimum phase was comparable. In contrast to conventionally managed stands, naturalness-promoting management creates fdp diversity. Furthermore, naturalness-promoting management preserves and enables the development of early and late optimum phases comparable to unmanaged stands, but does not conserve the medium optimum phases as found for conventionally managed sites.

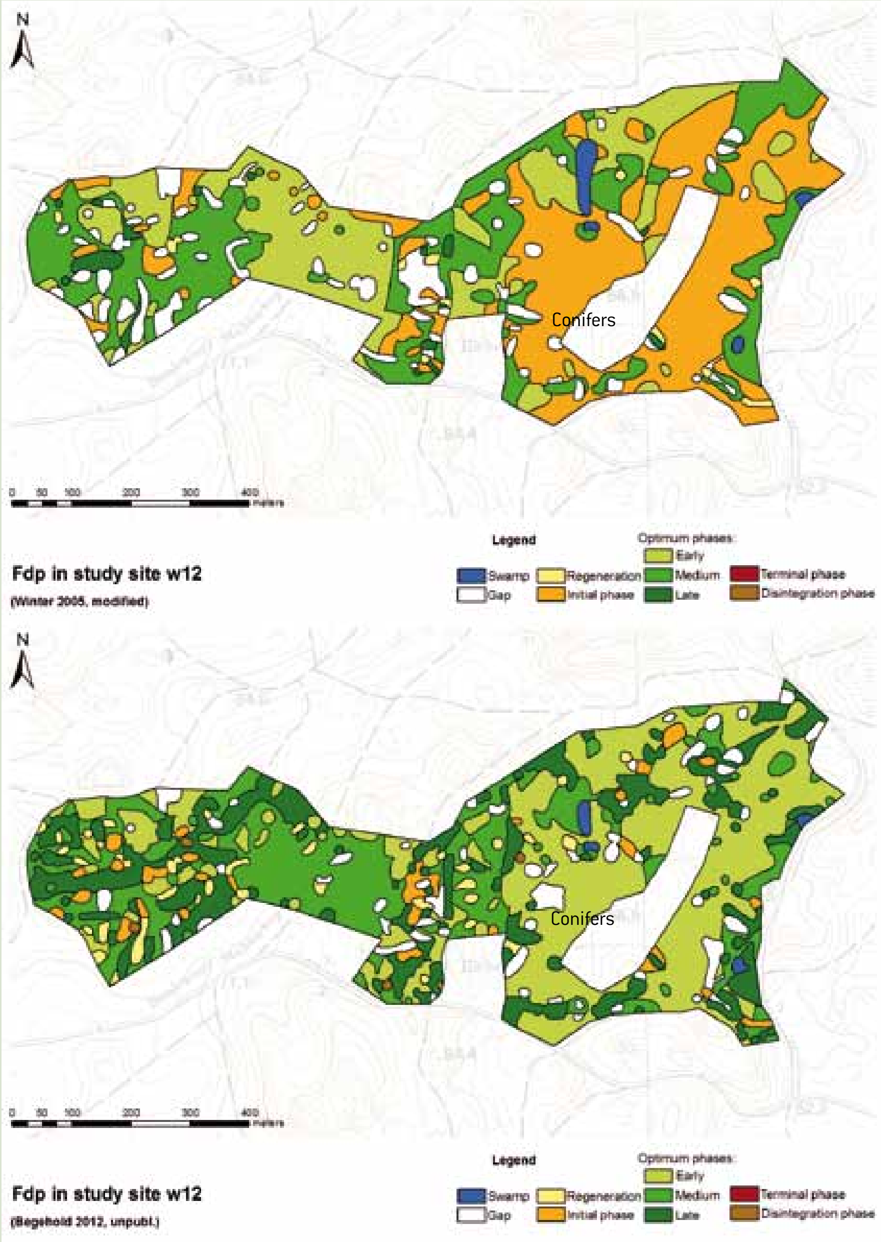


Figure 14. Development of forest development phases under naturalness-promoting management during the last decade (above 2002, below 2012).

Box 6. Old-growth forests have survived in some European countries.

As was stated at the beginning, forest management decisions have mostly been driven by economic considerations. Consequently, the answer to the question where and why do old-growth forests still exist in some European countries might be fundamental for integrated naturalness-promoting management and its monitoring. Is the existence of old-growth forests (forests minimally affected by man, mainly left to spontaneous development, containing old trees and deadwood, etc.) linked with their distance from foresters or their low timber value, or because natural sites are valued apart from wood production? This question was investigated in a study in the Czech Republic.

For use in the national environmental policy and nature conservation, a naturalness assessment of all Czech forests was performed using 30 criteria (direct human impact on stand development: 17 criteria; indirect human impact on stand development: three criteria; tree species composition: six criteria; deadwood: four criteria) (Anonymous 2008). The dichotomous criteria (yes, no) were classified in four equally weighted groups, thus the number of criteria within a group weighted the impact of the single criterion. The central forest database of the Czech Republic compiled at the Forest Management Institute was the primary source for the assessment – which is comparable with the National inventory data used for RANA. The naturalness assessment showed that only 30,000 ha of 2,568,000 ha of forested area matched the old-growth definition. In total, 490 old-growth sites ranging in area from 10 to 1,200 ha and exhibiting clumped distribution were found in the Czech Republic (Adam and Vrška 2009).

Four landscape types contain 67% of the old-growth forest area. These “protective” landscape types include long mountain slopes and high mountain plateaus with 50% of the old-growth area and karst and steep river valleys in lower locations with 17% of the old-growth area. The mountain slopes and high mountain plateaus have been settled at least since the 17th and 18th century. They represent mostly distant localities in harsh climate regions, but in the 18th century they were exploitable due to technological progress. They were colonised and first cut when the first ideas about nature protection spread across Central Europe. In fact, during the first forest exploitation, strict nature reserves of primeval and natural forests were deliberately established (1838 forest of Žofín, 1858 forest of Boubín).

Karst and steep river valleys at lower altitudes represent the borders of early human settlement. These localities were not exploitable during Neolithic and Middle Age settlement and were weakly productive sites for later exploitation. Middle Age colonisation moved to higher locations (highlands) due to better technological tools and better forest productivity of highland forests, ignoring some karst and steep river valley forests. Thus, these old-growth forests could be named old-growth forgotten by technological progress.

In conclusion, both historical nature conservation efforts as well as economic advantages at other forest sites maintained old-growth forests in the Czech Republic. Knowledge on the location of old-growth forests is essential for choosing the best available and comparable reference site for applying the RANA concept (Winter et al. 2010).

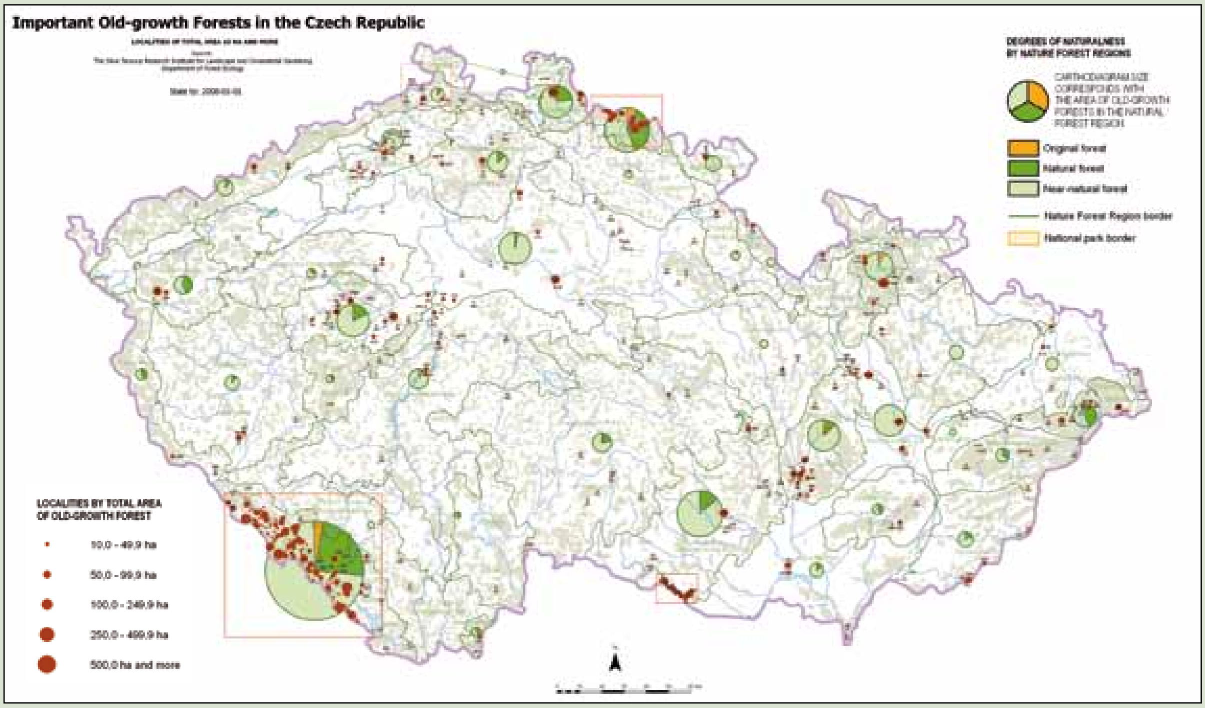


Figure 15. Map of important old-growth forests in the Czech Republic. Source: Modified from Adam and Vrška 2009.

References

Adam, D. and Vrška, T. 2009. *Important localities of old-growth forests. In: Hrnčiarová et al. (eds.). Landscape Atlas of the Czech Republic. Ministry of Environment and Silva Tarouca Research Institute. 209 p.*

Anonymous 2008. *Vyhláška č. 60/2008 Sb. o plánech péče, označování a evidenci chráněných území podle zákona č. 114/1992 Sb., o ochraně přírody a krajiny ve znění pozdějších předpisů. – Regulation No. 60/2008 on management plans, marking and register of protected areas according the Nature and Landscape Protection Act (No. 114/1992). Statute book 18: 946–975.*

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

Begehold, H. and Winter, S. (in prep). *Forest Development Phases in Lowland Beech Forests: Patch Dynamics within a Decade.*

Branquart, T. and Latham, J. 2007. *Selection criteria for protected forest areas dedicated to biodiversity conservation in Europe. In: Frank, G., Parviainen, J., Vandekerkhove, K., Latham, J., Schuck, A. and Little, D. 2007. COST Action E27 Protected Areas in Europe – Analysis and Harmonisation (PROFOR): Results, conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW). Vienna, Austria. Pp. 51–60.*

BUNR – Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit. 2007. *National Strategie zur biologischen Vielfalt. 180 p.*

***Burgess, P.F. 1971**. The effect of logging on hill Dipterocarp forests. Malayan Nature Journal 24:231–237.*

***CBD – Convention on biological diversity. 1992**. Convention on Biological Diversity, Rio: Secretariat of the Convention on Biological Diversity. United Environment Programme. 83 p.*

***Chape, S., Spalding, M. D. and Jenkins, M. D. (eds.). 2007**. The World's Protected Areas: Status, Values and Prospects in the 21st Century. University of California Press, Berkeley. 359 p.*

***Dullinger, S., Essl, F., Rabitsch, W., Erb, K.-H., Gingrich, S., Haberl, H., Hülber, K., Jarosik, V., Krausmann, F., Kühn, I., Pergl, J., Pysek, P. and Hulme, P.E. 2013**. Europe's other debt crisis caused by the long legacy of future extinctions. PANAS 110(18):7342–7347.*

***European Habitats Directive. 1992**. Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora.*

***FAO – Kapos, V., Lysenko, I. and Lesslie, R. 2002**. Assessing Forest Integrity and Naturalness in Relation to Biodiversity. Forest Resources Assessment Programme. Working Paper 54.*

***Gibson, L., Lee, M.L., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. and Sodhi, N.S. 2012**. Primary forests are irreplaceable for sustaining tropical biodiversity. doi: 10.1038/nature10425.*

***IUCN – International Union for Conservation of Nature and Natural Resources. 1980**. World Conservation Strategy – Living Resource Conservation for Sustainable Development. IUCN-UNEP-WWF.*

***MCPFE – Ministerial Conference on the Protection of Forests in Europe. 2002**. Improved Pan-European Indicators for Sustainable Forest Management. 6 p.*

***MCPFE – Ministerial Conference on the Protection of Forests in Europe. 2003**. Vienna Resolution 4: Conserving and Enhancing Forest Biological Diversity in Europe. Vienna, Austria. 32 p.*

***Michel, A. and Winter, S. 2009**. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. Forest Ecology and Management 257:1453–1464.*

***Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., Bruyn, L. de, Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. and Virtanen, R. 2010**. Biodiversity Differences between Managed and unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation Biology 24(1):101–112.*

***Rademacher, C. and Winter, S. 2003**. Totholz im Buchen-Urwald: Generische Vorhersagen des Simulationsmodells BEFORE-CWD zur Menge, räumlichen Verteilung und Verfügbarkeit. Forstwissenschaftliches Centralblatt 122:337–357.*

***Research and Development Project. 2012**. Umsetzung von Zielen der Nationalen Biodiversitätsstrategie in Wäldern: Untersuchung des Einflusses von naturschutzorientierter Bewirtschaftung auf Naturnähe und Biodiversität von Tiefland-Buchenwäldern", FKZ 3511 84 0100.*

***Remmert, H. 1978**. Ökologie – Ein Lehrbuch. Springer, Heidelberg, 363 p.*

***Tabaku, V. 2000**. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und -Wirtschaftswäldern. Cuvillier Verlag, Göttingen. 206 p.*

***Wilson, W.L. and Johns, A.D. 1982**. Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in east Kalimantan, Indonesia. Biological Conservation 24:205–218.*

***Wilson, C.C. and Wilson, W.L. 1975**. The influence of selective logging on primates and some other animals in East Kalimantan. Folia primatologica. 23:245–274.*

Winter, S. 2005. *Ermittlung von strukturellen Indikatoren zur Abschätzung des Einflusses forstlicher Bewirtschaftung auf die Biozönosen von Tiefland-Buchenwäldern. Determination of indicators for assessing the impact of silvicultural use on the biocoenosis of lowland beech forests in Germany. PhD thesis Technical University Dresden. 322 p.*

Winter, S., Fischer, H.S. and Fischer, A. 2010. *Relative quantitative reference approach on naturalness assessments. Forest Ecology and Management 259:1624–1632.*

Winter, S. 2012. *Forest naturalness assessment as a component of biodiversity monitoring and conservation management. International Journal of Forestry 85(2):293–304.*

1. 5 Silvicultural systems and multiple service forestry

Sven Wagner, Franka Huth, Frits Mohren and Isabelle Herrmann

Identifying structural elements within forest ecosystems is fundamental to understanding the link between management of forests and their ability to provide ecosystem goods and services (ESS)

The broad spectrum of silvicultural systems available today has evolved over time, and this evolution has been influenced by many different factors. In the past, providing material goods, e.g. timber, was the most important driver. Currently, the idea is to use silvicultural systems that allow for an array of ecosystem goods and services (ESS) within managed forests. The reason behind this is that in many regions demands for forest services have changed due to modified social circumstances. Since the 1950s and 60s, different social and environmental policy platforms have declared the approach of "multiple service forestry" as a suitable forest management tool to produce the required ESS. Gómez-Baggethun et al. (2010) have shown that since that time, definitions for ecosystem services have been used in different ways and influenced by a variety of actors. In many cases, multiple service forests still assume timber production and the provisioning of raw material as the leading principle. A similar pattern can be noticed for the descriptions of multiple service forestry (MSF, also referred to as multiple-use forestry). Therefore, we use Box 7 to explain some of the most common definitions for ESS and multiple service forestry as the basis for the following text.

Indeed, explanations and definitions of ESS and multiple service forestry are fairly theoretical, and some emphasis should be put into making them operational. Working with "structural elements" (SE) is an effective means of implementing the ideas of ESS and MSF into practical forest management and developing operational approaches, assuming the relevant ecosystem services can be related to the main structural elements of a forest stand. This leads to a practical operationalization of the concepts underlying this type of forest management without a priori valuation of individual services such as timber production. Box 8 explains the concept of SE and its connection to ESS. Forest management practice and forest enterprises deal with structural elements or structural attributes, although they are primarily interested in goods and services.

Although forest and environmental scientists have analysed forest ecosystems in many ways, for some structural elements, the relevance of their function for different ESS is unclear. This does not mean that there is no specific function, but that the function has not yet been unravelled. This situation applies to the spatial and temporal effects of some less frequent tree species in creating the specific ESS of water purification or aesthetics. In addition, the effects

Box 7. Ecosystem goods and services for multiple service forestry (MSF)

The Millennium Ecosystem Assessment (MA 2005) and The Economics of Ecosystems and Biodiversity (TEEB 2010) study are two important studies with international reputation that have been comprehensively presented to the public. These reports consider different ecosystem categories and have initiated a global discussion process within an interdisciplinary context. Taking both studies into consideration, ESS can be summarized as "[...] the benefits people obtain from ecosystems". Within forest ecosystems, ESS include the following four main categories that contain different types of goods/services (e.g. timber or public goods such as infrastructure or education):

- Provisioning services – these services describe the material output of forests such as food, water, timber, and fibre.
- Regulating services – these are services that affect the climate and regulate the quantity and quality of water, air, and soil.
- Habitat and supporting services – these services guarantee the provisioning of habitat for fauna and flora as an essential part of diversity.
- Cultural services – this component of ESS includes the non-material output associated with aesthetic and spiritual benefits.

Many countries have translated the theoretical framework of ESS into a legal framework of forest administration and environmental policy, with little modification. As a result, foresters have been instructed to manage the forest such that all of the overall policy aims of ESS are taken into account. Environmental authorities and forest policy have considered multiple service forestry (multiple-use forestry) as suitable to fulfil all of the above-mentioned requirements. Multiple service forestry is characterized by cross-scale management associated with attention to social, ecological, and economic interests, which are integrated into the overall forest management strategy as well as single stand management. However, it is important to verify whether the concept of multiple service forestry meets all the requirements mentioned. Economic theory and silvicultural research suggest that it is either not desirable or impossible to create a forest ecosystem that fulfils the demands of all ecosystem services equally. Therefore, an explicit consideration of multiple services and their trade-offs becomes important to provide a basis for decision making and choosing required management interventions.

of spatial transition zones between structural elements and their influence on a specific ESS is often unclear.

Furthermore, the function of a single structural element depends on the specifics of the forest ecosystem and its regional or local conditions, i.e. the function of a structural element is often context specific. We may take a single evergreen tree as an example of this context-dependency; within a pure evergreen coniferous stand, such a tree does not serve any specific aesthetic value, but when combined with deciduous trees in winter, it explicitly does.

The natural diversity of an ecosystem builds the ecological foundation of an integrative management approach in forestry through the diversity of structural elements

Box 8. Fundamentals – Services and structural elements (SE)

The feature of structural elements (SE) can be used to improve communication between forest ecosystem specialists, citizens interested in forests, and forest managers. Structural elements forge a link between the general term of "forest structure" and its meaning to ESS.

- Structural elements are the discrete parts of a forest ecosystem by which its physical structure in the horizontal and vertical dimensions is defined. Examples are crowns, branches, and leaves, which are species-specific, or diameter distribution, which may depend upon age composition, the amount of deadwood, and aspects of overall canopy structure, e.g. gaps.
- Structural elements contain specific properties that guarantee the provision of defined goods and services. They represent the medium for ESS, e.g. deadwood as a medium for saprophytes or a straight and healthy tree as a medium for timber.
- To provide services, single structural elements need adequate space. Here, the application ranges from square meters to hectares.
- The competition between services on one particular site is due to the spatial incompatibility of service providing structural elements. Incompatibility of services is a result of (neutral to negative) interaction between structural elements and space restrictions: in most cases, two structural elements cannot occupy the same space simultaneously, i.e. the exclusion principle in structural elements. For example, canopy gaps as structural elements favour species adapted to a higher light level (ecological niche), but a gap excludes the presence of canopy trees that favour shade tolerant species underneath.
- Combinations of single structural elements can lead to new services important for a higher spatial level. For example, aesthetic value increases when a mixture of a few evergreen and deciduous trees leads to a forest landscape in autumn and winter that is comparatively more attractive than a monospecific stand.
- In many cases, it is essential for the success of ESS provisioning using a structural element strategy to establish spatial networks of structural elements. This is particularly important for immobile species (e.g. slugs and snails) or extremely specialised species (e.g. Hermit beetles, Osmoderma eremita) as without spatial networks, it is impossible to perpetuate their metapopulations.

By definition, pure species ecosystems have a lower potential of structural element diversity than mixed forests. The general silvicultural idea of integrative utilization of structural elements is to find ecologically reasonable and spatially achievable arrangements to combine the elements in a constructive way. It is important to note that most forest enterprises are actors within an economically-oriented market, constrained by additional societal demands concerning biodiversity conservation and protection of water and soil resources. Therefore, forest enterprises have oriented the handling of structural elements towards operational processes and specific goals, mainly focussing on marketable goods, but accounting for additional rules and regulations. The much-discussed topic of the economic valuation of environmental goods and services (not our focus here) is derived from this point of view. Thus, to understand forest management, we have to switch from services and functions to objectives. Targeting the practicability of silvicultural strategies leads to an objective-oriented combination of different structural elements in a defined forest ecosystem (Figure 16). Landowners and most forest enterprises follow a deterministic approach of a set of specified treatments that result in predictable feedbacks in the forest, i.e. they favour a specified structural element that contains a harvestable good.

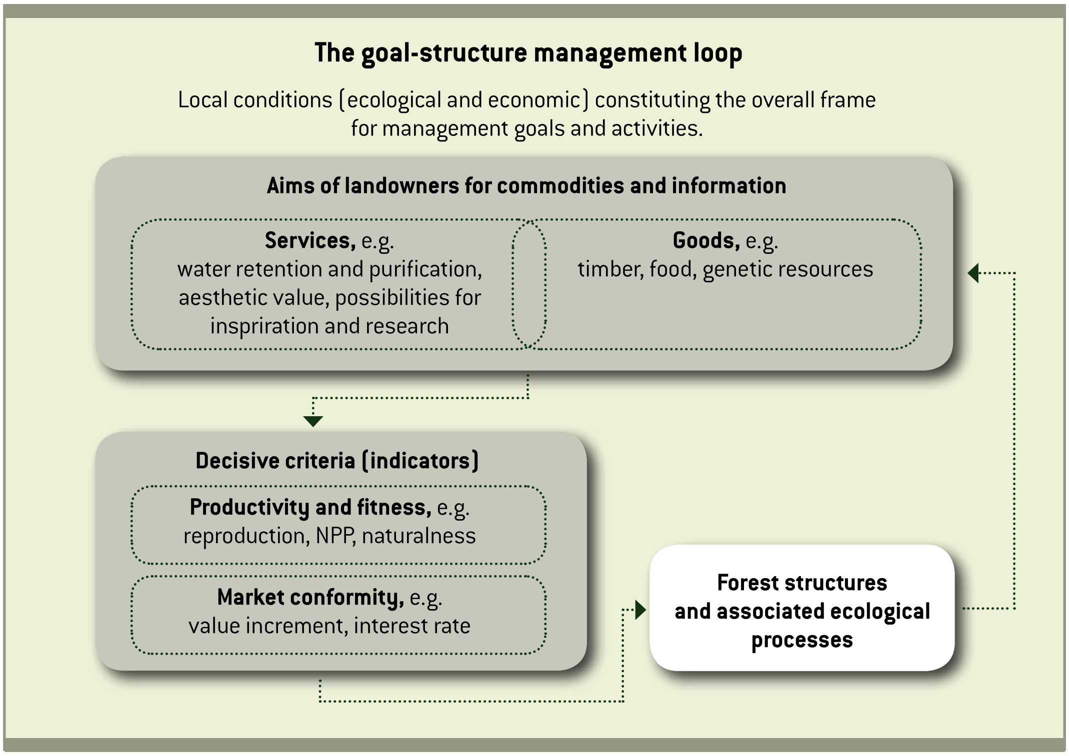


Figure 16. Schematic diagram showing the loops between ESS and SE integrated in the decision process by the local landowner.

Indicators and criteria allow assessment of the appropriateness of a chosen stand structure and silvicultural strategy to meet preset objectives

To confirm this statement, examples from real forestry may help. In this context, plantation forestry is characterized by simple combinations of one to a few structural elements leading to low complexity (e.g. trees of one species with homogenous growth parameters and equal age) and clear deterministic measures (i.e. stand establishment by planting, regular cutting regimes to increase homogeneity and apply machinery). In general, within such homogeneous forest systems, the productivity per unit (space and time) is high. Consequently, productivity indicators assess homogeneous stand structures as favourable for timber production.

By maximizing productivity in this sense, all other – obviously less-productive – structural elements are discriminated against due to the exclusion principle (Box 8). To this end, short rotation timber production is favoured at the expense of all other goods and services presented in Box 7. However, plantations are at a disadvantage compared to multi-structural stands when resilience-increasing ecological processes, adaptability to unpredictable changes in environmental conditions (e.g. climate change), and flexibility to changing markets are taken into account. From this perspective, plantation forestry is a one-way strategy that "puts all eggs in one basket".

Intensively managed single-tree selection systems (e.g. "Plenterwälder" or uneven-aged selection forests) are also linked to the structural element of a "single-tree"; but in contrast to simplified plantations, this element exhibits variety in different species (i.e. spruce, fir, and beech), age, and diameter. In addition, single-tree approaches may include selection of habitat trees or other structural elements relevant for services other than the provisioning of raw material. With this structural diversity, these single-tree selection systems better provide the opportunity to integrate different ESS on one site, for example high value timber of different shade-tolerant tree species, habitat features of old-growth stands, and high aesthetic value. With the given options for combining different species or different classes of diameters, the above-mentioned idea of a modular system comes close to reality in selection systems.

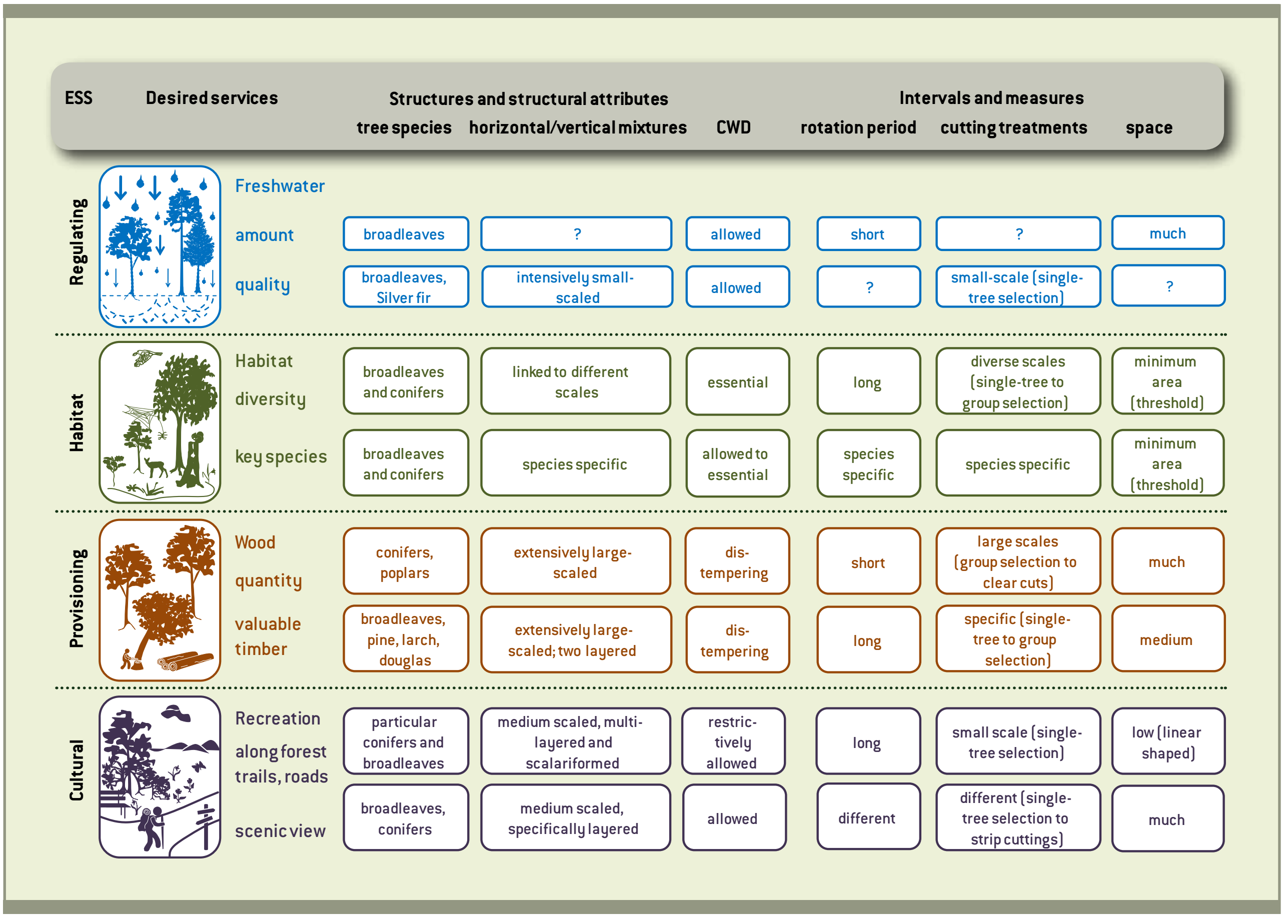
Some ESS are linked to the structural richness of forest ecosystems. However, the diversity in structural attributes in selection systems is accompanied by some weaknesses as well

As small gaps prevail in single-tree cuttings, the probability for light demanding species to reproduce is low. On an enterprise level with more than hundreds or thousands of hectares, a forest management strategy restricted to one silvicultural system, e.g. clear cutting or single-selection, results in a lack of key structures with important functions for a variety of processes and species within forest ecosystems. Thus, for the sake of multiple ESS it is not beneficial to solely rely on one silvicultural system or a few structural elements that meet current objectives, but rather to combine different systems to account for local variation in site conditions.

Landowners and society decide through their defined goals and chosen management strategies how to focus on or maximize ESS and which trade-offs are made in the combination of ESS. Goal-setting by the forest owner within a societal context determines the priority of separate ESS. Given that silvicultural strategies are manifold and adapted to different

> *A diversity of silvicultural systems and strategies across the landscape/ region is needed to increase diversity in structures, functions, and biota and consequently support a broad range of ESS*

regions, tree species, initial situations, and development stages, there is no lack of suitable silvicultural tools (thinning and cutting; pruning; regeneration using sowing, planting, or spontaneous regeneration; tending; etc.). However, regarding ESS it is a challenge for many forest practitioners to apply traditional knowledge of silvicultural systems and measures for more than solely timber production. Another problem is that mono-service forest management and research have been the guiding principles for a long time, thereby disregarding the use of silvicultural tools to optimize for multiple ESS (Figure 17).



ESS	Desired services	Structures and structural attributes			Intervals and measures		
		tree species	horizontal/vertical mixtures	CWD	rotation period	cutting treatments	space
Regulating	Freshwater amount	broadleaves	?	allowed	short	?	much
	quality	broadleaves, Silver fir	intensively small-scaled	allowed	?	small-scale (single-tree selection)	?
Habitat	Habitat diversity	broadleaves and conifers	linked to different scales	essential	long	diverse scales (single-tree to group selection)	minimum area (threshold)
	key species	broadleaves and conifers	species specific	allowed to essential	species specific	species specific	minimum area (threshold)
Provisioning	Wood quantity	conifers, poplars	extensively large-scaled	distempering	short	large scales (group selection to clear cuts)	much
	valuable timber	broadleaves, pine, larch, douglas	extensively large-scaled; two layered	distempering	long	specific (single-tree to group selection)	medium
Cultural	Recreation along forest trails, roads	particular conifers and broadleaves	medium scaled, multi-layered and scalariformed	restrictively allowed	long	small scale (single-tree selection)	low (linear shaped)
	scenic view	broadleaves, conifers	medium scaled, specifically layered	allowed	different	different (single-tree selection to strip cuttings)	much

Figure 17. Key structures, structural attributes, and characteristic measures to best serve a defined single ESS through forest management.

Structural elements become tools in a modular system that can mirror societal demands

The simplified overview in Figure 17 serves to clarify diverging structures and measures beneficial for optimizing specific ESS. Within this scheme, the intensity of conflicts between particular ESS is made explicit and becomes obvious since these conflicts are a result of incompatibility of structures (see Box 8). It is apparent that forest structures and tree species needed to maximize timber production, i.e. plantations, conflict with structural patterns beneficial to most of the other ESS. In decision making, this leads to trade-offs and choices for particular objectives and hence to transition management towards different forest structures. In contrast to this, similar structures, e.g. a tree species mixture or vertical layering, can be identified as being advantageous for several other ESS, excluding saw timber production. However, the more detailed knowledge becomes available in the future and the more focused forest management becomes, the more conflicts will arise. An example is coarse woody debris, which is needed for habitat improvement but often conflicts with timber revenue because large trees are left in the forest. In general, there will be more conflicts when available space decreases.

Based on this scheme, it becomes clear that today multiple services of managed forests are predominantly either a chance event or linked to a feature of the forest as such. To advance the intensity of multiple services provisioning beyond the fundamental level of what a particular forest provides, a specified multiple service concept must be developed.

Options for integrative multiple service forestry are bound by the question of available space. A successful methodological approach to integration of multiple services thus has to take into account and manage space conflicts

The current knowledge about silvicultural management strategies and spatial requirements of service relevant structural elements lead to the realisation that, under practical conditions, options for combining different structural elements are limited. Recalling the idea of a modular system, the combination of different structural elements in one forest site is used as a means to integrate element-associated ESS on that site. Here, we refer to one forest site as having a restricted size, i.e. typically less than 10 hectares. This integration concept follows a three-step approach in accordance with Lindenmayer and Franklin (2002). The first step defines the structural elements for the desired services. To continue along this path it is essential to know as much as possible about the links between structural elements and the relevant ESS. The second step is the allocation of a specified proportion of the forest to the different kinds of structural elements. Finally, the third step defines the spatial patterns in which the structural elements should be combined (Box 9 and Figure 18).

Box 9. The synthesizing idea – integration of a variety of structural elements supporting ecosystem services

The question of how to integrate and combine different ESS within a restricted forest area raises the issue of effective spatial allocation of structural elements. “Spatial optimization” is one example of a statistical technique for solving spatially explicit and complex problems. Hof and Bevers (1998) documented methods for different management strategies within ecosystems on the landscape level. Spatial optimization techniques are promising tools for integration problems because “...a great part of an ecosystem’s structure and function is spatial in nature” (Hof and Bevers, 1998). The following example shows an advanced spatial optimization for a combination of two ecosystem services at an intra-stand level. The aim of the optimization procedure was to combine low tending necessity (scaled by the level of a self-preserving mixture) for maintenance of a mixture of Norway spruce and European beech (i.e. production provision) with an active organic-rich fermentation horizon (supporting service) over the area of the stand. Thus, the example solely refers to step three of the above-mentioned three-step approach.

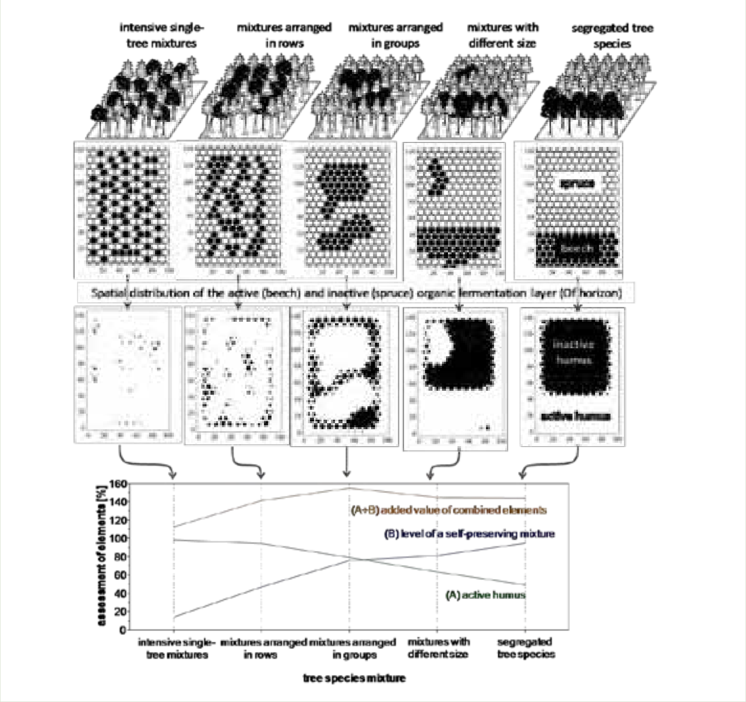


Figure 18. Different spatial arrangements of a beech (30%) and spruce (70%) mixture leads to different proportions of area with an active organic fermentation layer at the forest stand level and to different intensities of tending necessity for preserving the mixture due to unbalanced competition.

The spatial layout of the mixture (Figure 18, graph at bottom) that best serves both considered ESS simultaneously in this example is the group mixture.

Even though there are promising investigations to disentangle and quantify the links between forest structures and ESS, there is still a substantial lack of information. This especially applies to the issue of the relevance of regional conditions, differences between the development-stages of trees, and in general to information about rare species. In contrast to this, a great deal is known about dominant, economically important tree species and their ecological interaction processes such as competition or facilitation. As a result, the scope for decisions of forest practitioners is large, and a wide array of field experience is needed to make a final decision.

> *Once the links between structure and ESS have been identified and the underlying processes have been understood, the next step for silviculture is to design a dynamic system to promote and maintain the desired structure*

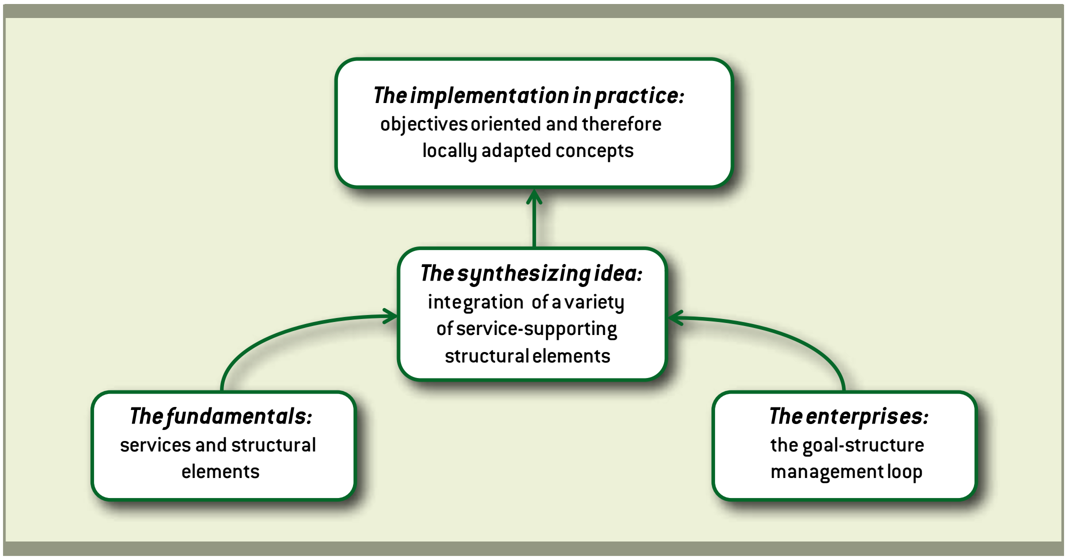


Figure 19. The rationale behind the presented concept to integrate multiple ESS into practical forest management on the stand level and with a local background.

Figure 19 shows the rationale behind the multiple-service forestry approach in this chapter. The tool for the integration of ESS within a particular forest area is the structure of the forest and the experience and expertise of the local forest practitioner. For the sake of operability, forest structures are broken down into structural elements. On one hand, the provisioning of ecosystem services or the functioning of supporting services is linked to single structural elements or sets of structural elements. On the other hand, forest management follows a deterministic approach and shapes the structure of the forest to best serve the objectives of the landowner within the possibilities provided by the local conditions, both ecological and social. Both views of "structure" may be synthesized into the integration of service-supporting structural elements on a particular site and thus yield multiple-services from that site. Finally, structural elements are often spatially mutually exclusive and objectives are diverse; therefore, in practice a locally adapted and objective oriented concept seems promising.

When implementation of multiple service forestry in harmony with the ESS concept in forest practice is the aim, forest enterprises have to be taken into account. As space is limited and objectives are landowner-specific and diverse, advocating for a homogeneous forest management strategy makes no sense. Instead, region and site specific, landowner specific, and service-combination specific concepts seem promising. For an implementation in practice, objective oriented and therefore locally adapted concepts must be developed, and for this local expertise and local experience are required. The more diverse the demand for structural elements in one forest is the more diverse and complex the silvicultural system must be. The tree species assemblage, the disturbance regime (e.g. gap size frequency distribution), diameter frequency distribution, production period length, acceptable loss of productivity due to other ESS, and amount of dead woody debris – among others – are key elements for designing an appropriate silvicultural system. As already stated above there is virtually no single silvicultural system that simultaneously fulfils all aims mentioned. However, objective oriented and therefore locally adapted concepts seem to be promising approaches; there is no single superior system. One of the key features here is to combine knowledge on different silvicultural systems – based on the ecological properties of the individual tree species – with site adapted ecosystem features and local knowledge, both in terms of ecosystem properties and societal demands.

References

Gómez-Baggethun, E., de Groot, R., Lomas, P.L., Montes, C. 2010. *The history of ecosystem services in economic theory and practice: From early notions to markets and payment schemes. Ecological Economics 69(6): 1209-1218.*

Hof, J.G. and Bevers, M. 1998. *Spatial optimization for managed ecosystems. Columbia University Press, New York, 258 p.*

Lindenmayer, D.B. and Franklin, J.F. 2002. *Conserving forest biodiversity: A comprehensive multiscaled approach. Island Press, London. 351 p.*

Millennium Ecosystem Assessment (MA) 2005. *Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC. 137 p.*

TEEB 2010. The Economics of Ecosystems and Biodiversity: *Mainstreaming the Economics of Nature: A synthesis of the approach, conclusions and recommendations of TEEB.*

1.6 Retention forestry: an integrated approach in practical use

Lena Gustafsson, Jürgen Bauhus, Jari Kouki, Asko Lõhmus and Anne Sverdrup-Thygeson

About 85% of all forestland globally is used for multiple functions, while a considerably smaller proportion is allocated to tree plantations and reserves (FAO 2010). Multifunctional forests supply a wide range of ecosystem services, including wood production, carbon storage, and non-tree forest products such as game, berries, and mushrooms. Tree diversity appears to be positively linked to various ecosystem services (e.g. Gamfeldt et. al. 2013), and biodiversity overall is fundamental for the provision, regulation, and support of ecosystem services (Millennium Ecosystem Assessment 2005). Thus, management considering the conservation of biodiversity is fundamental to the long-term maintenance of multifunctional forests.

Box 10. Development and current extent of retention forestry

The practice of retention forestry (synonyms include “variable retention”, “structure retention”, “retention approaches”, “green-tree retention”) was initiated in the Pacific Northwest of North America (Washington and Oregon, USA and British Columbia, Canada) about 25 years ago. The volcanic eruption of Mt. St. Helens in Washington in 1980 showed ecologists, with professor Jerry F. Franklin at Washington State University at the forefront, that many living trees survive even such a devastating catastrophe and recovery is quick, even in situations where almost all trees have fallen. In fact, the biological legacies of the past (intact patches of vegetation, surviving living trees, dead standing and fallen trees) are essential components for the recovery process. These legacies provide for a continuity of species populations and forest conditions. The retention approach gained rapid acceptance among forest owners and concession holders, probably at least partly since it was a way to soften accelerating criticism from the public and the environmental movement towards the practice of clearcutting. Within a decade it had spread to other states in the USA and other provinces in Canada as well as to Australia. Today, retention approaches are practiced on about 150 million hectares, and the trend is growing, with initiatives also being taken in South America, e.g. Argentina (Gustafsson et al. 2012).

Retention forestry is a model for the integration of environmental qualities into production forests. It is a new type of forestry that has emerged during the last decades and is now widespread on different continents. It is mostly associated with clearcutting but increasingly applied in selective harvest operations also. The core of the retention approach is that some structures and features of importance to biodiversity are retained at harvest, such as old trees, unusual tree species, dead trees, and special habitats. The selection of components is made in a well-planned and deliberate way, and they are retained over the long term.

Scientific information about natural disturbance legacies may guide retention approaches

Integrated forest management implies that efforts are made to uphold environmental qualities in production forests through well-planned harvest and management operations. The composition, structure, and processes of natural forests provide valuable guidance to retention techniques. Patterns and processes related to natural dynamics and succession are thus fundamental. After large-scale wildfires in boreal Europe, for example, it is rare that all trees are killed, and consequently many trees usually remain, in contrast to clearcutting. The post-disturbance phase is characterized by a mosaic of open spaces and patches of remaining living trees, and there is often also a high abundance of dead trees (Kuuluvainen 2009). Also, in forest landscapes characterized by continuous forest cover, such as in many parts of Central Europe, dead and living trees form essential links over time that are fundamental for the long-term viability of many species populations. However, while ordinary selection harvesting approaches look similar to natural gap disturbance regimes of temperate forests and can indeed provide for a continuity of forest microclimatic and soil conditions, they typically result in a large reduction of structural elements such as large old trees and deadwood (Kenefic and Nyland 2007, Vanderkerkhove et al. 2009).

In retention forestry the emphasis is just as much on what is left behind at harvest as on what is taken out

The lessons from disturbance ecology imply that a proportion of trees with important roles for biodiversity should be left unharvested. The spatial arrangement varies depending on the context, but most commonly single wildlife trees are left as well as patches of trees. Usually, priority is given to old trees, particularly those with hollows, deadwood within the crowns, and other special features, and to minority tree species (Bauhus et al. 2009). Amounts vary greatly between regions and landowners; European retention levels are low overall at 1–10% of the harvested area compared to parts of Canada and the US, where 10–20% is common, and Tasmania, where as much as 30% is often retained (Gustafsson et al. 2012).

Retention forestry is one component of multi-scale conservation

Conservation actions in forest landscapes mainly imply that trees are left unlogged, but the size of conservation areas varies enormously. Traditionally, rather large areas have been set aside as national parks and reserves, but there have also been smaller areas identified as having special conservation values. Retention forestry is a new conservation component that targets the small-scale level: individual trees and tree patches within the matrix of managed forests. The inclusion of this small-scale level supports and supplements current conservation networks. Since different species have different habitat demands and operate on different scales, a system that embraces all scales, from individual trees to thousands of hectares, is likely to be most efficient.

Box 11. The objectives of retention forestry

Retention forestry can achieve many objectives through providing a certain continuity of forest composition, structure, and functioning (Gustafsson et al. 2012). In particular it aims at:

- Sustaining and enhancing the supply of various ecosystem services, particularly the provisioning of biodiversity
- Maintaining certain (but not all) species associated with old forest but also promoting species, some of which are rare, that depend on living and dead trees in open conditions
- Increasing public acceptance of forest harvesting and options for future forest use
- Enriching the structure and composition of the post-harvest forest
- Achieving temporal and spatial continuity of key habitat elements and processes, including those needed by both early and late successional specialist species
- Maintaining connectivity in the managed forest landscape
- Minimizing off-site impacts of harvesting, such as on aquatic systems
- Improving aesthetics of harvested forests

Retention strategies can be integrated into all silvicultural systems

Traditionally, silvicultural systems aimed to provide adequate regeneration of the preferred tree species, secure stand establishment, and ensure a desired forest structure and distribution of tree size classes for provision of acceptable stand productivity through thinning, species regulation, fertilisation, etc., and finally the sustainable yield of desired forest products (Nyland 2002). The resulting silvicultural systems created either even-aged systems through clearfelling, seed-tree, and shelterwood methods or uneven-aged selection forests. Their focus on commodity production has led to a simplification of forests throughout the world (Puettmann et al. 2009). Structural elements that occur in all successional phases, such as trees with special features (large dead branches, cavities, etc.) and deadwood (standing, downed) are largely absent from forests managed for timber. Importantly, the traditional silvicultural systems did not consider the large range of natural variation of structures and conditions following natural disturbances (Figure 20) (Franklin et al. 1997). Even the traditional uneven-aged systems were lacking many elements of natural forests, particularly those of the old development phases (e.g. Vanderkerkhove et al. 2009).

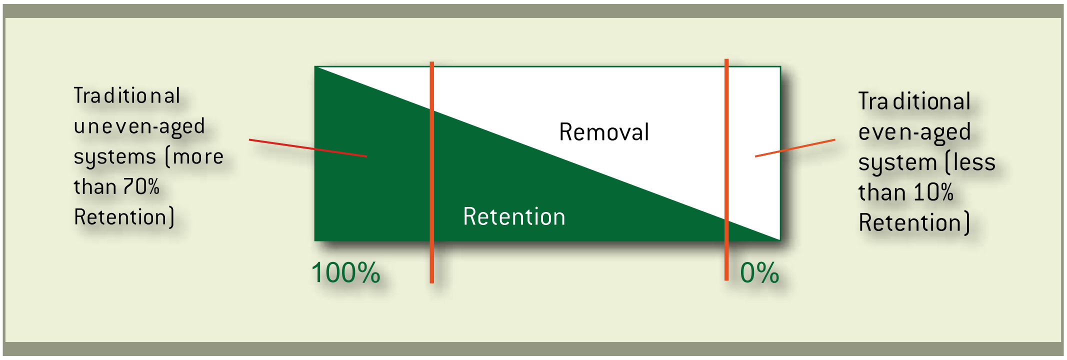


Figure 20. In forestry there is a wide variation in the amount of trees removed at harvest. Traditional uneven-aged management implies that most trees are left (approx. >70%), while in traditional clearcutting almost all trees are removed (approx. <10% are left). Retention forestry embraces typically a gradient of retention between 10% and 70%. Source: Modified from Franklin et al. (1997).

Retention is also required in selection forests

Components of retention forestry had already begun to be applied in Europe before the large breakthrough in North America. The development in Sweden exemplifies this. In this country, an obligation for forest owners to save important habitats such as certain swamp forests, patches with deciduous trees, and ravines as well as important wildlife trees at final harvest, was already written into the Forestry Act in the mid 1970s. There was an increase in the application through the adoption of a new forest policy in 1993/94 in which aspects of production and environment were given equal emphasis. A few years later, certification processes started (FSC and PEFC), with retention actions as core components. Development was similar in Norway and Finland, and the Baltic States quickly followed.

In Central Europe this development started later. Owing to the widespread adherence to close-to-nature forest management principles (Bauhus et al. 2013), there may have been less perceived need for deliberate action to maintain or restore critical forest structures. In Germany for example, this development was triggered by the 2009 amendment of the federal law for the conservation of nature, which translated the European Flora-Fauna-Habitat and Bird Protection guidelines into national law. Here, it was stated that only forest management that can demonstrate that it does not lead to a deterioration of populations of protected species is exempt from the strict requirement to protect each individual of these species as well as all of their reproduction and resting sites. It was recognized that populations of protected species can only be maintained through special provisions to increase habitat trees and deadwood in the matrix of managed forests (e.g. ForstBW 2010).

Retained structures help to maintain a higher level or facilitate a more rapid recovery of biodiversity and ecosystem functioning on site

Several hundred scientific studies relating to retention forestry have been published (Lindenmayer et al. 2012), including one review on studies from Europe and North America (Rosenvald and Lõhmus 2008) and one on studies from Northern Europe (Gustafsson et al. 2010). The studies largely agree that biodiversity is promoted when trees are retained, compared to traditional harvesting practices. The response varies depending on the species or species group in question, with an especially strong positive stand-scale response for ectomycorrhizal fungi, epiphytic lichens, and small ground-dwelling animals (Rosenvald and Lõhmus 2008). A number of large experiments on retention forestry have also been initiated, mostly in North America but also in Australia and Argentina. Very few experiments have so far been established in Europe, with the FIRE experiment in Finland being an exception (Figure 21).

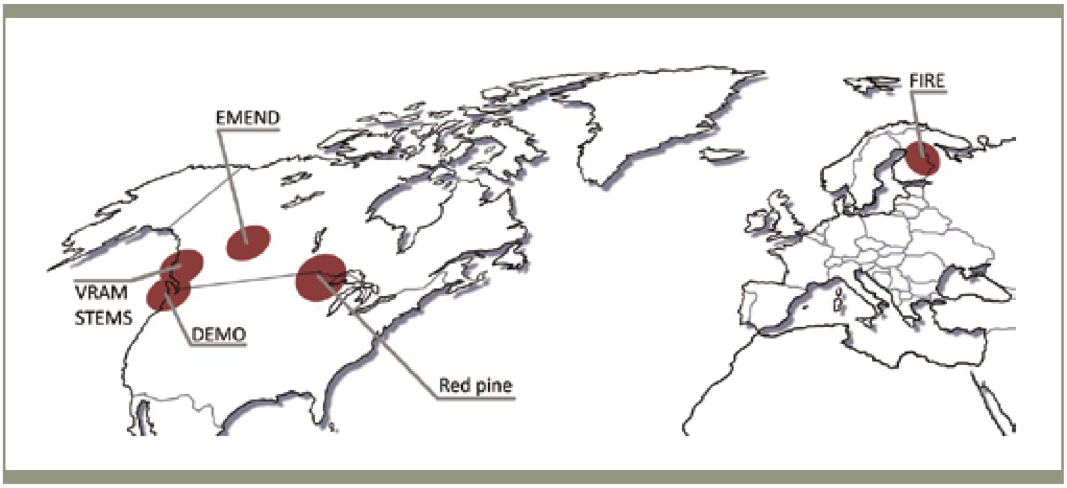


Figure 21. Several large experiments on retention forestry have been established, mostly in North America. In Europe there is only one large experiment, which is in Finland. There are also experiments in Australia and South America. DEMO – Demonstration of Ecosystem Management Options in Oregon and Washington, USA; EMEND – Ecosystem Management Emulating Natural Disturbance in Alberta, Canada; STEMS – Silviculture Treatments for Ecosystem Management in the Sayward in British Columbia, Canada; VRAM – Variable Retention Adaptive Management in British Columbia, Canada; and FIRE, a large-scale experimental facility for exploring fire and harvest, University of Eastern Finland. Source: Modified from Gustafsson et al. (2012).

Since retention forestry is such a young forestry model, there is large potential for its future development and improvement

Increased adaptation to regional conditions and also to landscape context would be an important step forward, as well as adjustment to site conditions. Very likely, increased efficiency would be reached, if the type of trees left as well as their spatial arrangement was based on knowledge of important habitats and species composition within the stand as well as in the surroundings.

Box 12. Retention forestry in practice – examples from Sweden and Germany

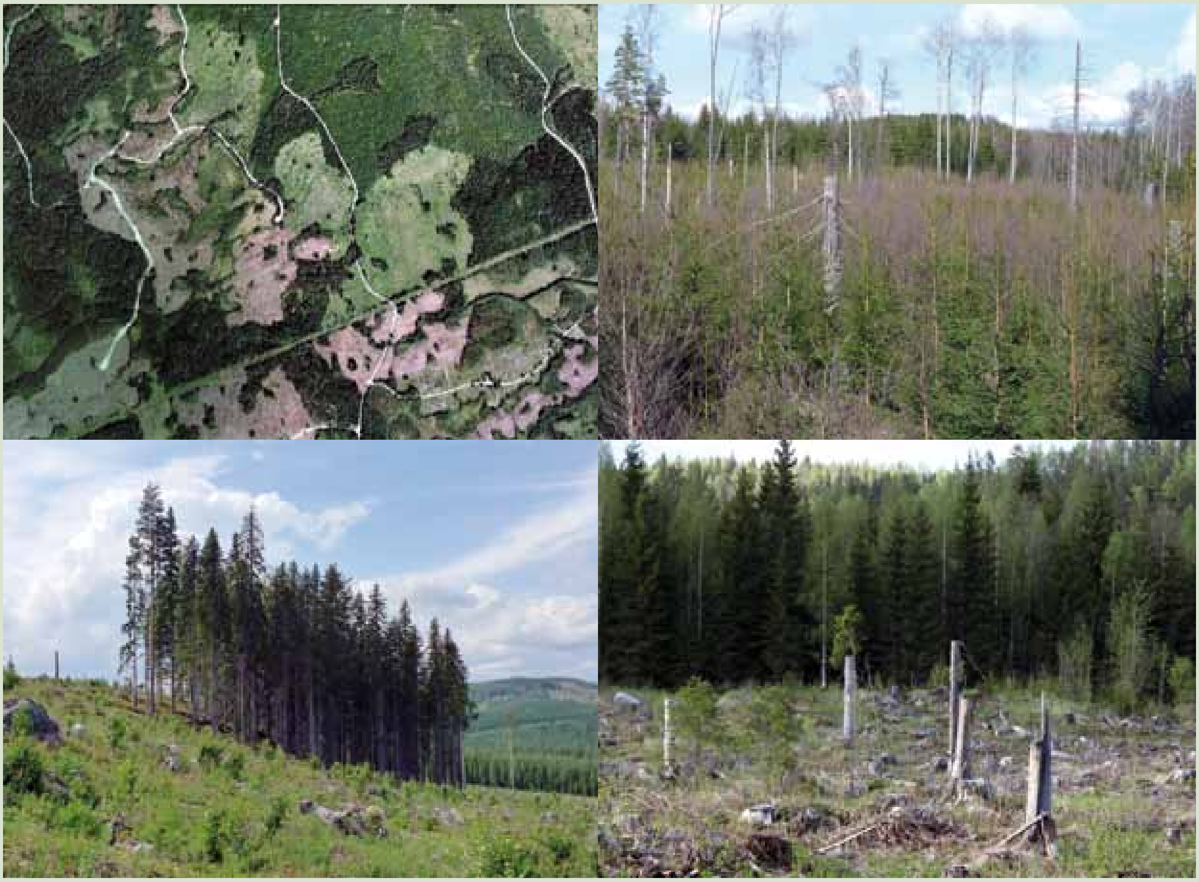


Figure 22. Sweden. Retention forestry is practiced on all 21 million hectares of production forest, i.e. on private as well as state-owned forestland, a requirement according to the Forestry Act and also included in certification standards. Retained edge zones and patches can be clearly seen in aerial photos (upper left; Dalarna, central Sweden; Google Earth). Since retention actions were introduced more than two decades ago, the young forests have been enriched with an overstorey of trees from the former stand (upper right; Östergötland, south Sweden). Trees are commonly left as retention patches (lower left; Hälsingland, central Sweden). A common restoration measure, and rather unique to Sweden, with the aim to increase the amount of deadwood, is to create high stumps, usually cut about 3 m above the ground (lower right; Hälsingland, central Sweden). Photos by L. Gustafsson.

Figure 23. **Germany**. Retention forestry is being practiced in all areas under forest certification (FSC, PEFC), which includes most public and a large share of private forests. Since there are practically no clearcuts, the retention of trees within selection forests focuses on habitat trees, standing dead trees, and logs. Commonly, the retention of ca. five old/habitat trees/ha is required (variation between 2–10 trees/ha). Trees are marked for retention during the regeneration phase (left), such as here in a 140-yr-old beech forest. Where these trees are retained in groups, additional individual trees with obvious hollows, nests, or other habitat features are to be retained. The right picture shows an old beech tree with patches of *Dicranum viride*, a protected moss species, marked for retention. On state forest land, in some states, single trees and forest stands/patches above a certain age (>180 years for beech, 250-300 years for oaks and conifers) are categorically retained, while in some other states categorical retention applies to all trees above a certain dimension (80–100 cm). In some cases (e.g. Bavaria) the quantitative goals for retention of habitat trees and deadwood vary with age and naturalness of the forest (more retention in high quality habitat). Photos by J. Bauhus

Box 13. Recommendations for management

- Inspect the stand before harvest to locate trees and tree groups of special value to biodiversity. They can be unusual tree species, especially old trees or hollow trees. Also, demarcate special habitats such as damp depressions, rocky slopes, or edge zones along watercourses. Also, map occurrences of large standing or lying dead trees.
- Save such trees and tree groups at harvest. If such special trees are absent, retain typical trees as these will later develop characteristics crucial for biodiversity. Document their location on property maps or in GIS.
- Keep these retention trees and areas intact, and avoid destroying deadwood during subsequent management actions.

References

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

Bauhus, J., Puettmann, K.J. and Kühne, C. 2013. *Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In: Messier, C., Puettmann, K.J. and Coates, K.D. (eds.). Managing Forests as Complex Adaptive Systems: building resilience to the challenge of global change. Routledge, The Earthscan forest library. Pp. 187–213.*

FAO – Food and Agricultural Organization of the United Nations. 2010. *Global Forest Resources Assessment 2010: Main Report. FAO Forestry Paper no. 163*

ForstBW (Hrsg) 2010. *Alt- und Totholzkonzept Baden-Württemberg. ForstBW, Stuttgart. 37 p.*

Franklin, J. F., Berg, D. R., Thornburgh, D. A. and Tappeiner, J. C. 1997. *Alternative Silvicultural Approaches to Timber Harvesting: Variable Retention Harvest Systems. In: Kohm, K. A. and Franklin, J. F. (eds.). Creating a Forestry for the 21st century. The science of ecosystem management. Island Press, Washington D. C. Pp. 111–139.*

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L, Kjellander, P., Ruiz-Jaen, M., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andrén, H., Moberg. F., Moen, J. and Bengtsson, J. 2013. *Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340 (DOI: 10.1038/ncomms2328).*

Gustafsson, L., Kouki, J. and Sverdrup-Thygeson, A. 2010. *Tree retention as a conservation measure in clear-cut forests of Northern Europe: a review of ecological consequences. Scandinavian Journal of Forest Research 25:295–308.*

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J.A., Wayne, A. and Franklin, J.F. 2012. *Retention Forestry to Maintain Multifunctional Forests: A World Perspective. BioScience 62:633–645.*

Kenefic, L. S. and Nyland, R. D. 2007. *Cavity Trees, Snags, and Selection Cutting: A Northern Hardwood Case Study. North. J. Appl. For. 24:192–196.*

Kuuluvainen, T. 2009. *Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge. AMBIO 38:309–315.*

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A. and Gustafsson, L. 2012. *A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conservation Letters 0:1–11. doi: 10.1111/j.1755-263X.2012.00257.x.*

MA – Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute.*

Nyland, R.D. 2002. *Silviculture: Concepts and Applications. McGraw-Hill Co., NY. 2ed.*

Puettmann, K.J., K.D. Coates, and C. Messier. 2009. *A Critique of Silviculture: Managing for complexity. Island Press, Washington, DC. 206 p*

Rosenvald, R. and Lõhmus, A. 2008. *For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. For. Ecol. Manage. 255:1–15.*

Vandekerkhove, K.; Keersmaeker, L. D.; Menke, N.; Meyer, P. and 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. For. Ecol. Manage. 258:425–435*

Key elements of biodiversity conservation in forests can be created by different species, species groups, or abiotic elements and can have a direct influence on other species by creating niches and microhabitats. Certain structures play an especially important role in ecosystem functioning and biodiversity, i.e. habitat elements that ensure essential niches for numerous species groups such as cavities in habitat trees, deadwood, or linear connecting structures. Effects of habitat fragmentation can be compensated for and gene flow between functionally isolated populations can be re-established through cross-linking elements in forest management (structural connectivity). For instance, for saproxylic organisms a forest stand consists of discrete habitat islands. For such organisms it is extremely important to have homogeneous habitat elements in a single forest stand.

2. Key elements of biodiversity conservation in forests

The sections of Chapter 2 highlight structural elements with a crucial impact on biodiversity conservation in forests. This chapter illustrates practical approaches to influence biodiversity at the management level and discusses the implications to forestry, focusing on habitat trees, deadwood, connectivity and fragmentation, successional stages, and disturbances. Additional emphasis is given on how to manage specialists from cultural legacies, target species, and endangered species groups. It is structured into six sections:

2.1 Habitat trees: key elements for forest biodiversity

Rita Bütler, Thibault Lachat, Laurent Larrieu and Yoan Paillet

Habitat trees are very large, very old, and dead or living microhabitat-bearing trees. They are of prime importance for specialised forest flora and fauna

Habitat trees are defined as standing live or dead trees providing ecological niches (microhabitats) such as cavities, bark pockets, large dead branches, epiphytes, cracks, sap runs, or trunk rot. Depending on their characteristics, habitat trees go by different names. Veteran, ancient, or monumental trees are individuals of remarkable age or size, whereas wildlife or cavity trees host animals such as woodpeckers and other cavity-nesting species. Habitat trees and the microhabitats they host are of prime concern for forest biodiversity as they can harbour many endangered specialised species of flora and fauna (see Box 14). At least 25 % of forest species depend on or benefit from deadwood and habitat trees. Many of them belong to the most threatened organisms in European temperate forest ecosystems.

Veteran trees have always caught man's attention and have consequently acquired a symbolic role. For example, justice was long administered under old lime or oak trees in Central Europe. However, despite their cultural importance, such trees have undergone a marked decline for diverse reasons: the loss of their symbolic value through cultural change and the establishment of modern forestry and agriculture accompanied by the abandonment of traditional forest uses. Today, veteran trees are a legacy of the past and are of exceptional importance given the hundreds of years required for a tree to reach this status.

The abundance and diversity of microhabitats strongly increase with tree diameter and bark thickness, and therefore typically with tree age (Bütler and Lachat 2009; Vuidot et al. 2011, Larrieu and Cabanettes 2012). In southwest Sweden, for example, Ranius et al. (2009) found that less than 1 % of the pedunculate oaks (*Quercus robur*) younger than 100 years of age had cavities where the inner space was wider than the entrance (>3 cm in diameter). Between 200 and 300 years of age, however, 50 % of the oaks harboured such hollows, while all the 400+-year-old trees had wide cavities (Ranius et al. 2009). The ecological value of a tree therefore increases with its age. For these reasons, particular attention is being given to veteran trees, and they are currently being inventoried in several countries to promote their preservation. In Europe, veteran trees may be found in three different types of ecosystems: relicts of orchards or traditionally managed forest zones (coppices with standards, wooded pastures), old-growth forests, or parks.

Box 14. Microhabitats associated with habitat trees and their importance for biodiversity.

Dead trees, snags, and trees with large amounts of canopy deadwood have been relatively well studied. They are a substrate for a considerable part of forest biodiversity and constitute feeding, roosting, foraging, nesting and, generally speaking, dwelling grounds for a variety of species, including vertebrates and invertebrates, plants (bryophytes and lichens), and saproxylic fungi. However, our knowledge remains incomplete as scientific investigations on tree microhabitats and their importance for biodiversity have mostly focused on cavities (see Winter and Möller 2008, Vuidot et al. 2011). Without aiming to be exhaustive, below we summarize the current findings on tree microhabitats and the biodiversity that depend on them. Four main types have been defined:

- Cavities: four types of cavities may be distinguished, depending on their origin and morphology
  - Woodpecker cavities: excavated/drilled out by woodpeckers for nesting, they play an important role for numerous secondary cavity dwellers (birds, bats, rodents (Gliridae), and meso-mammals (mustelids)) and invertebrates (spiders, beetles, wasps). For birds in particular, cavities seem to support a complex network of species involving primary cavity builders such as woodpeckers and a cohort of secondary cavity nesters.
  - Non-woodpecker cavities: created mainly during wood decaying processes, these cavities differ from those previously mentioned in that they originate mostly from injuries during the life of the tree. These cavities are mainly used by bats for roosting, but may also be used by small and large mammals, lizards, amphibians, and birds. The more mould they contain (i.e. the more the wood has decayed), the more specialised the species community they support. For example, the endangered beetle Osmoderma eremita closely depends on cavities with mould for its survival.
  - Dendrothelms: very specific cases where a cavity is temporarily or permanently filled with water. Several insects (mainly diptera) or microcrustaceans depend on dendrothelms, especially when the bottom of the cavity is decayed.
  - Root-buttress cavities: at the base of the tree, these cavities are used as shelters by micro and meso-mammals, birds, and amphibians.
- Cracks and loose bark: more abundant on snags and decaying trees, but also found on living trees damaged by natural causes (e.g. struck by lightning) or harvesting operations, such microhabitats are particularly important for bats, which specifically nest under the bark. Cracks and peeling bark are also used by crack-dwelling birds, hemiptera (flatbugs), and spiders.
- Fruit-bodies of saproxylic fungi: these fruiting bodies of saproxylic fungi indicate a certain level of biodiversity per se, but they also benefit other forest dwelling species such as beetles, diptera, moths, and flatbugs.
- Other microhabitats: epiphytes (e.g. ivy, lianas, lichens, and bryophytes), witch-brooms, and sap runs benefit insects (mainly beetles and moths) as well as birds. However, these microhabitats are poorly studied and more research is needed to specify their links with biodiversity.

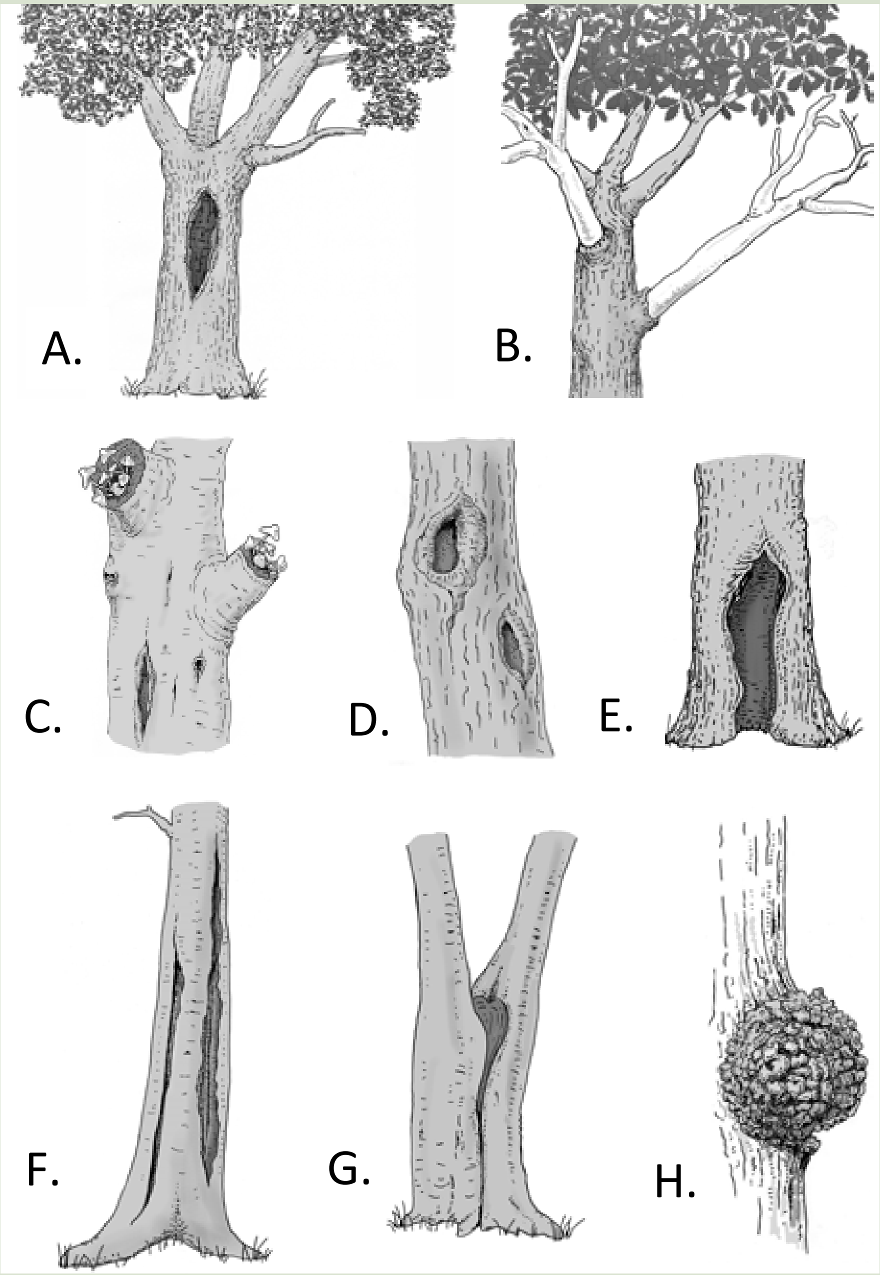


Figure 24. Different microhabitat types. A. Non-woodpecker cavity; B. Canopy deadwood; C. Fruit-bodies of saproxylic fungi; D. Cavities with mould; E. Root-buttress cavity; F. Cracks; G. Fork split; H. Burr. Source: © TU Berlin, Institut für Ökologie, Fachgebiet Ökosystemkunde/Pflanzenökologie. http://naturschutz-und-denkmalpflege.projekte.tu-berlin.de.

Habitat trees are common in unmanaged forests but require specific attention in managed forests

Changes in management practices in the 19th century marked the beginning of a dramatic decline in the number of old and hollow trees that had been maintained under specific management practices. This was especially true in the countryside, where pollarded trees, wooded pastures, and coppice with standards were common. Such habitat trees benefited many xerothermophilous species since, generally, they were well exposed to the sun. In most modern managed forests, logging systematically eliminates 'defective' trees with low economic value, which is often the case for trees hosting microhabitats or those with a high potential to develop them. In management aimed at producing large-diameter high-quality trees, microhabitat density is drastically reduced by positive tree selection during thinning and tending operations. As a consequence, microhabitat diversity and abundance are generally lower in managed than in unmanaged forests. This is also true for the number of trees hosting several different microhabitat types simultaneously (Winter and Möller 2008; Bütler and Lachat 2009; Larrieu et al. 2012).

Generally, the density of habitat trees with a diameter of over 70 cm remains less than 0.5 to 2 trees per hectare in managed forests (Bütler and Lachat 2009; Bütler et al. 2011), whereas 10 to 20 such trees occur in virgin forests in Central Europe and southern Scandinavia (Nilsson et al. 2002). On the other hand, certain types of microhabitats, such as dendrothelms (water filled tree holes) and bark losses, may be higher in managed forests as a consequence of harvesting activities (Vuidot et al. 2011; Larrieu et al. 2012).

Cavity-bearing trees are among the most important habitat trees for forest wildlife. Old cavities with decayed residue host several of the most threatened forest beetles

Cavities are probably the most well documented and studied type of tree microhabitat (Figure 25). Most cavities are produced either by avian excavators (woodpeckers) or by decay processes involving invertebrates and fungi, or by a combination of both (Cockle et al. 2012; see also Box 1). Snags are more likely to bear both woodpecker and non-woodpecker cavities than are living trees (Vuidot et al. 2011). However, snags generally account for less than 10 % of the standing trees in unmanaged forests and hardly exist at all in managed forests; this explains why most cavities (>80 %) are found in living trees (Larrieu et al. 2012).

The probability of cavity occurrence increases substantially with diameter in both live and dead trees, and greater wood thickness around cavities provides more buffered microclimatic conditions for sheltering bats or nesting birds. Consequently, cavity-nesting birds are less frequent in young trees than in older ones. There are also fewer cavity nesters in managed forests than in natural forests. However, cavity tree density has also been found to vary considerably among stands of the same age. Tree species also plays an important role. Even the amount of precipitation seems to positively influence the number of tree cavities. These

Figure 25. This sessile oak proves that woodpeckers may use the same cavity tree for several years. Old cavities can be re-used by secondary cavity users, both vertebrates and invertebrates (birds, bats, rodents, spiders, wasps, etc.). Photo by R. Bütler.

Figure 26. In French public forests, habitat trees to be maintained in managed areas are identified and marked to ensure they will be left untouched during thinning operations. Photo by Y. Paillet.

effects suggest that the distribution of tree cavities reflects the incidence of fungal heart rot in trees. Therefore, by reducing the number of fungus-bearing live trees, forest management is likely to have a broad-scale impact on cavity trees. In cavity-poor forests where wood decay processes are suppressed either climatically or by forest management, primary cavity nesters are consequently often rare.

Managing for natural features, including habitat trees, strengthens the ecological services that are becoming increasingly valued by society. Efficient management strategies include the retention of "old-growth islands" at the management unit level combined with the retention of habitat trees at the stand level when harvesting

Habitat trees have a low economic value yet have a high ecological value. Although this value is progressively recognized, they are still regularly removed in tending and harvesting operations. A shift in attitude in daily forestry practice towards their conservation may still often be needed. The retention of habitat trees suitably distributed across the landscape is a challenge for forest managers because such trees do not match silvicultural economic schemes. Snags and partially dead trees may also be a potential hazard for forest workers and visitors. Consequently, setting up a strategy of deliberate retention of habitat trees requires a

Box 15. Recommendations for management.

Conservation of (future) habitat trees should be an integral part of all forest operations, such as tending, thinning, and final harvest. For this purpose, specific indication on selection and density of such trees should be integrated in the operational guidelines.

At the stand level, at least five to 10 habitat trees per hectare should be retained to mitigate the effects of timber harvesting on organisms that depend on the structures provided by such trees. In selection systems, retention trees should be microhabitat-bearing trees (including snags) or non-vigorous low quality trees, which would be removed under conventional uneven-aged management. Generally, a combination of dispersed and aggregated retention is recommended ('variable retention') as wind damage is less pronounced in aggregated than in dispersed retention patterns. Furthermore, there is evidence that aggregated habitat trees provide better habitat for birds than do scattered individual trees. However, where scattered individual habitat trees already exist, they should be retained. In addition to retained habitat trees, trees likely to bear microhabitats in the future should be selected for recruitment; they should be properly identified and permanently protected from harvesting (Figure 26). Moreover, recruitment trees should be retained at each harvesting event at a rate that exceeds the number of senescent trees required. Both recruitment and retention trees can be marked in the field to guarantee their long-term conservation.

At the management unit level, complete forest stands should also be set aside where trees can complete their natural cycle, including senescence and decomposition. Strict forest reserves and old-growth islands are two instruments that promote habitat trees at this level. Generally limited in size to a few hectares, old-growth islands are often recommended to create stepping stones between larger protected forest areas.

In order to develop a functional network of old-growth elements, a combination of such larger and smaller set-asides should be completed with a good quality matrix of managed stands with habitat trees (see chapter 2.3 on connectivity).

shift in management attitudes and a reorientation of practices to encourage the development of old-growth structures. Retention at harvesting is justified based on two assumptions: first, retaining habitat trees at the stand level helps to maintain a higher level of biodiversity and better ecosystem functioning, and second, retained structures accelerate the recovery of biodiversity and ecosystem functioning in damaged systems (Bauhus et al. 2009). Depending on their location, habitat trees can be promoted at both the stand level and the management unit level (see Box 15).

> *Setting up a network of trees and stands that will never be logged is essential to guarantee the minimum habitat requirements of logging-sensitive species, though this appears incompatible with economic interests*

For example, the critical forest age threshold for a satisfactory diversity of lichens, mollusks, and birds in beech (*Fagus sylvatica* L.)-dominated forests ranges from 100 to 170 years in sub-montane forests and from 160 to 220 years in montane forests (Moning and Müller 2009). On the other hand, production forestry aims to shorten the rotation length in beech stands to less than 120 years to avoid the formation of red heartwood. Therefore, management strategies should be applied that guarantee a functional network of habitat trees and set-asides, without jeopardizing basic forestry goals. Considering that in natural forests in Central Europe, late developmental stages cover between 20 and 60 % of the surface area, and bear the majority of endangered forest biodiversity, it is essential to dedicate a sufficient share of the surface area in managed forests to approximate the level of biodiversity inherent in old-growth forests. Larrieu et al. (2012) recommend that a minimum of 10–20 % of the surface area of a management unit should be confined, in a more or less aggregated manner, to the conservation or recruitment of microhabitat-bearing trees. As stated before, these should not be the most valuable trees, most productive, or most accessible sites. Forest managers can take advantage of particular local features such as rocky outcrops, wetlands, or steep slopes to establish set-asides with minimal economic impact. However, set aside stands should not be confined only to marginal sites, but should be representative of all forest types available at the landscape level.

> *Habitat tradition – defined as the continuity in supply of old-growth, deadwood, and various forest structures – also seems to play an important role for preserving forest biodiversity*

Several authors have highlighted the importance of the continuity of deadwood supply and presence of old trees in the conservation of red-listed species, and Buse (2012) showed that relict saproxylic species are correlated with the continuity in forest cover. The retention of habitat trees both at the stand and management unit levels should therefore be planned to ensure long-lasting habitat continuity. However, a time gap may occur between the very old trees remaining today from abandoned traditional management and the next generation of habitat trees. To bridge this gap, it is possible to artificially accelerate the development of structures typically associated with old trees. This strategy involves wounding or killing younger trees, inoculating young trees with decay-forming fungi, or thinning to accelerate the rate at which trees develop structures such as hollows. Such active management may be limited to very specific cases, where few microhabitat-bearing trees are available and strong conservation issues have been identified, such as the presence of relic populations of endangered species.

> *Microhabitats could also be adopted for use as biodiversity indicators in European forests. A clear list of habitat tree features should be drawn up to help monitor microhabitats and correlate them to biodiversity levels*

Today, the importance of habitat trees for forest biodiversity is widely accepted and their ecological services are becoming increasingly valued by society. Consequently, foresters should consider them positively. Standing, these trees provide habitat for many species; fallen, they become a source of coarse woody debris and finally, through decay and nutrient cycling, become incorporated into the forest soil and contribute to maintaining important ecosystem functions. During the last few decades, the number of big trees, and consequently the number of habitat trees, has increased in some parts of Europe. For example, the number of trees with a diameter above 80 cm has almost doubled in Switzerland over the last 30 years, although this is not only explained by deliberate conservation efforts, but also by low market prices for wood. However, in many parts of Europe, the future of habitat trees (and their microhabitats) will also strongly interfere with policies on forest biomass production. Explicit conservation strategies will be needed to ensure that the increased demand for fuel wood and biomass will not lead to a strong decrease in habitat trees in managed forests since virtually all trees, even snags, can be harvested for this goal. Therefore, enacting harmonized measures to protect habitat trees and their microhabitats should be of prime concern.

References

Bauhus, J., Puettmann, K. and Messier, C. 2009. *Silviculture for old-growth attributes. Forest Ecology and Management 258(4): 525–537.*

Buse, J. 2012. *"Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. Journal of Insect Conservation 16(1):93–102.*

Bütler, R. and Lachat, T. 2009. *Wälder ohne Bewirtschaftung: eine Chance für die saproxylische Biodiversität. Schweizerische Zeitschrift für Forstwesen 160(11):324–333.*

Bütler, R., Bolliger, M., Senn-Irlet, B. and Wermelinger, B. 2011. *Naturwälder als Lebensraum. In: Brang, P., Heiri, C. and Bugmann, H. (eds.): Waldreservate: 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt Verlag, Bern, Stuttgart, Wien. Pp. 38–55.*

Cockle, K.L., Martin, K. and Robledo, G. 2012. *Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: Pathways of cavity production and implications for conservation. Forest Ecology and Management 264:210–219.*

Larrieu, L. and Cabanettes, A. 2012. *Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Canadian Journal of Forest Research 42(8):1433–1445.*

Larrieu, L., Cabanettes, A. and 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(3): 773-786.*

Moning, C. and Müller, J. 2009. *Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. Ecological Indicators 9(5):922–932.*

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G. and Ranius, T. 2002. *Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management 161(1–3):189–204.*

Ranius, T., Niklasson, M. and Berg, N. 2009. *Development of tree hollows in pedunculate oak (Quercus robur). Forest Ecology and Management 257(1):303–310.*

Vuidot, A., Paillet, Y., Archaux, F. and Gosselin, F. 2011. *Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144(1):441–450.*

Winter, S. and Möller, G.C. 2008. *Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255(3–4):1251–1261.*

2.2 Deadwood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity

Thibault Lachat, Christophe Bouget, Rita Bütler and Jörg Müller

> *Besides its major role for the conservation of saproxylic species, deadwood also contributes to carbon sequestration, nutrient supply, natural regeneration, and protection against falling rocks*

The awareness of the importance of deadwood in forest ecosystems has increased in recent decades. Today, deadwood is not only recognized as a key element for saproxylic species (species associated with the decay of wood on living and dead trees), but it is also known to play an important function for carbon sequestration, nutrient supply, and water retention. It might also enhance natural regeneration, particularly in mountain forests with perennial grasses. Furthermore, deadwood can also contribute to protection against falling rocks on steep slopes or play an essential role in other ecosystems, such as rivers and lakes with their spawning grounds. In this chapter, we will focus on deadwood within the forest ecosystem as a habitat or substrate for saproxylic biodiversity.

Even though data are mostly lacking, it is widely accepted that little deadwood was present in most Central European forests around 1900 as fuelwood was the most important source of primary energy. At this time, deadwood refuges were located in pasture forests with their veteran trees or in the stumps of coppiced forests. The situation changed when coal became the main energy source around 1910. After World War II, the amount of deadwood increased as a consequence of less intense forest management and lower demand for fuelwood (Speight 1989). Since 1990, an overall increase in deadwood has been noted based on data from European forests (FOREST EUROPE 2011). This may be due to increased compliance with sustainable forest management principles as well as to large windthrow disturbances (Priewasser et al. 2013). Consequently, the amount of deadwood is higher today than 100 years ago.

Forest managers often ask the question: “How much deadwood and what quality should there be in order to promote the conservation of saproxylic biodiversity?” Most of the time, the best answer is: it depends on the conservation goals or species of concern. Since habitat requirements differ between species in different forest types, it is highly unlikely that it will ever be possible to identify simple targets of deadwood that would guarantee the survival of the whole community of saproxylic species (Ranius and Jonsson 2007). Nevertheless, scientific work emerging in recent years may highlight some ecological thresholds that maintain a certain proportion of saproxylic diversity.

> *The survival of saproxylic species is not only dependent on the quantity, but also on the quality of deadwood, such as the tree species, diameter, or decay stage. However, the presence of a species is not a guarantee for good habitat conditions. It might be a legacy of the time when its habitat was still available*

Saproxylic species are used to living in a dynamic habitat such as deadwood, with changing physical and chemical characteristics over time. In order to maintain a local population, saproxylic species must therefore be able to colonise new suitable habitats at the right time. Depending on their ecology and habitat preferences, some saproxylic species have to find a new habitat after only a few months (e.g. colonisers of fresh deadwood or small branches), whereas other species can maintain a population for decades in one cavity tree with mould (e.g. Hermit beetle, *Osmoderma eremita*). If the density of a potential habitat is too low because of poor deadwood quantity or unsuitable habitat quality (e.g. a lack of big logs in an advanced stage of decay), the colonisation of new trees will not be sufficient to compensate for local extinction. The survival ability of saproxylic species is therefore not only dependent on the quantity, but also on the quality of deadwood. Generally, for species with narrow ecological niches (specialists) and/or species with limited dispersal ability, the extinction threshold will be more critical (Müller and Bütler 2010). The extinction threshold refers to the minimum size of a habitat suitable for a species above which the population persists and below which a population cannot survive. However, when a habitat is destroyed or is missing locally, most species dependent on this habitat will not disappear immediately. According to Tilman et al. (1994), a species population decline in response to habitat destruction occurs with a time delay, called the "extinction debt". This means that such a species could survive as "living dead" for a long time in an ecosystem that is no longer suitable in the long term. The observation of a specific species might thus be a legacy of the time when its habitat was still available. The dispersal of species associated with a short-lived habitat such as deadwood is still poorly understood. For instance, as more individuals of the Hermit beetle were investigated by telemetry, the migration distance of single species observed increased (Dubois and Vignon 2008). Here, it must be taken into consideration that only a few individuals are required to colonise a new forest patch over a long period of time. However, such single events are difficult to investigate.

At the stand scale, a high amount of deadwood under natural conditions not only leads to a larger diversity of substrates (e.g. a whole tree offers different diameters), but also to a higher deadwood surface area. According to the island theory (MacArthur and Wilson 1967), we can expect higher species richness on sampling units with a larger surface. Similarly, stands with high amounts of deadwood will generally harbour more saproxylic species than stands with low amounts of deadwood.

Even though the relationship between species number and the quantity of deadwood is well established for boreal forests (Martikainen et al. 2000), this relationship remains less clear for temperate forests in Central Europe. It seems that additional factors influence the saproxylic species community in these warmer forests. Nevertheless, even if the correlation between saproxylic biodiversity and deadwood amount is moderate, it is still positive, showing that

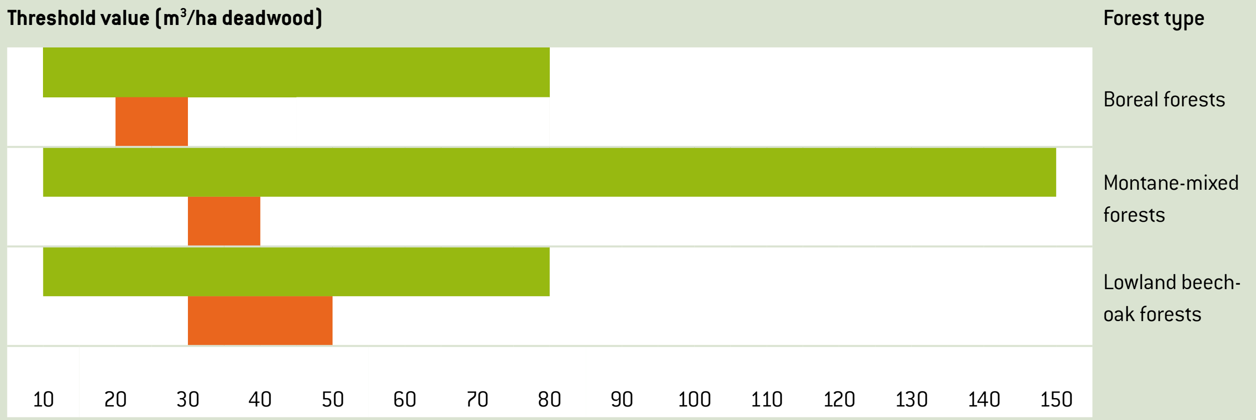
Figure 27. A large quantity of deadwood leads to a larger diversity of substrates. Consequently, stands with high amounts of deadwood will generally harbour more saproxylic species than stands with low amounts. Photo by R. Bütler.

any forest practices that enhance deadwood benefit saproxylic biodiversity (Lassauce et al. 2011).

Depending on the forest type, deadwood quantities ranging from 20 to 50 m^3/ha have been identified as a threshold to maintain the majority of saproxylic species. Very demanding species require more than 100 m^3/ha

Thresholds are mainly defined for single species. Still, for the conservation of whole communities, it is very useful to determine these thresholds at the community level. Consequently, it makes sense to consider as many species as possible when establishing habitat thresholds in order to maintain the entire deadwood species community. Müller and Bütler (2010) produced a literature review based on 37 thresholds for deadwood. Most of the species or species groups considered showed a peak at 20–30 m^3/ha for boreal coniferous forests, 30–40 m^3/ha for mixed-montane forests, and 30–50 m^3/ha for lowland forests. With these quantities of deadwood, the majority of the saproxylic species taken into consideration can be maintained. However, saproxylic species or species groups that need a high quantity of deadwood cannot be maintained in conservation schemes based on these ecological thresholds. For example, Moning and Müller (2008) found a threshold of 141 m^3/ha of deadwood for cavity-breeding birds. The parasitic fungus *Antrodiella citrinella* was only found in stands with more than 120 m^3/ha of deadwood (Bässler and Müller 2010). Both examples emphasize the necessity of forest reserves where forests can develop naturally, and deadwood amounts may reach quantities similar to primeval forests.

Table 6. Threshold values for dead wood (m^3/ha) in European forests for the occurrence of single species and species richness (after Müller & Bütler 2010), range in green, peak value in red.



Müller, J., and R. Bütler. 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.

Management practices that promote deadwood should be organized on large scales as the influence of deadwood on saproxylic species increases with increasing spatial scales. The temporal dimension should also be considered because the continuity of forest cover and deadwood availability might play a major role in the protection of saproxylic biodiversity

The influence of deadwood on saproxylic species should be considered at different spatial scales, specifically at local and regional or landscape scales. Okland et al. (1996) found that deadwood was an important factor at medium (1 km^2) and large scales (4 km^2) for species richness and composition, whereas only weak relationships were found at a small scale (0.16 ha). Franc et al. (2007) emphasized that the importance of deadwood increases with increasing spatial scales. This might influence management practices that promote deadwood, which should be organized on large scales in order to improve the conservation of saproxylic species. However, at the landscape level, the quantitative effect of deadwood on the saproxylic community is still poorly understood even though it is likely to be extremely significant. Here, two scales of forest management are affected: Logging operations are conducted on the stand scale (20–100 ha in Central Europe), whereas the planning of forest management for a decade is done on the landscape scale.

Moreover, not only should the spatial scale be considered, but also the temporal dimension. As deadwood is a dynamic habitat evolving with time, it should be available at the right time, place, and quality to be colonised successfully by a species in order for it to survive. This continuity in supply of deadwood refers to the habitat tradition. Brunet and Isacsson (2009) highlighted the importance of the continuity of deadwood and old trees for the conservation of red-listed species, and Buse (2012) showed that saproxylic species associated with primeval forest structures and features are correlated with the continuity of forest cover. Consequently, the continuity of forest cover and deadwood availability seem to play a major role in the protection of saproxylic biodiversity even though not all saproxylic species are sensitive to it. However, for sensitive species, this continuity enables their survival in stands without management, whereas they disappear from cultivated forests in which the habitat tradition has been interrupted (Müller et al. 2005). Furthermore, saproxylic species may have evolved to adapt to natural disturbance. The shift from naturally-disturbed to managed forests might not only relate to discontinuity but also to changes in the disturbance regime.

The diversity of deadwood in terms of tree species, diameter, decay class, and type (lying/standing) has a positive effect on the conservation of saproxylic species assemblages

Usually, if a large amount of deadwood can be found, a variety of deadwood features become available that enhance niche diversity, which in turn improves the survival ability of many saproxylic species. Even though the independent effects of deadwood quantity and quality have not yet been established, and quantity and quality might be highly correlated, the importance of different types of deadwood has already been noted in several studies. Consequently, maintaining diverse qualities of deadwood in terms of tree species, diameter, decay class, and type (lying/standing) has a positive effect on the conservation of saproxylic species assemblages. This is particularly important as ecological specialisation, often accompanied by low population density, makes species particularly vulnerable (Jönsson et al. 2008).

Most saproxylic species are either specialised on coniferous or broadleaved trees, and few generalists are known. Species with a narrower host-range are also known. However, the effect of tree species declines with the decomposition of deadwood

Host-tree associations of saproxylics can occur at different levels, from true specialist to host generalist. Coniferous and broadleaved trees are the broadest grouping of host-trees for saproxylics. For example, the majority of the saproxylic fungi and beetle species are either specialised on coniferous or broadleaved trees and few generalists are known. This separation of trees into two realms seems to be a universal pattern (Stokland et al. 2012).
However, behind this grouping, several species show a narrower host-range. The first colonisers in particular, such as bark beetles, are specialised on even a single tree species or genus. The effect of tree species on saproxylics declines with the decomposition of deadwood because of converging physical and chemical characteristics. However, the difference in species composition between coniferous and broadleaved trees remains throughout the decomposition process (Stokland et al. 2012).

Few large diameter logs cannot be substituted by many small ones for a given volume of deadwood because both have their own species assemblages. Large decay logs have been identified as essential for the conservation of saproxylic species as they are missing in most managed forests

The diameter of deadwood pieces does not have a direct effect itself on saproxylic species, but other factors are influenced by deadwood size, such as bark thickness (bark is thicker and rougher on big old trees than on young ones) and the surface-to-volume ratio (large trees have less surface per volume than small trees), which in turn influences moisture and temperature. Several studies have highlighted the correlation between the body size of saproxylic beetles and deadwood diameter. This correlation can be explained by the available resources, which can be considered as a limiting factor for larval development, and by the stability of the microclimate and the durability of the habitat as deadwood with a large diameter decomposes slower than deadwood with a smaller diameter (Gossner et al. 2013).

Larger pieces of deadwood are also more heterogeneous since they offer more ecological niches by bearing several decay classes and fungi, creating different microhabitats, which in turn influence the diversity of saproxylic species. However, while large-diameter and small-diameter deadwood harbour a similar number of species for a given surface or volume (Stokland et al. 2012), they do have their own species assemblages (Brin et al. 2011). Therefore, the substitution of a few large diameter logs by many small ones for a given volume of deadwood is not sufficient. Furthermore, Juutilainen et al. (2011) highlight that surveying only coarse woody debris may underestimate species richness and abundance of saproxylic species. A high diversity of deadwood diameters should be maintained to enable the conservation of saproxylic biodiversity. In general, in managed forests, we have a lack of large decayed logs (e.g. diameter above 50 cm for *Fagus sylvatica*), which have been identified as essential for saproxylic species.

Figure 28. Deadwood with large diameters (above 50 cm) is especially valuable for saproxylic species. Photo by T. Lachat.

During the decay process from fresh deadwood to mould wood, species assemblages and richness evolve in deadwood. Furthermore, how a tree dies has an important effect on the composition of the saproxylic community

Deadwood is known to be a dynamic habitat where local species extinctions are caused by gradual substrate destruction or deterioration due to wood decomposition, which in turn allows other species to establish themselves. The long-term persistence of these species requires successful colonisation of new patches (Jönsson et al. 2008). During the process from fresh deadwood to mould wood, the biotic and abiotic characteristics of this habitat/substrate change drastically. Roughly, three phases can be differentiated during the decay process for the succession of saproxylic species (especially invertebrates): the colonisation phase (invasion of fresh deadwood by primary saproxylics), the decomposition phase (primary saproxylics are joined by secondary saproxylics), and the humification phase (saproxylics are progressively replaced by soil organisms) (Stokland et al. 2012).

In addition to the species turnover with advancing wood decay, species richness is also strongly influenced by this process. For example, basidiomycetes show the highest species richness at intermediate decay stages of both broadleaved and coniferous trees. For beetles, several studies have demonstrated that the greatest species richness occurs at the beginning of the decay process for coniferous trees, whereas species richness peaks later for broadleaved trees, during mid or even late decay stages (Stokland et al. 2012).

How a tree dies has an important effect on saproxylic species composition. For example, an old tree might need several years, if not decades, to completely die and might remain as a standing dead tree (snag) before it falls down. Many different species will succeed in creating micro-habitats on such a tree, which in turn will harbour other species. In this case, tree death is a very complex and gradual process. If a tree is cut or dies suddenly because of windthrow or fire, colonisation will follow completely different pathways. However, these differences are bigger at the beginning of the decomposition period than at the end. This is because the characteristics of deadwood converge at the end of the decay process.

> *Abiotic factors such as temperature and humidity and biotic drivers such as predation and competition also strongly influence species assemblages occurring on deadwood*

Additional abiotic and biotic drivers also strongly influence species assemblages occurring on deadwood. Temperature and moisture are two of the main abiotic factors that might be influenced by the position of the deadwood, especially when it is standing (snag) or lying. A snag will be dryer than a log in contact with the soil and might be more sun-exposed. Again, it is not a matter of more or less favourable conditions for saproxylic species, but more a matter of different conditions that increase the survival ability of given species groups. Moist conditions are generally favourable to many fungi and bryophytes, whereas dry and hot conditions might be favourable to a whole range of saproxylic beetles and lichens. Similarly, it should be pointed out that similar substrates harbour different species assemblages when established in different environments, such as various trunk sections or branches in the canopy or on the forest floor (Bouget et al. 2011; Foit 2010). Other drivers, such as the presence of tree micro-habitats on living trees, could also influence the species assemblages living in deadwood.

Regarding biotic interactions, we may also mention species interactions about which we still know very little, but which are probably crucial. Even though some succession pathways are

> *Deadwood has been increasing over the last decade throughout Europe. However, the conservation goals for saproxylic species have not yet been achieved as the quantitative thresholds determined for the conservation of most saproxylic species have generally not been reached in commercial forests*

well known between some fungi and beetle species or between prey and predators (see e.g. Stokland et al. 2012), most of the interactions within the saproxylic food web remain unknown as there are many (e.g. competition or commensalism).

Today, several schemes are used for the management and promotion of deadwood in the forest ecosystem. Apart from the conservation of the last primeval forests, segregative measures such as forest reserves and old-growth islands are compulsory to stimulate high deadwood amounts. These high quantities are required by the most demanding saproxylic species. Their requirements for high deadwood quantity and quality range are not compatible with commercial forests, where the amount and diversity of deadwood substrates as well as the input/output dynamics of deadwood have changed. As even the quantitative thresholds determined for most saproxylic species are much higher than the general amount of deadwood found in commercial forests, Müller and Bütler (2010) recommended establishing a network of forest stands with between 20–50 m^3/ha of deadwood rather than aiming for a lower mean in all stands.

In general, the amount of deadwood has been increasing over the last decade throughout Europe. However, this does not mean that the conservation goals for saproxylic species have already been achieved. The significantly increasing demand for renewable energy resources such as fuelwood – to reduce dependence on fossil fuels and thereby limit greenhouse gas emissions – might drive an intensification of forest management in the future. Consequently, the amount of large over-mature trees and deadwood might be reduced. Such an intensification of management is expected to have a negative effect on saproxylic biodiversity. However, with increasing awareness on the part of forest owners and managers of the need for the conservation of biodiversity, an intensification of forest management may be done with sustainable, adaptive forest management. This can only be achieved with the help of all participants, including researchers, conservation managers, and decision makers.

Figure 29. Many saproxylic species such as longhorned beetles not only need deadwood, but also sunny places with inflorescences where adults feed on pollen and nectar. Photo by B. Wermelinger.

The ecological threshold for deadwood quantities of between 20–50 m^3/ha should be reached within a network of forest stands at the landscape scale rather than aiming for a lower mean amount in all stands

Box 16. Recommendations for management

The conservation of saproxylic biodiversity depends on the quantity and quality of deadwood. Generally, a high quantity of deadwood is associated with high diversity within this habitat (different size, decay stages, tree species, position), which in turn increases its ecological value for saproxylic species. The majority of these species can be maintained with the following amounts of deadwood (Müller and Bütler 2010):

- 20–30 m^3/ha for boreal coniferous forests
- 30–40 m^3/ha for mixed-montane forests
- 30–50 m^3/ha for lowland forests

These quantitative thresholds are much higher than the general amount of deadwood available in commercial forests. It is therefore recommended to establish, at the landscape scale, a network of forest stands with deadwood quantities between 20–50 m^3/ha rather than to aim for a lower mean in all stands. Since high demanding saproxylic species require deadwood amounts above 100 m^3/ha, unmanaged forests are compulsory for their conservation. Particular attention should be given to deadwood of large diameter and in advanced decay stages as these are generally lacking in managed forests. For example, for the most dominant tree species in European temperate forests, *Fagus sylvatica*, deadwood logs above 50 cm in diameter should be maintained in the stands.

References

Bässler, C. and Müller, J. 2010. *Importance of natural disturbance for recovery of the rare polypore Antrodiella citrinella Niemela & Ryvarden. Fungal Biology 114:129–133.*

Bouget, C., Brin, A. and Brustel, H. 2011. *Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management 261:211–220.*

Brin, A., Bouget, C., Brustel, H. and Jactel, H. 2011. *Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of Insect Conservation 15:653–669.*

Brunet, J. and Isacsson, G. 2009. *Restoration of beech forest for saproxylic beetles – effects of habitat fragmentation and substrate density on species diversity and distribution. Biodiversity and Conservation 18:2387–2404.*

Buse, J. 2012. *"Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. J Insect Conserv 16:93–102.*

Dubois, G. and Vignon, V. 2008. *First results of radio-tracking of Osmoderma Eremita (Coleoptera: Cetoniidae) in French chestnut Orchards. Revue D Ecologie-La Terre Et La Vie:131–138.*

Foit, J. 2010. *Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. Agricultural and Forest Entomology 12:133–141.*

FOREST EUROPE, UNECE and FAO 2011. *State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe.*

Franc, N., Gotmark, F., Okland, B., Norden, B. and Paltto, H. 2007. *Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biological Conservation 135:86–98.*

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W. and Müller, J. 2013. *Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27(3):605–614.*

Jönsson, M., Edman, M. and Jonsson, B. 2008. *Colonization and extinction patterns of wood-decaying fungi in a boreal oldgrowth Picea abies forest. J Ecol 96:1065–1075.*

Juutilainen, K., Halme, P., Kotiranta, H. and Monkkonen, M. 2011. *Size matters in studies of dead wood and wood-inhabiting fungi. Fungal Ecology 4:342–349.*

Lassauce, A., Paillet, Y., Jactel, H. and 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.*

MacArthur, R. and Wilson, E. 1967. *The theory of island biogeography. Princeton.*

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., and Rauh, J. 2000. *Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94:199–209.*

Moning, C. and Müller, J. 2008. *Environmental key factors and their thresholds for the avifauna of temperate montane forests. Forest Ecology and Management 256:1198–1208.*

Müller, J., Bussler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J. and Zabransky, P. 2005. *Urwald relict species – Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie online 2:106–113.*

Müller, J. and 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.*

Okland, B., Bakke, A., Hagvar, S. and Kvamme, T. 1996. *What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5:75–100.*

Priewasser, K., P. Brang, H. Bachofen, H. Bugmann, and T. Wohlgemuth. 2013. *Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. European Journal of Forest Research 132:231-240.*

Ranius, T. and Jonsson, M. 2007. *Theoretical expectations for thresholds in the relationship between number of wood-living species and amount of coarse woody debris: A study case in spruce forests. Journal for Nature Conservation 15:120–130.*

Speight, M. 1989. *Saproxylic invertebrates and their conservation. In: C. o. Europe (ed.). Nature and Environment, Strasbourg. Pp. 81.*

Stokland, J., Siitonen, J. and Jonsson, B. G. 2012. *Biodiversity in dead wood.*

Stokland, J., Siitonen, J. and Jonsson, B. G. 2012. *Biodiversity in dead wood. Cambridge University Press. Pp 509.*

Tilman, D., May, R., Lehman, C. and Nowak, M. 1994. *Habitat destruction and the extinction debt. Nature 371:65–66.*

2.3 Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements

Kris Vandekerkhove, Arno Thomaes and Bengt-Gunnar Jonsson

Large quantities of deadwood and a high density of old and hollow trees (further called "habitat trees", see chapter 2.1) are characteristic elements of natural forests, especially of the old-growth phases (Harmon et al. 1986). These phases can cover up to 50 % of the area in natural forests (e.g. Meyer and Schmidt 2008) but are often absent or rare in managed forests, even in forests under close-to-nature management. Indeed, in commercial forests, only rejuvenation and mature stand phases are common, and other developmental phases are "shortcut" by the final harvest of the stand (Christensen and Emborg 1996; Bobiec 2002). Also, in selective harvests and thinnings, "defective" trees referring to these old-growth phases (hollow, dead, and languishing trees) are often removed. Yet, an important share of forest biodiversity is strictly or primarily dependent on these elements for its survival, especially saproxylic species, that is species that depend on deadwood (Stokland et al. 2012). Siitonen (2001) calculated that a decline of the total amount of coarse woody debris by over 90 % may lead to the disappearance of at least 1/4, and more probably over 1/2, of all saproxylic species. If this habitat loss is combined with habitat fragmentation, this proportion is expected to be even larger. As a result, most species dependent on old-growth elements and phases have become threatened.

> *Conservation of biodiversity in commercial forest stands is mainly a question of retention of specific elements to overcome the "harvest shortcut"*

Old-growth elements such as hollow trees and deadwood emerge on their own if the manager allows them to develop. For instance, the net build-up of deadwood in recently set-aside stands in mid-European forests (which have a low initial deadwood amount) can reach on average 1–1.5 m³/ha/year without any heavy disturbance taking place (e.g. Vandekerkhove et al. 2009). At this pace, they may reach "natural" levels of deadwood after 50 to 100 years. Some old-growth elements may take even longer to redevelop once they are gone, such as old standing decorticated trees and highly decayed large logs. Reservation and retention of these elements is essential, as "restoration" may literally take ages (see Box 17). Still, even in sites where restoration is the only option, it is important to make the effort and slowly but gradually work towards the redevelopment of old-growth elements.

Box 17. Management strategies for conservation of old-growth elements: “the triple R”

- **Reserve**: safeguard existing relics of old-growth (or other patches with high value or potential) from harvest, by conserving them in delineated areas such as forest reserves and national parks, but also in smaller delineated patches, often called “set-aside patches”, “key habitats”, or “ilôts de scénescence”.
- **Retain**: intentionally keep a number of dead, old, or other habitat trees in the stand during thinning and final harvests. Such retention trees are key elements in the managed forest “matrix”.
- **Restore**: even when none such old-growth elements are present at the moment, a policy can be applied to allow them to develop in a premeditated pattern and network.

This concept has been originally developed and applied as the “Variable Retention Harvest System” for the old-growth forests of the Pacific Northwest (Franklin et al. 1997, Lindenmayer and Franklin 2002). However, it can also be applied to temperate forests where no old-growth elements remain, but where a “management for old-growthness” is integrated in the silvicultural practice (Bauhus et al. 2009). It is mainly a question of intentionally “letting things happen”. Indeed, hollow trees and deadwood emerge by themselves if the manager allows them to develop and build up.

> *In order to be effective for the conservation of saproxylic biodiversity, these old-growth elements should be arranged in a functional network*

The successful survival of a population of a species is only possible if its reproduction and immigration are able to compensate for losses through dispersal, mortality, and predation. Saproxylic species are peculiar in that their habitat is ephemeral: indeed, hollow and dead trees are only temporarily available and may only be suitable as a habitat for certain species for an even shorter period of time (Jonsson 2012). Thus, the survival of a population of a species will depend on the ability and opportunity to colonise newly available habitat before the original habitat is lost.

> *Saproxylic organisms can be considered as populations that live on melting icebergs and that need to be able to reach the next suitable iceberg before the original one is gone*

Box 18. The theory of island biogeography and metapopulations

The **principles of island biogeography** were developed by MacArthur and Wilson (1967), who examined species diversity on larger and smaller islands, closer and farther away from the mainland.

Their basic conclusion was that species richness is higher on larger islands than on smaller ones, and higher on islands closer to the mainland than on remote ones. It is basically explained by the fact that the influx of species from the mainland (the source population) to an island decreases with the distance to be crossed. On larger islands, more habitat diversity may be present, making the island suitable for more species, and larger, less extinction-prone populations can build up.

Set-aside areas and habitat trees are for old-growth-dependent species like a network of "old-growth islands" and stepping stones in a "sea" of young and mature forest. Like in the typical island biogeography, larger habitat patches may support larger (sub-) populations for longer periods (lower extinction risk), and patches closer to large source populations also have a greater chance of being colonised.

The theory of **metapopulations** was mainly developed and described by Hanski (1999). It states that a population of a species can be composed of a number of separate subpopulations, each living in discrete patches of suitable habitat, but able to swiftly migrate from one site to another. All these subpopulations together form one so-called "metapopulation".

Individual sites and sub-populations may go extinct, but as long as the sum of interchanging subpopulations is viable, the population may survive. In some cases (for example, an archipelago with breeding cormorants), the discrete sites are stable over time. In some cases, such as for dead trees, suitable sites will disappear over time and reappear elsewhere. Some individuals (or seeds) may disperse from one site to reach these new sites by chance (e.g. fungi, see further), while others may actively search for new sites (e.g. beetles). In this case, we speak of a "habitat tracking dynamics"

As long as enough habitat patches are available and within reach for colonisation, a viable metapopulation of a species can be built-up or sustained and guarantee the survival of a species. By contrast, when establishment rates are too low, the metapopulation will decline and eventually go extinct. This process can be slow and lag behind the loss of habitat. Species may still be present although their habitat requirements are no longer met. This is called an "extinction debt" (e.g. Hanski 1999). Similarly, recolonisation of newly established suitable habitats may also be delayed because species are not able to reach them or have not yet established new populations, the so-called "immigration credit" (e.g. Jackson and Sax 2009).

The colonisation of suitable habitat by a species is the joint result of successful dispersal and successful recruitment (e.g. Jonsson et al. 2005). Dispersal is the ability to actively spread. This can be done through seeds, spores, or flying adult individuals and can be random or target-directed. Recruitment is the ability to establish and reproduce on the newly reached habitat patch. This strongly depends on the suitability of the habitat itself. Some species may be very selective, while others more indiscriminate. Success is strongly determined by species-dependent dispersal and recruitment potential.

> *A functional network of old-growth elements enables target species to develop and sustain viable metapopulations. Continuity and connectivity in time and space are essential elements*

Such a network involves smaller and larger non-intervention patches that are interconnected by "corridors" and "stepping stones" of habitat trees in the managed forest matrix. The functionality of the design is dependent on the habitat requirements and dispersal ability of species.

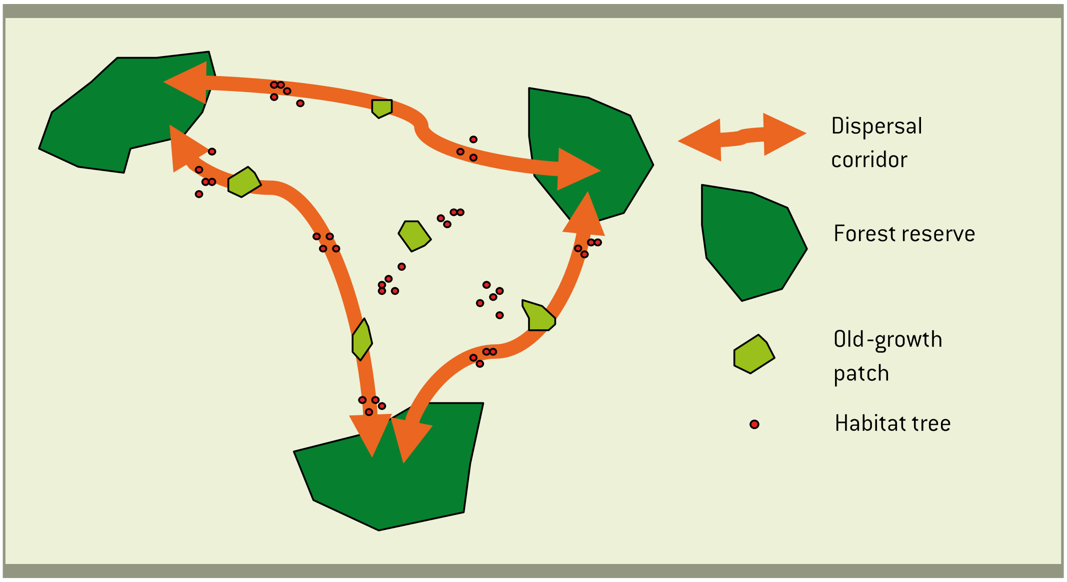


Figure 30. Schematic representation of a functional network of old-growth elements: larger set-asides (reserves >10 ha) are interconnected through set-aside patches (1–5 ha) and individual habitat trees. Areas with higher densities of habitat trees can form "corridors", but a qualitative "matrix" can also be crossed by most target species. Source: Lachat and Bütler 2007.

> *Like other organisms (e.g. vascular plants), saproxylic species can be subdivided into different life-strategies, from fast-colonising ruderals to stress-tolerant sedentary survivors*

Some species have a typical "ruderal" strategy: they invest in high reproduction and high dispersal capacities. They manage to quickly colonise newly available habitat over a long distance and produce a large number of offspring. Bark beetles are typical examples of such species. They need this strategy because time is short; they live on very short-lived habitat (such as freshly dead cambium) or must be first in order to successfully compete with other species.

On the other side of the spectrum are species that are very slow colonisers, producing little offspring, often only reproducing after several years. They have a strategy of "persistence", with long individual life spans. Typical species here are beetles living in wood mould in cavities of very old living and dead trees. The mould is very hard to digest, with little nutritious value, so development is slow, but the cavities may persist for many decades, even centuries. Many other species have an in-between strategy, with high or low dispersal abilities. They may have specific habitat requirements or may be able to survive in harsh environments where hardly any other species can survive.

> *The required configuration of a functional network of habitat is strongly dependent on these life strategies: fast colonisers require a continuous supply of (often very short-lived) habitat over larger areas; slow colonisers are often dependent on the conservation and enlargement of relict habitat islands*

As the saproxylic community is so diverse in its life strategies, the design of the network of old-growth elements should account for all these differences in order to be functional. It should guarantee continuity in time and space of suitable and renewing habitat.

We illustrate this theory with some species groups:

Forest birds are a well-studied group of good dispersers. Woodpeckers are often used as indicators for forest biodiversity. The habitat requirements of woodpecker species are indeed quite diverse. The Great Spotted Woodpecker (*Dendrocopos major*) and the Black Woodpecker (*Dryocopus martius*) are less restrictive than others; they can feed on living middle-sized trees and only need a few suitable nesting trees in their territory in order to survive. Others, such as the Middle Spotted Woodpecker (*Dendrocopos medius*), are more selective as they need large broadleaved trees with moss-rich branches to feed on (e.g. Pasinelli 2007). Finally, Three-toed (*Picoides tridactylus*) and White-backed Woodpeckers (*Dendrocopos leucotos*) are very selective in their habitat and need high densities of standing dead trees for feeding and breeding (at least 30 m^3/ha, and over 50 m^3/ha, respectively) (Angelstam et al. 2003; Bütler et al. 2004; Müller and Bütler 2010). It is clear that a few retention trees per ha may be a sufficient functional network for the first species, but the Middle Spotted Woodpecker will also need a sufficient amount of old-growth patches and a high density of old retention trees in the matrix (Pasinelli 2007; Müller et al. 2009). This was clearly illustrated in areas like Belgium and Holland, where Great Spotted and Black Woodpeckers quickly responded to improved habitat conditions, while the Middle Spotted Woodpecker took much longer but now also successfully recolonises newly suitable habitat (Vandekerkhove et al. 2011). For White-backed and Three-toed Woodpeckers, several larger old-growth patches of at least 20–100 ha are needed to form a successful breeding territory, so they are often restricted to conservation areas. Still, retention trees and key habitats in managed forest may constitute the necessary stepping stones in between the reserves in order to create a wide-scale regional functional network for a viable metapopulation of these species.

Saproxylic fungi are in principle very good dispersers; they produce millions of spores that can be spread over hundreds of kilometres (e.g. Stenlid and Gustafsson 2001). However, only a very small fraction of the spores actually spread over longer distances. The vast majority of spores fall within a few meters of the fruiting body. Given the enormous number of spores, there is still a fair chance for some spores to travel over long distances. This small fraction is crucial to establish new populations in distant localities (Stenlid and Gustafsson 2001). In contrast to birds and insects, the spores cannot actively search for suitable substrate to germinate and thus depend entirely on chance, although some may be dispersed by insects (Jonsson 2012). Moreover, even when a viable spore reaches a distant new substrate and is able to germinate, another compatible spore must reach the same substrate in order to mate and produce a dikaryotic mycelium that in its turn is able to produce fruit bodies and new spores (Stenlid and Gustafsson 2001). This process makes the development of a reproductive new mycelium at longer distances much less likely than would be expected from its reproductive and dispersal capacity. A study on the colonisation capacity of *Fomitopsis rosea* in Sweden (Edman et al. 2004) showed that even with deposition rates of 10 spores per m^2 per hour and the availability of suitable substrate, no colonisation was registered after 5 years. The mere occurrence of spores and presence of suitable substrate does not necessarily guarantee colonisation (Jonsson et al. 2005). Examples have shown that for many species of fungi that are not too specific in their substrate requirements, the actual density of suitable habitat appears sufficient to allow the steady development of new viable populations (Vandekerkhove et al. 2011). However, a number of highly selective species, such as the Bearded Tooth (*Hericium erinaceus*), are still rare or absent. They are often related to very specific, rare and transient substrates (such as wounds or rot holes of overmature trees). If their habitat is temporarily missing or the density of suitable habitat is too low, these species may easily fail to arrive in time, especially if source populations are distant (Christensen et al. 2005). Sites with a high occurrence of suitable substrate such as forest reserves, retention islands, and old tree rows not only locally increase the incidence of spores reaching suitable habitat and thus the chances of successful establishment, but also allow further development of larger local populations with a lower risk of local extinction. These new satellites may in the future develop to become new sources for further expansion (Siitonen 2001; Jonsson et al. 2005). Some species, however, appear to be restricted to large areas with amounts of deadwood over 100 m^3/ha, such as *Antrodiella citrinella* (Bässler and Müller 2010). Such species are "out of reach" for integrative management and require larger non-intervention areas.

For **saproxylic beetles**, habitat requirements and availability influence the possibility for recolonisation in much the same way as they do for saproxylic fungi, but the process is complicated by the extremely diverse dispersal potential of the different species (Jonsell et al. 1999). Some species, which are often linked with highly ephemeral habitats (such as bark beetles) have a high dispersal capacity, and are short-lived themselves. Species inhabiting stable deadwood microhabitats (such as species in wood mould) have low dispersal rates and also live longer (first described by Southwood 1977). Brunet and Isacsson (2009) found that non-

Box 19. Setting up a functional network: some 'rules of thumb'

For fauna, **minimum viable metapopulations** (to ensure population survival and maintenance of genetic variation) require an estimated minimum population size of 4,000 to 5,000 individuals (Frankham 1995). For species with multi-year lifecycles, viable metapopulations may be smaller (for species with a generation time of 5 years, an "effective breeding" population of at least about 200 individuals, corresponding with a total population of 2,000 individuals, is needed to avoid inbreeding – Hamilton, 2009).

For some beetle species such numbers may occur on a single tree, while others need at least ten to several dozens of suitable trees within the dispersal range (e.g. *Osmoderma*). For most species, distances of 1–2 km are within this range, while others (again, such as *Osmoderma* and *Lucanus*) rarely cross distances of over a few hundred meters.

Depending on the target species, the design of the network will be more diffuse (appropriate for most species) or concentrated around relict populations (appropriate for slow colonisers, often rare target species).

For many species, a typical network of old-growth elements (as described above) will work if they are not "spread too thin". A consistent network should therefore combine the following elements:

- one or several larger non-intervention areas (>10 ha, up to several hundred hectares)
- a network of "key habitats" (minimum size for set-aside patch >1 ha – Müller et al. 2012)
- a distance of 1–2 km between these set-aside areas is fine for most species but may be problematic for some (Brunet and Isacsson 2009).
- a suitable, qualitative matrix that allows good dispersal to the set-asides, but also provides habitat in itself for many species. Preserve at least 5–10 habitat trees per ha (large dead trees, old trees, hollow trees, etc.), both clusters and individual trees, and both sun-exposed and shaded trees (*for more details: see also chapter 2.1 on habitat trees*).
- for the specific group of dispersal-limited species requiring habitat continuity, look for "hotspots" and relict areas where a dense and local functional network of set-asides can be created in order to allow long-term viable (meta)populations to develop. Also take into account the relict hotspots for these species that are located outside the strict boundaries of the forest.
- and finally, be realistic. Typical "Urwald" indicator species will not settle for less; larger conservation areas will remain indispensible for their conservation. Integrative management can contribute by providing a better transit-matrix, but will not be able to harbour viable populations of these species.

Beyond the forest complex: the need for functional networks on a larger landscape scale

On a larger landscape scale, metapopulation authority Ilkka Hanski recently suggested his "third of a third" rule of thumb (Hanski 2011). He states that in a landscape where at least one-third of the area consists of suitable habitat for a "habitat specialist", loss of metapopulations due to fragmentation is not expected. Within this one-third, again one-third of the habitat should be managed (or set aside) to create ideal conditions for conservation (of the species). In this approach, he is stressing the need for some kind of aggregation of conservation efforts and set-asides to reach a sufficient amount of suitable habitat in functional "interweaving" networks at a larger landscape scale. At the same time, it is also stressed that these networks should not only cover less productive and more remote areas, but should encompass all habitat types.

selective species were not affected by isolation from old-growth forest, but for more selective or dispersal-limited species (that are therefore often rare and red-listed), there was already a significant effect after just a few hundred meters. Some species appeared unable to cross a 2 km section of unfavourable habitat. Jonsell et al. (1999) concluded that the fungi-inhabiting species they studied could colonise suitable substrate within 1 km of their point of origin, but already observed reduced colonisation over a distance of 150 m. For some species, such as *Osmoderma eremita*, dispersal over distances of over 200 m is even unlikely (Hedin et al. 2008). Thomaes (2009) calculated that stag beetle (*Lucanus cervus*) colonisation over a period of about 30 years does not exceed a radius of about 1 km. Moreover, some of these non-mobile species are very selective in their habitat. They are dependent on sites with high spatio-temporal continuity of habitat related to natural forests ("Urwaldreliktarten") and are therefore often used as indicator species for habitat continuity (Müller et al. 2005). For most saproxylic beetles, an integrative retention network approach with clusters of habitat trees and retention islands at reachable distances (of a few hundred meters) will provide a functional network to build viable populations. For the non-mobile species of wood mould, a conservation strategy should be focused on the localisation of relict populations and the conservation and extension of their habitat in the immediate surroundings (Hedin et al. 2008; Thomaes 2009). At present many of these species are mainly found in pollard trees and orchards in the open countryside (Alexander 2008), sometimes bordering the forest. Connectivity networks for these species should therefore also focus outside the strict boundaries of the forest.

A functional network of old-growth elements should be tailored to these different life strategies and therefore requires the combination of larger and smaller set-asides, intertwined with a dense enough network of habitat trees, both dead and alive

We can conclude that functional networks of retention trees and islands in managed forests are indispensable for the conservation of old-growth-related biodiversity. Integrative and segregative conservation approaches in forests are indeed complementary and essential in order to reach overall forest biodiversity conservation goals (Frank et al. 2007). A recent paper by Gossner et al. (2013) indeed concluded that the complete species richness of saproxylic species can only be guaranteed through a combination of managed forests with an ambitious retention strategy (resulting in an average deadwood amount of at least 20 m³/ha), combined with a network of strict conservation areas that function as source-populations for the managed areas and simultaneously harbour the most critical species that are restricted to "Urwald" conditions.

Box 20. From theory to practice: the network of retention trees and set-aside areas of the Sonian Forest (Flanders-Belgium).

The Sonian forest, located at the southern edge of Brussels, has a specific management history that has resulted in a very high density of old trees and forest stands, mainly beech. In the part of the forest managed by the Flemish Forest Administration alone (2,500 ha), almost 400 ha of forest stands are over 180 years old, some even more than 230 years. These stands contain high densities of very large trees, sometimes up to 20–30 trees per ha. Over the whole inventoried area, more than 7,000 trees of > 3 m girth were registered. About half of these trees occur in the old stands, and the rest are widely spread over the area as individual trees and old avenues. Amounts of deadwood in the managed stands are currently still low (< 10 m³/ha). The whole area is registered as a Special Area of Conservation (Habitat directive) and Protected Landscape. The site is a hotspot for many species groups that are related to old beech forests, such as bats, mycorrhizal and saproxylic fungi, epiphytic mosses and lichens, saproxylic hoverflies, and beetles (e.g. *Stictoleptura scutellata*, *Gnorimus nobilis*).

A functional network of retention trees and set-asides was developed in the framework of the new management plan (Brichau et al. 2013). This network contains one large strict forest reserve (over 200 ha) and 75 ha of smaller strict set-aside areas (5–10 ha each). They are interconnected by 250 ha of "senescence islands" and a dense network of retention trees comprising individuals and groups. For these trees, a dynamic approach is used: individual trees may still be cut (dangerous or exceptionally high value trees) but should be compensated by ingrowth from smaller size classes. The overall number should remain at least at the current level of 7,000, and the senescence islands should retain their "old-growth character", so no final cuts will be done there, only very selective fellings. When they eventually break down completely and lose their old-growth function, they can be reintegrated in the managed stand, but should be replaced by a new site.

Selection of the islands and retention trees is primarily based on their current occurrence, starting the selection in the remaining old stands. However, interconnection between retention areas and individual old retention trees was also taken into account.

The retention elements will be integrated in a matrix where a management of selective harvest and group fellings with retention trees will be applied that will guarantee the required ingrowth of old trees, and should also lead to higher amounts of deadwood. Dead and dying trees remain in the retention islands, and also in the other stands, at least up to the threshold of approximately 10 m³/ha.

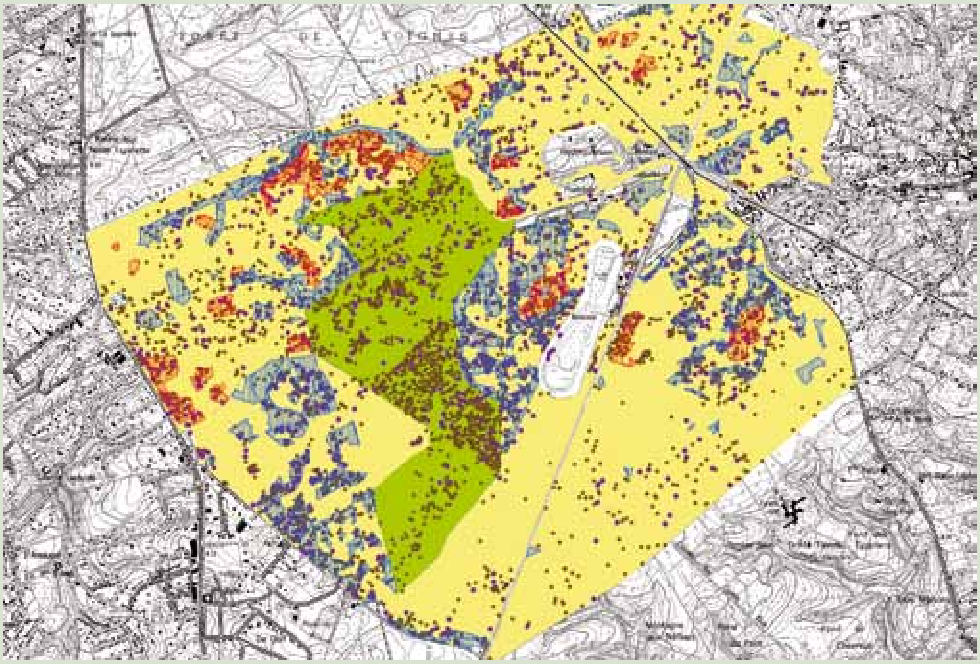


Figure 31. Part of the Sonian forest, showing the strict forest reserve (green), set aside areas (red), senescence islands (blue), and position of very large trees >3 m (brown) and > 3.50 m girth (purple).

References

Alexander, K.N.A. 2008. *The special importance of traditional orchards for invertebrate conservation, with a case study of the BAP priority species the Noble* Chafer Gnorimus nobilis. *Landscape Archaeology and Ecology 7:12–17.*

Angelstam, P.K., Bütler, R., Lazdinis, M., Mikusiński, G. and 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.*

Bässler, C. and Müller, J. 2010. *Importance of natural disturbance for recovery of the rare polypore* Antrodiella citrinella *Niemelä & Ryvarden. Fungal Biology 114:129–133.*

Bauhus, J., Puettmann, K. and Messier, C. 2009. *Silviculture for old-growth attributes. Forest Ecology and Management 258(4):525–537.*

Bobiec, A. 2002. Living stands and dead wood in the Białowieź a Forest: *suggestions for restoration management. Forest Ecology and Management 165:125–140.*

Brichau, I., Huvenne, P., Vaes, F., De Groote, M., Emmerechts, W., Vandekerkhove, K., Roelandt, B., Raes, D., Bartolomees, E., Van de Leest L., Bennekens J. 2013. *Uitgebreid bosbeheerplan Zoniënwoud. ANB, Brussels.*

Brunet, J. and Isacsson, G. 2009. *Restoration of beech forest for saproxylic beetles – effects of habitat fragmentation and substrate density on species diversity and distribution. Biodiversity and Conservation 18:2387–2404.*

Bütler, R., Angelstam, P., Ekelund, P. and Schlaepfer R. 2004. *Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-alpine forest. Biological Conservation 119:305–318.*

Christensen, M., Heilmann-Clausen, J., Walleyn, R. and Adamćik, S. 2005. *Wood-inhabiting fungi as indicators of nature value in European beech forests. In: Marchetti, M. (ed.) Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality. EFI Proceedings 51: 229–237.*

Christensen, M. and Emborg, J. 1996. *Biodiversity in natural versus managed forest in Denmark. Forest Ecology and Management 85:47–51.*

Edman, M., Kruys, N. and Jonsson, B.G. 2004. *Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on experimental logs. Ecological Applications 14:893–901.*

Frank, G., Parviainen, J.,Vandekerkhove, K., Latham, J., Schuck, A. and Little, D. (eds.). 2007. *COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW).Vienna, Austria. 211 p.*

Frankham, R. 1995. *Effective population size/adult population size ratios in wildlife: a review. Genetical Research 66:95–107.*

Franklin, J.F., Berg, D.R., Thornburgh, D.A. and Tappeiner, J.C. 1997. *Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (eds.). Creating a Forestry for the 21st century. The Science of Ecosystem Management. Island Press, Washington, DC. Pp. 111–139.*

Gossner, M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. and Müller J. 2013. *Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27(3):605–614.*

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.John Wiley and Sons.*

Hanski, I. 1999. *Metapopulation ecology. Oxford University Press. 313 p.*

Hanski, I. 2011. *Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio 40:248–255.*

Hamilton, W. D. 2009. *Population Genetics. Wiley-Blackwell, Chichester UK.*

Harmon, 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. and Cummins, K.W. 1986. *Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.*

Hedin, J., Ranius, T., Nilsson, S. and Smith, H. 2008. *Restricted dispersal in a flying beetle assessed by telemetry. Biodiversity Conservation 17:675–684.*

Jackson, S.T. and Sax, D.F. 2009. *Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology and Evolution 25:153–160.*

Jonsell, M., Norlander, G. and Jonsson, M. 1999. *Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3:145–161.*

Jonsson, B. G., Kruys, N. and Ranius, T. 2005. *Ecology of species living on dead wood – lessons for dead wood management. Silva Fennica 39:289–309.*

Jonsson, B.G. 2012. *Population dynamics and evolutionary strategies. In: Stokland, J.N., Siitonen, J. and Jonsson, B.G. (eds.) Biodiversity in Dead Wood (Ecology, Biodiversity and Conservation). Cambridge University Press.*

Lachat, T. and Bütler, R. 2007. *Gestion des vieux arbres et du bois mort; îlots de sénescence, arbres-habitat et métapopulations saproxyliques. Report WSL and EPFL, Lausanne for OFEV.*

Lindenmayer, D.B. and Franklin, J.F. 2002. *Conserving Forest Biodiversity. A Comprehensive Multiscaled Approach. Island Press, Washington DC. 351 p.*

MacArthur, R. H. and Wilson, E. O. 1967. *The Theory of Island Biogeography. Princeton University Press, New York.*

Meyer, P. and Schmidt, M. 2008. *Aspekte der Biodiversität von Buchenwäldern – Konsequenzen für eine naturnahe Bewirtschaftung. Beiträge aus der NW-FVA, Band 3:159–192.*

Müller, J., Pöllath, J, Moshammer, R. and Schröder, B. 2009. *Predicting the occurrence of Middle Spotted Woodpecker Dendrocopos medius on a regional scale, using forest inventory data. Forest Ecology and Management 257:502–509.*

Müller, J., Büssler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J. and Zabransky, P. 2005. *Urwald relict species– Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2: 106–113.*

Müller, J. and 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.*

Müller, M., Lachat, T. and Bütler, R. 2012. *Wie gross sollen altholzinseln sein? Schweizerisches Zeitschrift für Forstwesen 163:49–56.*

Pasinelli, G. 2007. *Nest site selection in middle and great spotted woodpeckers* Dendrocopos medius *and* D. major*: implications for forest management and conservation. Biodiversity and Conservation 16:1283–1298.*

Pianka, E.R. 1970. *On r and K selection. American Naturalist 104:592–597*

Siitonen, J. 2001. *Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49:11-41.*

Southwood, T. 1977. *Habitat, the Templet for Ecological Strategies? Journal of Animal Ecology 46: 336–365*

Stenlid, J. and Gustafsson, M. 2001. *Are rare wood fungi threatened by inability to spread ? Ecological Bulletins 49:85–91.*

Stokland, J.N., Siitonen, J. and Jonsson, B.G. (eds.) 2012. *Biodiversity in Dead Wood (Ecology, Biodiversity and Conservation). Cambridge University Press.*

Thomaes, A. 2009. *A protection strategy for the stag beetle (Lucanus cervus, (L., 1758), Lucanidae) based on habitat requirements and colonisation capacity. In : Buse, J., Alexander, K., Ranius, T. and Assmann, T. (eds.). Saproxylic Beetles – their role and diversity in European woodland and tree habitats. Proceedings of the 5th Symposium and Workshop on the Conservation of Saproxylic Beetles. Pensoft Publishers. Pp. 149–160.*

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. and Verschelde, P. 2009. *When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-West- and Central Europe. Forest Ecology and Management 258:425–435.*

Vandekerkhove, K., De Keersmaeker, L., Walleyn, R., Köhler, F., Crevecoeur, L., Govaere, L., Thomaes, A. and Verheyen K. 2011. *Reappearance of old growth elements in lowland woodlands in northern Belgium: do the associated species follow? Silva Fennica 45(5): 909-936.*

2.4 Natural disturbances and forest dynamics in temperate forests of Europe

Thomas A. Nagel, Miroslav Svoboda and Momchil Panayotov

Forest ecosystems are dynamic; their composition and structure are in a continuous state of change. These changes are driven by a variety of processes that operate at different spatial and temporal scales, ranging from small-scale competitive interactions to millennial scale changes in climate. One of the most important drivers of forest dynamics is natural disturbance, the subject of this chapter. All forest ecosystems are influenced by disturbances, whether by occasional death of canopy trees caused by pathogens, by widespread low severity mortality caused by drought or herbivory, or by severe stand-replacing fires, blowdowns, or insect outbreaks, to name a few. A key concept in the field of ecology that emerged in the last century was the recognition that plant community structure and composition are not in equilibrium, but are dynamic due to the influence of natural disturbances (Pickett and White 1985).

> *The defining structural and compositional patterns of a given forest are largely the result of a particular natural disturbance regime, characterized by the different types of disturbances in a forested ecosystem and the frequency, severity, and size distribution of these disturbances*

For example, in many temperate forests worldwide, where fires and other stand replacing disturbances rarely occur, forest dynamics are typically driven by relatively continuous, small-scale mortality of canopy trees (i.e. gap dynamics) that leads to finely structured, uneven-aged stands dominated by late successional, shade tolerant species. At the opposite extreme, some boreal forests experience a regime of high-severity stand-replacing fires, leading to a patchwork of forest stands at different successional stages on a landscape. Such examples, however, are oversimplifications because natural disturbance regimes in a given region are often complex and vary in space and time. In other words, the temperate forest in the example above may occasionally experience moderate severity mortality from storms or heavy snow, and parts of the boreal forest may go through long periods without severe disturbance that are driven by single-tree mortality. In addition to variation in the timing and severity of disturbances, further complexity is imparted by landscape heterogeneity, feedbacks linked to current vegetation and prior disturbances, and interactions among multiple disturbance types. Understanding natural disturbance regimes and the complexity they impart on forest ecosystems has important implications for integrative forestry that blends timber production and biodiversity conservation. A central idea is that silviculture practices that emulate natural disturbances are likely to maintain native biodiversity (Hunter 1999). The underlying assumption is that all species living in a given forest ecosystem evolved under the natural structural and compositional variability created by a given disturbance regime, such that maintaining these conditions via forest management will safeguard against biodiversity loss. This range of historical variation in natural ecosystem patterns and processes is often referred to as "Natural or Historical Range of Variation" (NRV or HRV) (Landres et al. 1999).

A sound understanding of how natural disturbance processes influence forest structure and composition at different spatial and temporal scales is key for successful conservation of biodiversity in integrative forestry

In the following section, we briefly overview the disturbance regimes in two important forest types in the temperate zone of Europe, namely, beech dominated (including mixed beech-fir forests) and Norway spruce forests. We focus on these two forest communities not only because they cover a large part of the European landscape, but also because old-growth conditions still exist for these forest types in the region and provide necessary reference conditions to study natural disturbances and forest dynamics. It is important to note, however, that existing old-growth remnants of these forest types mainly occur in relatively remote regions of the Dinaric Mountains, Carpathian Mountains, and the eastern Alps, and may not represent the broader range of disturbance patterns found in these forest types over the entire European region. As such, the discussion that follows is mainly relevant for the broader Central and Southeastern regions of Europe where these forest types occur.

Despite a rich history of important research in these old-growth remnants during the 20th century, disturbances, especially intermediate and high severity events, received relatively little attention. Early studies mainly centered on detailed descriptions of stand structure and phytosociological descriptions of plant communities over space. The conceptual model that emerged from this work suggested that relatively continuous mortality of single canopy trees (small-scale gap dynamics) maintained an equilibrium structure and composition at stand scales. Moreover, compositional heterogeneity across stands was mainly attributed to variation in site conditions rather than disturbance history. More recently, many studies have investigated the role of natural disturbance processes in more detail in these remaining old-growth remnants. As a result, traditional views have gradually expanded to include a more non-equilibrium view of forest ecosystems due to natural disturbances.

In contrast to traditional conceptual models of natural forest dynamics that emphasized stability, ecologists and foresters now accept a non-equilibrium view that highlights the role of natural disturbance as an important driver of forest dynamics

Pure beech and mixed beech-conifer communities cover much of the forested landscape in mountain regions of Europe. Because large high severity disturbances are very rare or absent in this region, relatively continuous mortality of large old canopy trees is an important driver of stand dynamics. Old trees may die from a number of different, often interacting processes, such as pathogens that cause wood and root decay, moderate intensity wind, heavy snow, and drought. This type of mortality is often referred to as “endogenous” or “background” mortality because it is linked to tree life span (Figure 32), even if the ultimate event that kills the tree is “exogenous”, that is, an external process linked to abiotic and biotic factors, such as wind, snow, insects, and pathogens.

Figure 32. Standing dead fir and elm trees in the Perućica forest reserve, an old-growth mixed beech-fir forest in Bosnia and Herzegovina. This type of endogenous “background” mortality of old canopy trees leads to finely structured, uneven-aged stands typical of most temperate forests. Photo by T. Nagel.

While there is no doubt that background tree mortality plays a central role in the dynamics of these forests, recent studies highlight that it may not account for all the variability in forest structure and composition found in old-growth stands. For example, several studies that have examined characteristics of canopy gaps reveal that most canopy openings encountered in a stand are small and formed by the death or one or two trees (i.e. background mortality), yet larger openings several thousand square meters in size with multiple snapped and uprooted gapmakers are also encountered (Drösser and von Lüpke 2005, Nagel and Svoboda 2008, Kucbel et al. 2010). Studies that use tree-ring evidence to reconstruct patterns of disturbance several centuries past support findings from gap studies (Splechtna et al. 2005, Nagel et al. 2007, Firm et al. 2009, Šamonil et al. 2012). First, they show that tree mortality is variable in time; some decades experience higher rates of disturbance than others. Second, while most decades indicate low severity disturbance (i.e. gap dynamics or background mortality), periodic peaks in disturbance are sometimes observed. Large canopy gaps and disturbance peaks found in tree-ring reconstructions are likely related to strong winds associated with storm events, although heavy snow or ice accumulation could also be responsible. To summarize, while no studies have found evidence of high-severity stand replacing disturbances over extensive areas in beech dominated forests, periodic disturbances that create intermediate levels of canopy damage likely play an important role in many forests.

> *Direct observations of intermediate severity damage following storms in temperate old-growth forests show complex patterns of mortality, ranging from scattered individual gaps to small blowdown patches*

Such events may have an important influence on tree regeneration (Nagel and Diaci 2006). For example, scattered gaps created in a stand will increase the amount of diffuse light throughout the understory of a stand, which may lead to increased recruitment of shade tolerant species, such as beech (Figure 33). In contrast, larger openings may facilitate recruitment of less shade tolerant species that coexist in these stands, such as maple, ash, and elm, especially in areas where advance regeneration of shade tolerant species is less abundant (Nagel et al. 2010).

Unlike the beech dominated forests described above, naturally occurring Norway spruce forests in the mountains of Central and Southeastern Europe have experienced widespread stand replacing windthrow and bark beetle outbreaks in recent decades (Figure 34). These disturbances raised considerable controversy because the traditional view holds that such events are not part of the natural disturbance regime in the region, but rather an outcome of previous management practices that created homogeneous (i.e. forests comprised of single species of similar size) areas of Norway spruce. Because homogeneous forests are generally

Figure 33. Typical damage patterns from recent intermediate severity wind disturbances in two beech dominated forest reserves in Slovenia. Photos by T. Nagel.

Figure 34. Windthrow followed by bark beetle outbreak in a Norway spruce forest in the Bistrishko braniste reserve, Bulgaria. The damaged forest was composed of trees with similar size and age (100–130 years). Photo by M. Panayotov.

Figure 35. Widespread bark beetle mortality in Norway spruce forests in Šumava National Park and the Bavarian Forest spanning the Czech Republic and German border. Approximately 10,000 ha of forest were killed between 1994 and 2012. Photo by Z. Krenova.

more susceptible to high severity disturbances, particularly biotic disturbance agents such as pathogens or insect outbreaks, the recent events mentioned above may be a result of land use practices centuries in the past that promoted such structures. An alternative explanation is that large areas of homogeneous spruce forests developed following naturally occurring stand-replacing disturbances caused by storms, bark beetle outbreaks, or interactions between the two disturbance types.

Are widespread stand replacing disturbances part of the natural range of disturbance variability in Norway Spruce forests or do they reflect the legacy of past management? Are such events novel processes due to climate change? Recent research provides some insight into these questions. Dendroecological research in both the Tatra Mountains and the Bohemian Forest, two regions that experienced widespread high-severity disturbances from windstorms and bark beetle outbreaks in recent decades, suggests that high-severity disturbances periodically occurred in these areas during the past two centuries (Zielonka et al. 2009, Svoboda et al. 2012). In the Tatra region, unusually intense "bora" winds create conditions for repeat stand-replacing disturbances, while data from historical archives suggest both storms and bark beetles are important disturbance agents in the Bohemian region. Other dendroecological studies in primary Norway spruce stands highlight the variability in historical disturbance regimes over the broader region of Central and Southeastern Europe. For example, Szewczyk et al. (2011) documented a history of small-scale gap disturbances in the northwest Carpathians, while Panayotov et al. (2011) reconstructed a wide range of disturbances in the Rila Mountains of Bulgaria, spanning small-scale gap dynamics to windthrow patches between 1 and 10 ha in size.

Implementing practical forestry measures that emulate natural disturbance processes is challenging and often fraught with difficulties

In the following section, we briefly touch upon general implications for forest management regardless of the forest type or disturbance regime. For simplification, it is useful to break this discussion down into landscape, stand, and tree scale decisions (e.g. Hunter 1999).

At the landscape and stand level, the severity, frequency, and spatial pattern of disturbances can provide a framework for forestry decisions. From a practical forestry point of view, species composition, rotation period, silvicultural system, spatial and temporal arrangement of regeneration, stand and landscape level age structure, and annual harvest are all potential measures that could be used to mimic the landscape level reference conditions. A major obstacle is the lack of landscape scale reference conditions where disturbance processes and forest dynamics can be studied in Central Europe. Nevertheless, recent research shows that spatial and temporal variability in disturbance processes is greater than that suggested by traditional models. This would imply that landscape scale management should not only mimic late successional forest structure and composition, but successional stages and structural complexity that arise from moderate to high severity disturbances as well. The proportion of these different stages on the landscape mosaic, however, would require careful consideration. Forestry decisions should try to mimic landscape-level variability based on clearly defined goals and existing reference conditions for a given area. The choice of rotation period together with the regeneration system and annual harvest rate could be used to assure that the desired landscape-level stand age structure will be maintained (Hunter 1999). Maintaining late successional conditions would require mimicking low and occasional intermediate severity disturbances accompanied by an appropriate regeneration system with sufficient recovery periods between individual interventions. Maintaining early successional stages may be as simple as incorporating naturally disturbed habitats into forest management without the post disturbance treatments that are conventionally applied.

Forest management at the landscape scale should not only mimic or restore late successional forest structural and compositional patterns, but also successional stages and structural complexity that arise from higher severity disturbances. The latter goal, for example, could be partly achieved by simply refraining from salvage logging after high severity disturbances on some sites

At the stand and tree level, biological legacies of natural disturbances are an important focus of natural disturbance based management, acting as critical habitats for many organisms in forested landscapes. Management of veteran trees and deadwood are well known examples of how forestry decisions can emulate late-successional reference conditions. For example, maintaining medium and large sized standing and lying logs in various stages of decay in both late-successional (low light) and early successional (high light) habitats is crucial for long term persistence of a variety of saproxylic organisms. Deadwood on the forest floor also acts as an important regeneration substrate for trees on some sites. Retaining a certain amount of green trees, snags, and uprooted and broken trees are thus key practices following natural disturbance in managed forests. Incorporating more complex spatial and temporal patterns of harvesting that go beyond strict silvicultural systems (e.g. single tree selection, group selection, or shelterwood systems) are also needed to emulate the highly variable mortality patterns that often result from natural disturbances.

> *Understanding the historic range of natural disturbance variability is necessary for gauging the influence of climate change on disturbance regimes and forest dynamics*

Thus far, we have focused mainly on historical patterns of natural disturbances and how they can serve as a reference for contemporary forest management. However, it is critical to emphasize that management based on historical reference conditions could become less relevant if climate change predictions prove true (Millar et al. 2007). Climate change is likely to not only cause shifts in forest vegetation, but also future disturbance regimes (Dale et al. 2001). One example that is particularly relevant for Norway spruce forests in the region is that warmer summers may permit several annual generations of bark beetles (Wermelinger 2004), potentially facilitating more frequent and severe outbreaks, especially when coupled with drought weakened trees. Despite potential climate driven changes, a sound understanding of the historical range of disturbance variability is needed to gauge future changes. Furthermore, management systems that enhance structural complexity and increase species diversity over stand and landscape scales should foster adaptation to climate change, although monitoring, adaptive management, and embracing a non-equilibrium view of disturbance regimes due to climate instability will be key for success (Mori 2011).

References

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., and Wotton, B. M. 2001. *Climate change and forest disturbances. Bioscience 51:723–734.*

Drösser, L. and von Lüpke, B. 2005. *Canopy gaps in two virgin beech forest reserves in Slovakia. Journal of Forest Science 51:446–457.*

Firm, D., Nagel, T.A. and Diaci, J. 2009. *Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management 257:1893–1901.*

Hunter Jr., M.L. 1999. *Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK. 698 p.*

Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J. and Klimas, V. 2010. *Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. European Journal of Forest Research 129:249–259.*

Landres, P. B., Morgan, P. and Swanson, F.J. 1999. *Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.*

Millar, C. I., Stephenson, N. L. and Stephens, S. L. 2007. *Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17:2145–2151.*

Mori, A. S. 2011. *Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48:280–292.*

Nagel, T. A. and Diaci, J. 2006. *Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Canadian Journal of Forest Research 36:629–638.*

Nagel, T. A., Levanic, T. and Diaci, J. 2007. *A dendroecological reconstruction of disturbance in an old- growth Fagus-Abies forest in Slovenia. Annals of Forest Science 64:891–897.*

Nagel, T. A. and Svoboda, M. 2008. *Gap disturbance regime in an old-growth Fagus-Abies forest in the Dinaric Mountains, Bosnia-Herzegovina. Canadian Journal of Forest Research 38:2728–2737.*

Nagel, T. A., Svoboda, M. and Rugani, T. 2010. *Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. Plant Ecology 208:307–318.*

Panayotov, M., Kulakowski, D., Dos Santos, L. L., and Bebi, P. 2011. *Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. Forest Ecology and Management 262:470–481.*

Pickett, S. T. A. and White, P. S. 1985. *The ecology of natural disturbance and patch dynamics. Academic Press, New York.*

Šamonil, P., Dolezelova, P., Vasickova, I., Adam, D., Valtera, M., Kral, D.J. and Sebkova, B. 2012. *Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. Journal of Vegetation Science.* In press.

Splechtna, B. E., Gratzer, G. and Black, B. A. 2005. *Disturbance history of a European old-growth mixed-species forest – A spatial dendro-ecological analysis. Journal of Vegetation Science 16:511–522.*

Svoboda, M., Janda, P., Nagel, T., Fraver, A. S., Rejzek, J. and Bace, R. 2012. *Disturbance history of an old-growth sub-alpine Picea abies stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science 23:86–97.*

Szewczyk, J., Szwagrzyk, J. and Muter, E. 2011. *Tree growth and disturbance dynamics in old-growth subalpine spruce forests of the Western Carpathians. Canadian Journal of Forest Research 41:938–944.*

Wermelinger, B. 2004. *Ecology and management of the spruce bark beetle Ips typographus – a review of recent research. Forest Ecology and Management 202:67–82.*

Zielonka, T., J. Holeksa, P. Fleischer, and P. Kapusta. 2009. *A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. Journal of Vegetation Science 21:31-42.*

2.5 Conservation and management of specialised species: sustaining legacies of natural forests and cultural landscapes

Per Angelstam, Marine Elbakidze and Asko Lõhmus

There is a need to sustain legacies of both natural forests and cultural landscapes for the conservation of specialised species that are not provided with habitat in landscapes managed to maximise the production of wood, fibre, food, and energy

After a brief review of European landscape history, we conclude that maintenance of specialised species requires consideration of legacies of both naturally dynamic forests and pre-industrial cultural landscapes. Next, we propose the need for conservation, management, and restoration in the context of intensified use of forests and abandonment of cultural woodlands across entire landscapes. Two key issues include gathering knowledge about performance targets regarding how much habitat different species need and developing knowledge-based dialogue. While the focus is on the European continent, the arguments in this chapter are generally applicable.

Understanding landscape history is critical for the conservation of natural and cultural biodiversity, i.e. species, habitats, and processes in natural forests and cultural landscapes

The European continent was once dominated by naturally dynamic forests. During Millennia, however, most of Europe's forests and woodlands were gradually transformed into cultural landscapes with traditional agro-silvo-pastural land use systems linked to village systems with integrated use of wood and non-wood products (Box 21). Along in the gradient from the centre to the periphery of a traditional village, there was an increased amount of habitat for species adapted to natural riparian, coastal, and mountain grassland ecosystems in the village's fields, meadows, pastures, and grazed forests. Many tree-inhabiting old forest species found habitat in large remnant trees, pollards, and coppice trees in the wooded grasslands of the infields. Other natural forest species often found habitat in the outfield woodlands.

However, the advent of more intensive forestry and agriculture reduced both natural forests and cultural woodlands. To maintain specialised species, the focus shifted to creating protected areas in forests and wetlands with free development, as well as agri-environmental schemes aimed at maintaining cultural landscapes. However, to create functional habitat networks of both protected areas (such as Natura 2000) and specially managed areas, a landscape perspective is necessary. This means considering the quality, size, and total area of patches with high conservation value and the extent and hostility of the areas in between these patches on the one hand, and encouraging collaboration among actors representing different land use and land covers on the other. To conclude, conservation of biodiversity in landscapes involves visions of both natural forest dynamics and traditional management of cultural landscapes, albeit with different proportions depending on the landscape history.

Box 21. The traditional village system

Natural forests and woodlands were shaped by traditional management long before the development of industrial forestry and intensive agriculture. A significant proportion of the world's forests and woodlands are still managed by local and indigenous communities. Such cultural landscapes are usually based on a traditional village system with centre-periphery zoning, from houses, gardens, and fields to mowed and grazed grasslands to forests (i.e. the ancient system of *domus, hortus, ager, saltus,* and *silva* (e.g. Elbakidze and Angelstam 2007). Landscapes located in the periphery of economic development often host remnants of both near-natural ecosystems and traditional agro-silvo-pastural land use systems (Angelstam et al. 2013a). The species assemblages in a local forest and woodland landscape may thus have both natural forest and cultural landscape origins.

> *The maintenance of species and landscapes with forests, woodlands, and trees requires consideration of legacies of both naturally dynamic forests and pre-industrial cultural landscapes*

Maintaining species in viable populations requires a range of disturbance regimes to sustain the heterogeneity in ecosystem habitats and processes that support different species. The term naturalness captures the need to understand the extent to which managed landscapes differ in terms of species, habitats, and processes. Such disturbances include both natural abiotic and biotic as well as anthropogenic factors (Table 7). As advocated within the natural disturbance regime paradigm for close-to-nature forest management, the management regimes chosen for different forest environments must correspond with the ecological past of different forest types (Angelstam 2006). This poses new challenges to silviculture (Puettmann 2010).

Figure 36. A near-natural forest landscape in the Hungarian Börzsöny Mountains after windfall (left) and forest fire in an open Scots pine forest on sandy sediments in NW Russia (right). Photos by Per Angelstam.

Three main natural forest disturbance regimes are characteristic in forest ecosystems (e.g. Angelstam and Kuuluvainen 2004): (1) succession after stand-replacing disturbance from young forest to old-growth with shade-intolerant species in the beginning and shade tolerant species later on, (2) cohort dynamics on dry sites, and (3) gap dynamics in moist and wet forest (Figure 36). For the open woodland conditions typical of cultural landscapes, natural analogues can be seen in ecosystems where tree growth is limited by climate, soils, or complex relationships between abiotic or herbivore-induced disturbance and vegetation response (Figure 36).

Table 7. Examples of common abiotic, biotic, and anthropogenic disturbances that affect the maintenance of natural and cultural biodiversity.

Disturbances	Natural biodiversity vision	Cultural biodiversity vision
Wind	Uprooting creates deadwood, bare soil, and special microhabitats	Deadwood is often removed and used as fuel
Flooding	Natural stream dynamics creates important aquatic and riparian habitat	Irrigation and draining often occur, as well as active flooding to benefit productivity of meadows and pastures
Fire	Larger patches, lower frequency	Smaller patches, higher frequency
Large herbivores	Browsers dominant	Grazers dominant
Insects and fungi	Important natural disturbances	Not important
Human activity	Not important, unless restoration measures are needed	Vital, includes mowing, pasturing, pollarding, coppicing, shredding, etc.

Figure 37. A traditional pre-industrial cultural landscape in the Carpathian Mountains in Ukraine. Usually centred around a village street with farm houses, traditional villages have a characteristic zonation from the centre to the periphery. These zones include: (1) built-up area with farm houses, a church, and a local administration building; (2) vegetable and fruit gardens; (3) fields; (4) hay meadows; (5) pastures; and (6) forests, all of which satisfy different needs of land users. Photo by Per Angelstam.

Traditional pre-industrial management of grasslands, woodlands, and forests by grazing, mowing, and tree management at different intensities produced a structurally diverse landscape (Figure 37). For example, mountain pastures with diverse and rich flora, hay meadows, small arable fields with hedgerows, and other structural elements are the result of centuries of traditional management of the land. Species-rich and structurally diverse biotopes along fences and stone walls also provide habitats for forest species. Extensive grassland management favours light-demanding vascular plants and associated animal species, and traditional management of arable lands creates favourable conditions for species depending on open space and field-forest edges (Bezák and Halada 2010).

> *Intensified use of forests and abandonment of cultural woodlands are two processes that are currently taking place simultaneously in European landscapes. This involves both challenges and opportunities for the conservation of both natural forest species and culture followers*

Box 22. Natural forest and cultural landscape legacies – Carpathian Mountains as an example

The Carpathian Mountains host Europe's most extensive tracts of mountain forest, the largest remaining natural mountain beech and beech/fir forest ecosystems, and areas of old-growth forest remnants (Angelstam et al. 2013a, Pâtru-Stupariu et al. 2013). There are remnants of forests dominated by gap dynamics in shade-tolerant beech and other broad-leaved forest, succession after windfall, ice storms, and riparian cohort dynamics in flood-plain forests. Furthermore, the Carpathians contain some of the most intact, wild river systems in Europe. Many of the last flooded forests are found in the valleys of the Carpathians. Due to the occurrence of elements of naturally dynamic forests, such as large old trees, deadwood, and slow-growing trees in cultural landscapes, forest species can occur outside areas normally characterised as natural forest, e.g. in wooded grassland with trees managed to provide leaf fodder, fruit, and material for tools.

As a consequence, the region hosts populations of specialised species as well as area-demanding large carnivores and herbivores that have become locally extinct or very rare elsewhere in Europe. Additionally, there are many endemic species. The Carpathian Mountains form a vital corridor for the dispersal of plants and animals between forests and woodlands in Europe's North and South.

The natural forest and cultural landscapes in Europe are presently developing in different directions. Natural forest biodiversity trends are following a diversity of trajectories, including (1) protection in reserves and national parks, (2) intensification of forest harvesting, (3) emerging ideas of close-to-nature silviculture, and (4) recreational and tourist use of forests. Cultural landscapes are developing along three different trajectories and (1) often remain with traditional use outside the EU, (2) change due to intensive agriculture and urbanization, and (3) are abandoned and afforested as a consequence of depopulation of rural areas within the EU. These trajectories provide better opportunities for rewilding by landscape restoration than to sustain those specialised species that were favoured by the pre-industrial cultural landscape. To maintain cultural biodiversity, the methods employed in the pre-industrial cultural landscape, or their analogues, need to be considered. Without a deep understanding of local knowledge and perceptions of landscape, it will be difficult to combine local and scientific knowledge into landscape management for biodiversity conservation.

Changes in the conditions for land use, such as reduction of subsidies and the reduced profitability of primary production in cultural landscapes, provide opportunity for rewilding as a means of restoring the level of naturalness of the landscape (Bauer et al. 2009). The term rewilding appeared in the 1990s as the idea of large-scale conservation aimed at restoring and protecting core areas, providing connectivity among them, and protecting or reintroducing top predators and keystone species (e.g., Soulé and Noss 1998). Reintroduction of large herbivores and carnivores as well as prescribed burning and stream restoration are good examples of strategies to initiate uninfluenced processes while excluding long-lasting human interventions aimed at sustaining ecological processes and recovery of natural forest legacies in terms of habitats and the associated species. Based on a study of public attitudes towards nature and rewilding processes in Switzerland, Bauer et al. (2009) recommended initial assessment of the attitudes among involved stakeholders towards nature and rewilding and a participatory process when managing landscape change. Even in the UK, which has a long history of land use, Carver (2007) concluded that a core of significant wild lands remain that can be built on to create a spatially continuous network of wilder areas for the benefit of people and wildlife. Navarro and Pereira (2012) thus argued that rewilding should be recognized by policy-makers as one of the possible land management options for rural development, including tourism, in Europe, particularly in marginal areas.

There are two main complementary strategies to sustain the legacies of cultural biodiversity in wooded landscapes dominated by modern land use. The first is to support surviving social systems or the conservation community in order to continue historical land use. This strategy is limited by the funds available, public interest, and people's ability to create new products or markets for traditional goods. For example, the plant conservation value of the once widespread Fennoscandian wooded meadows (a priority habitat in the EU) depends on mowing, which has been locally reinforced by allocating conservation funds to special managed reserves (Sammul et al. 2008). Research has provided an evidence base to decide whether overgrown sites should be restored as wooded meadows or preserved as future broad-leaved forests with ancient trees (Palo et al. 2013). In Northern Europe, small patches of a range of cultural habitats in managed forests can be protected as "key habitats" (Timonen et al. 2010). Similar approaches exist for conserving the biodiversity of ponds and culturally significant groves, but in most cases only a part of the historical diversity can be sustained.

The second strategy uses and develops the opportunities provided by modern land use. Clear-cuts, road verges, drainage ditches, power line rights-of-way, military training grounds, and mining areas serve as examples of forest openings that are created and subjected to various disturbance regimes without special conservation costs. Clear-cuts with soil scarification could provide future habitats for several threatened grassland plants (Pykälä 2004), while retaining selected important structures during clear-cutting has led to the global approach of retention forestry, enhancing, inter alia, habitats for many early-successional species (Gustafsson et al. 2012). The potential of such emerging "novel habitats" is a priority of conservation research.

> *Knowledge about reference landscapes for biodiversity can be gained by studying remnants of natural and cultural landscapes as well as landscape history*

Understanding both natural and cultural legacies of the past in reference landscapes is an important starting point for the maintenance of biodiversity. Key research questions about ecosystems include what processes lead to which habitats and how much thereof species need. Regarding social systems, regionally adapted approaches to governance and territorial planning need to be developed and applied.

Whyte (1998) concluded that areas of “retardation” and tradition are still concentrated in Northern Europe, the Atlantic periphery, and mountain areas of Central Europe, the Mediterranean, and the Caucasus. Economic remoteness in Europe thus has both east-west and lowland-mountain dimensions. In the European continent’s mountain ecoregions, the co-occurrence of these two dimensions explains why such regions are hotspots for natural and cultural biodiversity (Box 22) and thus important both for conservation in situ and as references for biodiversity restoration elsewhere.

Maintaining natural and cultural biodiversity requires management of species, habitats, and processes across entire landscapes

Maintaining biodiversity is an integral part of the general normative challenge of sustainability. Designing land management systems that emulate historical natural and cultural landscape disturbance regimes is a major challenge that requires the collaboration of private, public, and civic sectors. Maintaining and restoring natural and social capital of village systems and functional networks of protected areas as well as implementing policies of sustainable management of land and water are crucial. The European continent thus forms a quasi-experiment with stark contrasts among countries and regions regarding natural and cultural biodiversity. Europe can be seen as a landscape-scale laboratory for systematic studies of interactions between ecological and social systems to support the development of an integrated landscape approach to biodiversity conservation and cultural heritage (Box 23, Axelsson et al. 2011).

Box 23. Recommendations for an integrated landscape approach to maintain biodiversity and ecological sustainability

The term integrated landscape approach captures the need to consider a larger functional geographical area when addressing sustainability, including ecological sustainability, and to include both social and ecological systems and their interactions. Deconstructing the landscape approach, Axelsson et al. (2011) identified five core features: (1) a focus on a large area of tens of thousands, up to millions, of hectares depending on the sustainability issues; (2) collaboration among multi-level partners representing all societal sectors and fields of interest; (3) a commitment to sustainable development and an analytic approach to address sustainability; (4) production of new knowledge to identify useful traditional knowledge for socially robust solutions; and (5) sharing of knowledge and experience.

How much is enough? Performance targets as norms for assessment of sustainability

The introduction of sustained yield forest management and intensive agriculture generally lead to a reduction in deadwood, functional connectivity, and intact areas of natural woodland and cultural landscapes. A major challenge is to identify, and use as guidelines for management, evidence-based performance targets for biodiversity conservation rather than negotiated targets such as forest certification, or the state of the environment in already managed and altered landscapes. It is also critically important that land management becomes spatially explicit at several spatial scales ranging from trees and stands to landscapes and regions. Additionally, participatory conservation management planning with societal arenas for combining top-down planning with bottom-up implementation is crucial.

While various lists of indicators of sustainable forest and other forms of land management have been elaborated, their comprehensive monitoring and comparing with performance targets describing the desirable states remains a challenge. For considering the role of ecosystems as sustainable providers of natural capital, the naturalness concept is useful for defining benchmarks. For the conservation of species, non-linear responses of species to habitat loss can be used to formulate performance targets (e.g. Villard and Jonsson 2009, Törnblom et al. 2011). To define how much habitat is enough for the persistence of species in the long term, available knowledge can be used to formulate evidence-based norms that define the amount of forest properties adequate for species populations (Angelstam et al. 2013b). A key issue is that there are large differences in the amount of different habitats in landscapes with different histories. A good example is that the amount of downed deadwood found in naturally dynamic forest is much higher than that found in today's managed forested landscapes, which explains why specialised focal species are present in the former but absent in the latter (e.g. Roberge et al. 2008).

Informed dialogue that aims at enhancing stakeholder collaboration in landscapes and regions is a prerequisite for successful conservation of natural capital. Biosphere Reserves, Model Forests, and LTSER are examples of concepts that promote this

There are several approaches to establish dialogue among actors. Ideally, adaptive management teams should be formed whereby researchers, land managers, and policy-makers share decisions and responsibilities toward the success or failure of the strategy they jointly adopt. The Model Forest concept, which supports the formation a partnership between individuals and organisations sharing the goal of sustainability, is one example (IMFN 2008). UNESCO's Biosphere Reserve concept is another (Elbakidze et al. 2013). Both concepts imply that a management unit consisting of an actual landscape with its characteristic ecosystems, actors' economic activities, and stakeholders is used as a site for syntheses, innovation, development, and education. Similarly, the network for Long Term Socio-Economic and Ecosystem Research (LTSER) platforms aims at place-based integration of monitoring and assessment of landscape sustainability, with all stakeholders playing a role (Haberl et al.2006).

To maintain viable populations of all naturally occurring forest species in Europe, legacies of habitat structures and ecosystem functions in both natural forests and cultural landscapes need to be considered

Biodiversity conservation in Europe's landscapes is based on both natural and cultural visions. We argue in favour of a novel win-win oriented approach to research and development, which is based on exchanging knowledge and experience gathered over a long period in different countries and regions, and which adaptively integrates both natural and cultural legacies with modern land use. This will be of mutual benefit for both science and practice, and thus for the continued sustainable use and conservation of natural resources that provide the basis for human well-being and quality of life.

Ultimately, acknowledging and adopting this perspective requires the gradual development of a new transdisciplinary profession able to facilitate ecosystem management in landscapes and social-ecological systems. This necessitates improved mutual feedback between the science, engineering, and art of integrated natural resource management and governance and regionally adapted solutions (e.g. Elbakidze et al. 2013).

References

Angelstam, P. 2006. *Maintaining cultural and natural biodiversity in Europe's economic centre and periphery. In: Agnoletti, M. (ed.). The Conservation of cultural landscapes. CAB International. Pp. 125–143.*

Angelstam, P., Elbakidze, M., Axelsson, R., Čupa, P., Halada, L., Molnar, Z., Patru-Stupariu, I., Perzanowski, K., Rozylowicz, L., Standovar, T., Svoboda, M. and Törnblom, J. 2013a. *Maintaining cultural and natural biodiversity in the Carpathian Mountain ecoregion: need for an integrated landscape approach. In: Kozak J., Ostapowicz, K., Bytnerowicz, A. and Wyżga, B. (eds.). Integrating nature and society towards sustainability. Springer. DOI: 10.1007/978-3-642-12725-0_28*

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

Angelstam, P., Roberge, J.-M., Axelsson, R., Elbakidze, M., Bergman, K.-O., Dahlberg, A., Degerman, E., Eggers, S., Esseen, P.-A., Hjältén, J., Johansson, T., Müller, J., Paltto, H., Snäll, T., Soloviy, I. and Törnblom, J. 2013b. *Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: the Swedish Forest Stewardship Council standard as a case study. AMBIO 42(2):229–240.*

Axelsson, R., Angelstam, P., Elbakidze, M., Stryamets, N. and Johansson, K.-E. 2011. *Sustainable development and sustainability: Landscape approach as a practical interpretation of principles and implementation concepts. Journal of Landscape Ecology 4(3):5–30.*

Bauer, N., Wallner. A. and Hunziker, M. 2009. *The change of European landscapes: Human-nature relationships, public attitudes towards rewilding, and the implications for landscape management in Switzerland. Journal of Environmental Management 90: 2910–2920.*

Bezák, P. and Halada, L. 2010. *Sustainable management recommendations to reduce the loss of agricultural biodiversity in the Mountain Regions of NE Slovakia. Mt Res Development 30(3):192–204.*

Carver, S. 2007. *Rewilding in England and Wales: A Review of recent developments, issues, and concerns. USDA Forest Service Proceedings RMRS-P-49: 267–272.*

Elbakidze, M. and Angelstam, P. 2007. *Implementing sustainable forest management in Ukraine's Carpathian Mountains: The role of traditional village systems. Forest Ecology and Management 249:28–38.*

Elbakidze, M., Hahn, T., Mauerhofer, V., Angelstam, P. and Axelsson, R. 2013. *Legal framework for biosphere reserves as learning sites for sustainable development: a comparative analysis of Ukraine and Sweden. AMBIO 42(2):174–187.*

Gustafsson, L., Baker, S., Bauhus, J., Beese, W., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A. and Franklin, J.F. 2012. *Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62:633–645.*

Haberl, H., Winiwarter, V., Andersson, K., Ayres, R. U., Boone, C., Castillo, A., Cunfer, G., Fischer-Kowalski, M., Freudenburg, W. R., Furman, E., Kaufmann, R., Krausmann, F., Langthaler, E., Lotze-Campen, H., Mirtl, M., Redman, C. L., Reenberg, A., Wardell, A., Warr, B. and Zechmeister, H. 2006. *From LTER to LTSER: conceptualizing the socioeconomic dimension of long-term socioecological research. Ecology and Society 11(2):13.*

IMFN 2008. *Model Forest development guide. Ottawa: International Model Forest Network Secretariat.*

Navarro, L. M. and Pereira, H. M. 2012. *Rewilding abandoned landscapes in Europe. Ecosystems 15:900–912.*

Palo, A., Ivask, M. and 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.*

Pătru-Stupariu, I., Angelstam, P., Elbakidze, M., Huzui, A. and Andersson, K. 2013. *Using spatial patterns and forest history to identify potential high conservation value forests in Romania. Biodiversity and Conservation 22(9):2023–2039.*

Puettman, K.J. 2010. *Silvicultural challenges and options in the context of global change: "Simple" fixes and opportunities for new management approaches. Journal of Forestry(September 2010):321–331.*

Pykälä, J. 2004. *Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. Applied Vegetation Science 7:29–34.*

Roberge, J.-M., Angelstam, P. and Villard, M.-A. 2008. *Specialised woodpeckers and naturalness in hemiboreal forests – deriving quantitative targets for conservation planning. Biological Conservation 141:997–1012.*

Sammul, M., Kattai, K., Lanno, K., Meltsov, V., Otsus, M., Nõuakas, L., Kukk, D., Mesipuu, M., Kana, S. and Kukk, T. 2008. *Wooded meadows of Estonia: Conservation efforts for a traditional habitat. Agricultural and Food Science 17:413–429.*

Soulé, M. and Noss, R. 1998. *Rewilding and biodiversity: complementary goals for continental conservation. Wild Earth 8:19–28*

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. and Mönkkönen, M. 2010. *Woodland key habitats in northern Europe: concepts, inventory and protection. Scandinavian Journal of Forest Research 25:309–324.*

Törnblom, J., Angelstam, P., Degerman, E., Henrikson, L., Edman, T. and Temnerud, J. 2011. *Catchment land cover as a proxy for macroinvertebrate assemblage structure in Carpathian Mountain streams. Hydrobiologica 673:153–168.*

Villard, M.-A. and Jonsson, B.-G. 2009. *Setting conservation targets for managed forest landscapes. Cambridge University Press*

Whyte, I.D. 1998. Rural Europe since 1500: *Areas of retardation and tradition. In: Butlin, R.A. and Dodgshon, R.A. (eds.) An historical geography of Europe. Oxford University Press.*

2.6 Managing for target species

Bengt Gunnar Jonsson and Juha Siitonen

> *By focusing only on structural features we risk overlooking species with particular demands*

Forest conservation management often focuses on maintaining general habitat features such as natural tree species composition, uneven age structure, and perhaps most importantly, the presence of old and dead trees. The most widely used strategy for maintaining biodiversity is to emulate natural forest dynamics at the stand and landscape levels. For example, selective cutting or partial cutting can be used as alternatives to traditional clear-cutting, and untreated habitat patches, individual retention trees, and deadwood can be retained in the cutting area. The basic assumption is that by mimicking natural disturbances it should be possible to maintain the structural features and processes that are important for species. The general justification for focusing on structural features instead of species is that there are simply too many species to take into account the habitat requirements of each individual species. Therefore, it is often necessary to use structural features as surrogates for species (Figure 38).

Although this so-called coarse filter approach (*sensu* Hunter et al. 1988) probably captures the demands of many forest species, it may still not secure all aspects of forest biodiversity and risks overlooking some species with particular demands. It may even be potentially deceiving as the mere presence of particular structural features does not guarantee the presence of all species associated with the forest type in question. It is therefore advisable to include a set of target species in the management strategies to ensure that the more demanding species actually maintain viable populations, which also provides an evaluation of the success of the management. This is often referred to as a fine filter approach to conservation management. Including a set of well-selected target species may be an important complement to general measures and provides managers with a biological “receipt” on the outcome of implemented actions.

Box 24. The coarse and fine filter approaches

The concept of coarse and fine filter approaches dates back at least 25 years (Hunter et al. 1988). Originally it was related to the idea of securing particular habitat types by setting aside a representative network of reserves (coarse filter) while recognizing that this might be insufficient to secure viable populations of all species and that there is hence a need to complement the coarse filter with actions directed to individual species. In its development the concept has, however, expanded to include the identification and maintenance of general habitat features in management (coarse filter) as surrogates for species diversity as well as species-specific habitat requirements (fine filter) for those species that might not be secured by the general measures. It can be seen as a conceptual framework for conservation planning. When identifying how much of a particular habitat feature is needed, it is critical to consider its natural range of variability (Landres et al. 1999), while at the species level, the focus is on the individual requirements and population dynamics of each species. This is a broad starting point for conservation actions: for instance, the EU's Birds and Habitats Directives call for favourable conservation status of both the designated habitat types (based on structures and functions) as well as associated typical species and hence include both the coarse and fine filter approaches.

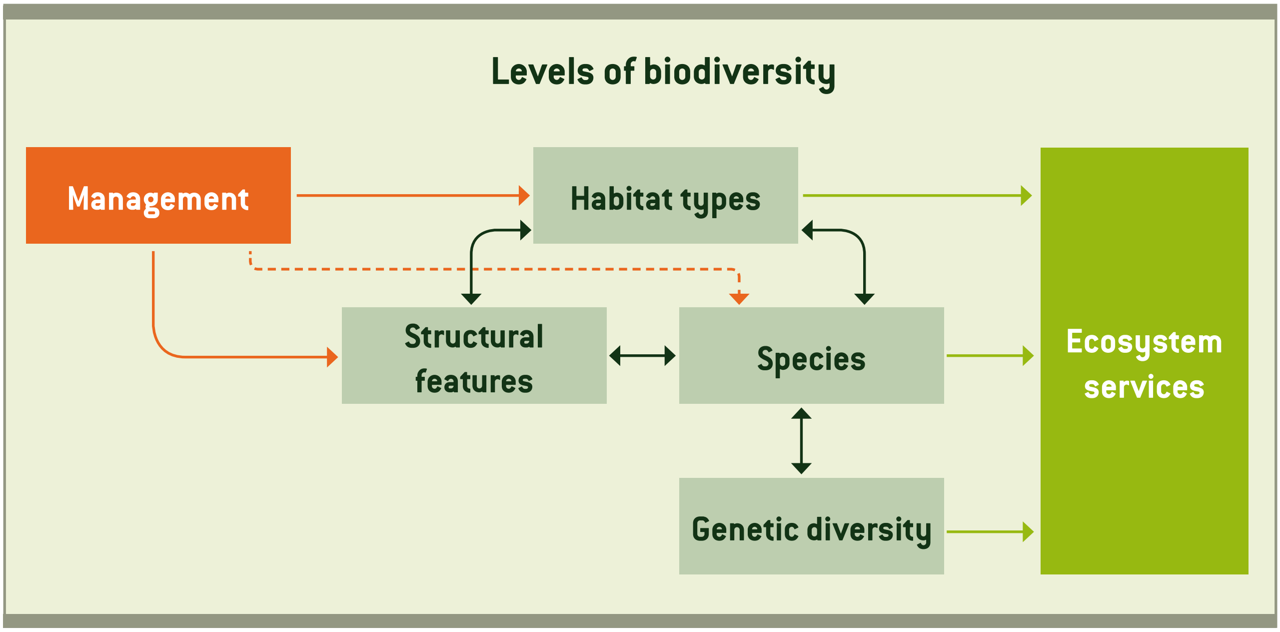


Figure 38. Components of biodiversity. In general, three levels of biodiversity are distinguished: genetic, species, and ecosystem diversity. From the management point of view, it is useful to add one additional aspect of biodiversity: structural features. The different components of biodiversity are interconnected, and together they produce ecosystem services. Management is practically always directed to either maintaining certain habitat types or structural features (the coarse filter approach). Even when the focus is on individual species (the fine filter approach), we actually manage particular habitat types or structural features that are needed to maintain their populations.

Careful selection of target species is a critical stage for complementing the coarse filter approach and evaluating management outcomes

As not all species can be considered, selecting representative target species is an important step. At least two different aspects should be considered to guide management. First, species to be selected should include those that are not covered by the general management measures, i.e. specialist species demanding particular habitat structures and substrates that are difficult to provide. Secondly, they should also include species that are easy to monitor and can be used as monitoring tools for assessing whether the chosen management results in desired outcomes.

In addition, the choice of target species also needs to consider what is actually limiting their occurrence in the forest landscape. The limiting factor is critical to address and can be used as a template to compare management options. For selecting target species we recommend that four types of species, limited by different factors, should be considered: **resource-limited**, **area-limited**, **dispersal-limited**, **and process-limited species.** As a framework for the selection of target species, we believe that this will allow us to better envision the range of habitat requirements that forest species exhibit. Basically, this is nothing more than dissecting into pieces the simple, general statement that all species need a continuity of the right kind of resources in sufficient amounts within their dispersal range. For an individual species, the four limiting factors are not mutually exclusive but can affect with different intensities (Figure 39). In the following, we will use species dependent on deadwood (saproxylic species) as examples. While many other substrates and habitat types are important for forest biodiversity, deadwood is one of the most critical habitat features in most managed forest types.

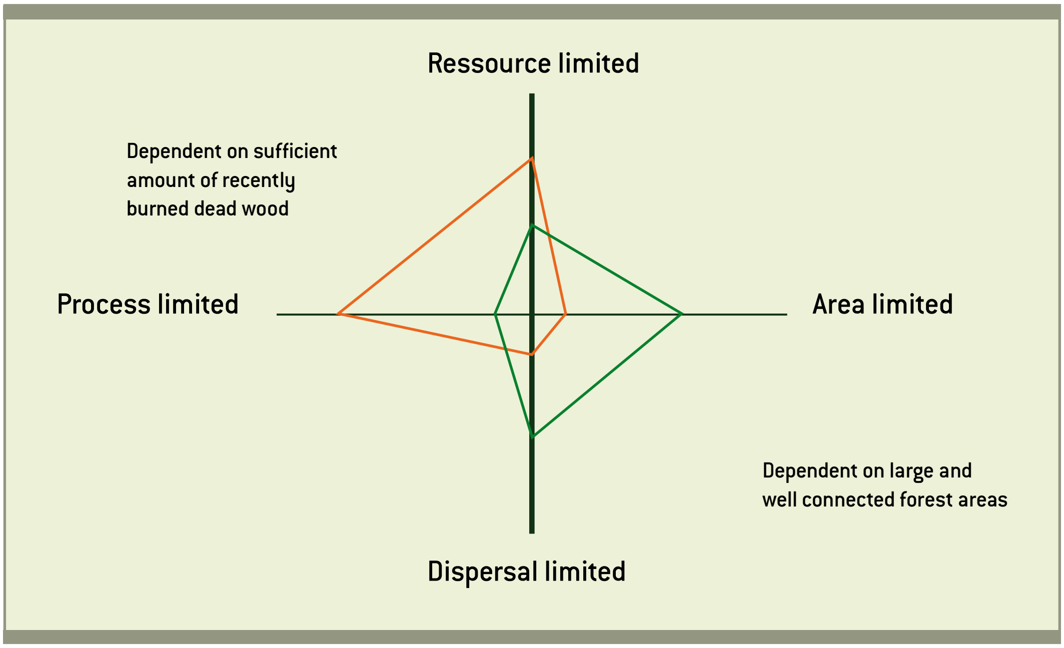


Figure 39. Species are limited by different factors, and by selecting target species representing these factors, management can secure suitable conditions for a wider range of species. This star-diagram includes an example of a species (red lines) dependent on recently burned wood (process and resource) and a species dependent on larger areas of well connected habitats (area and dispersal). The set of limiting factors in these two species is completely different.

Ideally, target species affected by different limiting factors should be selected since this will improve the general relevance of conservation management measures

Resource-limited species. The simplest reason why a species may be missing from a forest stand or the entire landscape is that suitable resources are missing. Regarding saproxylic species, deadwood is not a homogenous substrate. It comes in many different forms, and even with apparently high total volumes, particular types of deadwood might still be missing. Different tree species, decay stages, tree diameters, causes of death, and combinations of these factors all potentially represent specific substrates for some target species. Management should ideally ensure that the full range is available (Figure 40.).

In intensively managed forests with relatively short rotation times, particularly large-diameter trees in advanced decay stages are scarce or missing. For instance, the majority of threatened polypore species associated with beech in Denmark were only recorded on logs that were > 70 cm in diameter (Heilmann-Clausen and Christensen 2004) – a truly rare substrate in managed forests. Another example of a rare substrate is large decorticated snags of pine. These so-called "kelo trees" were probably historically common in lowland forests with pine throughout Europe, but are among the first deadwood types to decline when forests are harvested. Nowadays they occur in higher numbers only in remote boreal areas and in a few remaining lowland sites, such as the Białowieza primeval forest (Niemelä et al. 2002).

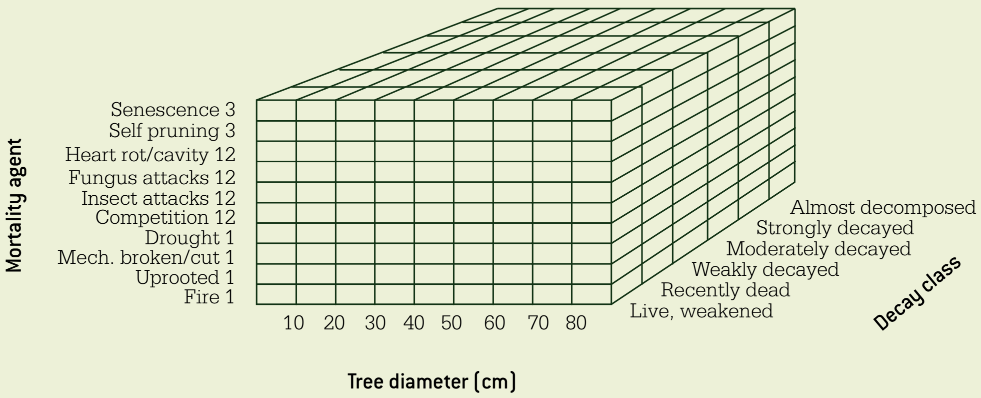


Figure 40. Deadwood is more than just total volume. It is critical to also consider different types of deadwood since many species are specific to certain deadwood qualities. The figure exemplifies for a single tree species the variability in three important factors; tree size, decay class, and mortality agent. All these, as well as different tree species, are required to provide the full range of substrate types. Source: Modified from Stokland et al. 2012.

Figure 41. A: The Middle Spotted Woodpecker (*Dendrocopos medius*) is a good example for an area-limited species (photo by Alain Saunier). B: The hermit beetle (*Osmoderma eremita*) is a dispersal-limited species inhabiting old hollow trees (photo by Heinz Bußler). C: The larvae of the beetle *Pytho kolwensis* live under the bark of fallen spruces in old-growth spruce-mire forests. The species is both dispersal- and process-limited and depends on continuous local tree mortality (photo by Reijo Penttilä). D: The ascomycete species *Daldinia loculata* grows on fire-killed birch trees in forest fire areas. Several insect species are associated with this fungus (photo by Reijo Penttilä). E: The jewel beetle (*Melanophila acuminata*) is a classical example of a strongly fire-dependent (pyrophilous) species. It has infrared sensors to locate ongoing forest fires (photo by Petri Martikainen). F: The flat bug species *Aradus laeviusculus* is one of the many insect species that colonize burned areas right after forest fires. Species associated with forest fires are process-limited (photo by Petri Martikainen).


B)


C)


E)


D)


F)

Area-limited species. Many rare specialist species require not only specific resources but also sufficiently large patches of habitat where the amount of the critical resource exceeds a species-specific threshold value. A range of studies focusing on woodpeckers illustrate how specialised woodpecker species need relatively large areas of forest with sufficient amounts of deadwood. For instance, the White-backed Woodpecker feeds its nestlings mainly with longhorn beetle larvae and other large larvae living in dead deciduous trees. For successful reproduction, one nesting pair needs at least 50 ha of deadwood-rich deciduous forest (Aulén 1988). At the landscape scale, the average basal area of deciduous snags should exceed 1.4 m^2/ha over an area of 100 ha for a high occurrence probability of this species (Roberge et al. 2008). Furthermore, in order to maintain a viable White-backed Woodpecker population comprising several nesting pairs within a certain area, this good-quality deciduous forest needs to cover at least 10–20 % of the landscape, otherwise the population will gradually disappear (Carlsson 2000). For the Middle Spotted Woodpecker (Fig. 41A), the minimum area of a breeding territory is about 15 ha (Kosiński 2006), and at the landscape scale, the occurrence probability of the species becomes high when the basal area of large-diameter deciduous trees exceeds 1 m^2/ha over an area of 100 ha (Roberge et al. 2008). Another example is the Three-toed Woodpecker: at least 1.3 m^2/ha of snags (corresponding to a volume of about 15 m^3/ha) over an area of 100 ha of coniferous forest is needed to sustain this species (Bütler et al. 2004). It should be noted that these examples concern conditions needed to host one or a few pairs of the species and not necessarily what is required to maintain a viable population over a larger landscape.

Dispersal-limited species. Species living on temporary substrates such as decaying trees are dependent on repeated dispersal. However, their dispersal ability varies in relation to the specific longevity of their substrate and habitat. Some may occur only during one summer on their substrate, as for instance most bark beetles utilizing the cambium of recently dead trees, while other species may utilize the same substrate unit for decades. The durability of substrate constitutes a strong selection pressure, and as a consequence, different species have widely varying dispersal capacities. The fragmentation of the forest landscape and the loss and growing isolation of specific habitats or habitat features pose a special threat to those species adapted to long lasting, but currently declining, substrates.

Species living in tree hollows serve as a good example. The hermit beetle (*Osmoderma eremita*) (Figure 41B) lives in hollows of large and old oaks and other deciduous trees. In Northern Europe about 85 % of the individuals remain in the tree where they were born. Of those leaving the tree, most disperse less than 200 m, which means that they usually remain within the same stand (Ranius and Hedin 2001; Hedin et al. 2008). The species has become threatened because of its low dispersal capacity, combined with the decline of wood pastures and other habitats with old hollow trees, and it is included into the Habitats Directive. To maintain species like the hermit beetle, it is important to secure local continuity of the critical substrate and, as far as possible, increase connectivity between suitable forest stands.

Process-limited species. Some species occur mainly or exclusively in particular successional stages. For these species the disturbance processes driving the succession need to be maintained. For saproxylic species these may include fire, wind, flooding, and other processes that generate dead trees. In some cases a species may be specifically dependent on the local continuity of its substrate, and although potentially characterized as dispersal-limited, it can also be considered as process-limited as it is strongly dependent on the processes generating its substrate. An example is the beetle *Pytho kolwensis* (Figure 41C) inhabiting fallen spruce trees that have died a few years earlier. Due to its low dispersal ability and its occurrence during a relatively short time span in individual logs, it is strongly dependent on continuous local tree mortality (Siitonen and Saaristo 2000).

In many forest ecosystems, fire has played a significant role. *Daldinia loculata* (Figure 41D) is a wood-decaying ascomycete that occurs in Northern Europe and with scattered occurrence also in Central Europe. It appears exclusively on fire-killed birch trees and is hence strictly connected to forest fires. In a study from central Sweden, Wikars (2001) showed a strong correlation between fire-dependent insects and the frequency of birch trees with *D. loculata*. The details of the interaction are not fully understood, but many of the fire-dependent insects were found to live inside the fruit bodies of the fungus, indicating a strong association. Another example comes from insects breeding in fire-killed trees directly after forest fire. Some of these are so dependent on fire areas that they have developed infrared sensors to locate ongoing forest fires, the jewel beetle *Melanophila acuminata* (Figure 41F) being a classic example. Other species, including several flat bugs (*Aradus* spp.) (Figure 41E), colonize the burned area directly after fire. These fire-dependent species often have remarkable dispersal abilities.

Analysis of thresholds can provide managers with quantitative target values, but there are limitations

A critical question in addressing the limiting factor is "how much is enough?" If a single answer could be given, managers would have a powerful tool and target to work with. However, given the large number of forest species and aspects to consider, this is a notoriously difficult question to answer. Searching for quantitative thresholds is a valid and important research challenge, and for some species and habitat features quantitative targets are available. Regarding how much of the original habitat that needs to be retained at the landscape scale, most empirical and theoretical studies point to a level around 20 % (e.g. Hanski 2011). There are also examples of quantitative targets for individual species, such as those presented for the woodpeckers above. Although these estimates provide guidance, care must be taken when they are implemented. Even if we can assume that thresholds in limiting factors do occur for the majority of species, they are likely to vary among species, species groups, and even for the same species that occurs in different regions (e.g. Ranius and Fahrig 2006, Müller and Bütler 2010). Translated to the *whole forest biota*, this suggests that for many factors we cannot give a single answer besides the general statement of "the more the better". Yet, by carefully selecting target species representing a range of limiting factors, we can provide suitable conditions for at least these species, and by fulfilling their habitat requirements, we can expect to help many other species.

Box 25. Recommendations

There are indeed many species, even if we only consider threatened saproxylic species, and we cannot simultaneously take into account all of their habitat requirements. Careful selection of target species should include species of special concern (e.g. those included into Birds and Habitats directives, red-listed species), but also species suitable for evaluation of management outcomes. By recognizing that different species are limited by different factors, a link to a wider range of concerns can be made. This would also help to integrate the local stand level factors (enough resources in single stands) with landscape level targets (suitable habitats within dispersal distances and sufficient amount of habitat to sustain viable populations).

One possible solution is to reduce a larger set of species into a more limited number. This was done by Tikkanen et al. (2007). Originally their study system included about 140 species. They were grouped based on their preferred microclimatic conditions (sunny, indifferent, or shady), host tree species, decay stage, and quality of the tree (e.g. snag or log). Tikkanen et al. were able to form only 27 groups in which the habitat requirements of the species overlapped. This appears to be a promising approach that can be used in selecting a representative set of target species.

Identifying thresholds for critical habitat and landscape factors, as well as critical population sizes and the spatial requirements thereof, is needed in order to provide management with relevant quantitative targets. These are available for some species, but ideally we should have information for many other species with different limiting factors. Assessing threshold conditions is an important first step for implementing target species strategy in conservation management.

Management includes numerous trade-offs, and it is unlikely that all objectives can be met within the same forest stand. This includes not only conflicts between economy and species habitat requirements, but also among target species. Their requirements are likely to differ, making it impossible to provide suitable conditions, in any specific forest, for all target species. This suggests that explicit choices have to be made concerning what aspects should be emphasized in individual forest stands, and that conservation planning, including integration approaches, must consider the landscape scale. This is even more important as populations of many species utilize and need large parts of the landscape for their long-term survival.

References

Aulén, G. 1988. *Ecology and distribution history of the white-backed woodpecker* Dendrocopus leucotos *in Sweden. Swedish University of Agricultural Scaiences, Department of Wildlife Ecology, Report 14. 194 p.*

Bütler, R., Angelstam, P., Ekelund, P. and Schlaepfer, R. 2004. *Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biological Conservation 119:305–318.*

Carlsson, A. 2000. *The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (Dendrocopus leucotos). Forest Ecology and Management 131:215–221.*

Hanski, I. 2011. *Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio 40:248–255*

Hedin, J., Ranius, T., Nilsson, S.G. and Smith, H.G. 2008. *Restricted dispersal in a flying beetle assesed by telemetry. Biodiversity and Conservation 17:675–684.*

Heilmann-Clausen, J. and Christensen, M. 2004. *Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management 201:105–117.*

Hunter, M.L., Jacobson, G.L. and Webb, T. 1988. *Paleoecology and the coarse-filter approach to maintaining biological diversity. Conservation Biology 2:375–385.*

Kosiński, Z. 2006. *Factors affecting the occurrence of middle spotted and great spotted woodpeckers in deciduous forests – a case study from Poland. Annales Zoologici Fennici 43:198–210.*

Landres, P. B. Morgan, P. and Swanson, F.J. 1999. *Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.*

Müller, J. and 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.*

Niemelä T, Wallenius, T. and Kotiranta, H. 2002. *The Kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Botanical Journal 47:91–101.*

Ranius, T. and Fahrig, L. 2006. *Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scandinavian Journal of Forest Research 21:201–208.*

Ranius, T. and Hedin, J. 2001. *The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows. Oecologia 126:363–370.*

Roberge, J.-M., Angelstam, P. and Villard, M.-A. 2008. *Specialised woodpeckers and naturalness in hemiboreal forests – deriving quantitative targets for conservation planning. Biological Conservation 141:997–1012.*

Siitonen, J. and Saaristo, L. 2000. *Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. Biological Conservation 94:211–220.*

Stokland, J., Siitonen, J. and Jonsson, B.G. 2012. *Biodiversity in Dead Wood. Cambridge University Press, Cambridge, UK.*

Tikkanen, O.-P., Heinonen, T., Kouki, J. and Matero, J. 2007. *Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: cost-effective measures for multi-species conservation. Biological Conservation 140:359–372.*

Wikars, L.-O. 2001. *The wood-decaying fungus Daldinia loculata (Xylariaceae) as an indicator of fire-dependent species. Ecological Bulletins 49:263–268.*

Processes, functioning, and structures in forest ecosystems directly and indirectly depend on the species assemblages they consist of. In addition to floristic composition, faunistic elements play a key role in forest ecosystems. They serve as catalysts in nutrient cycling and provide links between plants, fungi, and micro-organisms. In analysing forest biodiversity, it is therefore of paramount importance to identify the appropriate indicator species groups. This may pose a challenge to ecologists since among the estimated 5,000 species that could be expected in a typical Central European forest, only a few species groups fulfil the criteria for serving as indicators for forest ecological evaluations. These criteria include a sufficient number of species to occupy the range of niches that are representative for the complexity of structures in Central European forests, sufficient ecological knowledge, identification on the species level, and coverage of a broad range of functions and trophic levels (e.g. saprophagous, phytophagous, zoophagous) within an ecosystem.

Aegolius funereus

3. Indicator species groups and their thresholds of habitat requirements

Chapter 3 presents selected species groups and discusses management options for these specific groups. The main focus of this chapter is on the complexity of meeting various habitat requirements and their potential thresholds in Central European forests. The sections focus on a few selected species groups where sufficient expert knowledge is available to illustrate the complexity of the topic. The chapter is structured into seven sections:

3.1 Forest birds and their habitat requirements

3.2 Forest insects as indicators

3.3 Forest-specific diversity of vascular plants, bryophytes and lichens

3.4 Biodiversity of mycorrhizal fungi as a crucial player in forest ecosystem functioning

3.5 Lichens: sensitive indicators of changes in forest environment

3.6 Spiders in forest ecosystems

3.7 Snails and slugs as indicators of sustainable forest management


Hericium flagellum


Cucujus cinnaberinus

3.1 Forest birds and their habitat requirements

Pierre Mollet, Simon Birrer and Gilberto Pasinelli

Bird populations act on large scales and, on such large scales, are good indicators for forest biodiversity and management

Bird communities in forests across Europe vary in species number and composition. At large spatial scales, this variation is mainly driven by climate. Climate and other natural factors such as topography, water availability, and soil productivity are also important at local scales. However, on these relatively small scales, in most forests the main driver of structural diversity and hence the availability of resources important for birds is human activity. In Central, Western, and Southern Europe, almost all forests have been extensively exploited by humans for many hundreds, sometimes even thousands, of years. Regional differences in socio-economic systems and processes have led to a large diversity of forest types across Europe, with differing value as habitat for birds. Europe's forests will experience changes in the future associated with area increase as a result of agricultural abandonment, climate change, and increasing demand for wood for fuel and timber.

For securing future forest bird species diversity, it will be crucial to develop management strategies that maintain a diversity of structures across the whole forested surface, providing key resources for birds

All birds need resources for foraging and breeding. Some species have additional habitat requirements not directly linked to foraging or breeding, but necessary for exhibiting species-specific behaviour. For instance, the Eurasian Woodcock *Scolopax rusticola* is a species that needs open forest patches for its crepuscular display flight (roding), whereas both breeding and foraging can take place in rather dense forest. Translating habitat requirements of forest birds into elements that can be more or less directly modified by forestry results in the following list. For further reading on forest bird ecology we recommend Fuller et al. (2012) and Scherzinger (2011).

Tree canopy. The canopy layer with its enormous biomass of twigs, branches, and either leaves or needles provides a diverse habitat for invertebrates and thus a rich foraging resource for insectivorous birds. For bird species feeding on seeds or fruits, the canopy provides a rich foraging ground as well. The canopy is also important for large birds of prey that nest in tree canopies but forage outside the wooded area, usually on agricultural land.

Gaps, shrub layer, and field layer. Gaps in the canopy, usually the result of human activity, storms, avalanches, landslides, bark beetle activity, the death of single old trees or fire, are quickly colonised by more or less light-demanding shrubs and herbs. This vegetation layer can develop differently depending on gap size, soil conditions, and humidity. In larger gaps, it is often dominated by a dense shrub layer composed of small trees up to 3–4 m in height that offers nesting and foraging opportunities for species such as the Blackcap *Sylvia atricapilla* or Garden warbler *Sylvia borin*. In small gaps with still rather shady conditions or in gaps on poor soil there is sometimes just a field layer consisting of low shrubs such as Vaccinium spp., herbs, and grasses interspersed with patches of bare ground. In such low and heterogenous field layer vegetation, various ground nesting birds such as grouse (*Tetrao* ssp. and *Bonasa bonasia*) or the Wood Warbler *Phylloscopus sibilatrix* find good nesting opportunities.

Sometimes, there are large gaps in the forest with just a few scattered single standing trees left and a matrix of sparse low vegetation and bare soil. For an important group of bird species, one example being the Redstart *Phoenicurus phoenicurus*, this is a preferred habitat structure. These birds are cavity-breeders and feed on arthropods they find on open ground. Large gaps also provide open space that can be important for nocturnal foraging flights of the Eurasian Nightjar *Caprimulgus europaeus*. In today's European Forests, whether they are managed for producing wood or unmanaged, such structures are rare because large gaps are usually filled rather quickly by shrubs and herbs. Long-term maintenance of this kind of habitat seems to be possible only through human activity other than forestry, i.e. grazing (cattle, sheep, or goats, depending on local conditions) or regular fires.

Figures 42 and 43. The combination of open ground with scattered trees standing upright is a very good habitat for cavity-breeding birds that feed on arthropods on sparsely vegetated ground, one example being the Redstart *Phoenicurus phoenicurus*. The 310-hectare pine-oak forest in Valais, Switzerland in figure 1 burnt down in 2003. In following years, the number of breeding pairs of the Redstart on this surface, absent before the fire, rose to 97 in 2008, then fell again to 86 in 2010 (Sierro et al. unpublished data). Photos by T. Wohlgemuth (left) and B. Rüegger (right).

Old trees and deadwood. Deadwood in its many different forms contains a large invertebrate resource that is important for insectivorous birds such as woodpeckers, particularly in winter. Apart from that, rot holes develop in dead and decaying wood, providing nest sites for secondary cavity nesters not capable of excavating nest holes such as tits *Parus* ssp. or the Eurasian Nuthatch *Sitta europaea*. Single old trees are important for many bird species because such trees usually offer more dead branches, rot holes, decaying wood, and cavities than young trees. The availability of dead branches and cavities is further affected by tree species composition. For example, oak *Quercus* ssp. offers more such structures than beech *Fagus silvatica* and is also known for its highly fissured bark where specialised arthropod-gleaners such as the Middle Spotted Woodpecker *Dendrocopos medius* and tree creepers *Certhia* ssp. find food. Dead stems are a particularly valuable habitat element for forest birds when they are standing upright. Lying deadwood may still offer food for woodpeckers but does not serve as a resource for hole-breeders.

Old stands. For some bird species, notably the White-backed Woodpecker *D. leucotos* and the Three-toed Woodpecker *Picoides tridactylus*, a few single old trees with deadwood elements are not sufficient. Populations of these species solely occur in stands with a high amount of deadwood on large surfaces of several hundred hectares. The White-backed Woodpecker in particular seems to depend heavily on high amounts of deadwood and has suffered dramatic population declines in many countries due to forest management (Czeszczewick and Walankiewicz 2006; Virkkala et al. 1993).

Figure 44. The White-backed Woodpecker *Dendrocopos leucotos* is an indicator for large old forests with a high amount of deadwood, typically not present in managed forests. Photo by J. Peltomäki.

Tree species. Bird communities differ between coniferous and broadleaved forests. In the former, the number of species seems to be generally lower than in the latter (Mosimann et al. 1987). Some bird species, such as the Three-toed Woodpecker or the Coal Tit *Parus ater*, are largely confined to coniferous forests. Others, such as the Middle Spotted Woodpecker or the Golden Oriole *Oriolus oriolus*, occur in broadleaved forests only. Many bird species, however, such as the Great Spotted Woodpecker *D. major* or the Chaffinch *Fringilla coelebs*, do not seem to depend on the occurrence of particular tree species at all. They regularly occur in coniferous, mixed coniferous, and broadleaved woods. In the latter, population densities can be higher, presumably as a result of higher food availability compared to mixed and coniferous forests. Planting coniferous tree species in lowland forests where the natural vegetation would primarily consist of broadleaved species results in habitat loss for species requiring broadleaved stands and hence reduces forest bird diversity (Baguette et al. 1994; du Bus de Warnaffe and Deconchat 2008). In addition, heavily managed conifer plantations are typically harvested at rather young ages such that structural diversity remains relatively low.

Forest birds reflect the diversity of their habitats. Some species are good indicators for openness of forests; some, for stands with closed canopies; others, for large trees with many holes; and still others, for short-term successional stages after forest fires. Different forest management strategies help to maintain forest bird diversity

In addition to the above-mentioned habitat elements, which are all influenced by forestry more or less directly, there is another habitat requirement that usually has little to do with forestry but should nevertheless be considered by forest managers in some situations. Capercaillie *Tetrao urogallus* negatively responds to human presence (Brenot et al. 1996, Thiel et al. 2011), particularly in winter and in the lekking and breeding season. Human-induced disturbance is not necessarily a problem in the vast and contiguous boreal forests, but it can be critical for the local survival of the species in the southern parts of its range where suitable habitats are usually small and fragmented. Forest managers can help to reduce disturbance by avoiding road construction in Capercaillie habitats.

For maintaining avian forest biodiversity, European forests should provide all the above-mentioned habitat elements on the whole forested surface

The questions still to be answered relate to quantity, spatial distribution, and extent: how many old and dead trees are needed in a given area? What percentage of the managed forest surface should be rather open, with a well-developed shrub layer, and how much should consist of closed-canopy stands? How large can or should such stands be? What is the maximum distance between two elements of the same type for avoiding critical isolation effects?

So far, unfortunately, there is no scientific data to answer these questions, the required quantity of deadwood being the only exception. Müller and Bütler (2010) provide a meta-analysis of 37 studies investigating threshold values. Eight of these studies contain data about birds. Based on Müller and Bütler (2010), it is possible to recommend deadwood quantities for managed forests, categorised into three forest types: lowland beech-oak forests, montane mixed beech-fir-spruce forests, and alpine-boreal spruce-pine forests (Table 8). If these recommended deadwood volumes can be provided in managed forests, almost all bird species depending on deadwood will find appropriate habitats. We are convinced, however, that it will still be necessary to establish a well-connected system of unmanaged large forest reserves across the whole landscape, where deadwood amounts can still be much higher. Only with such a system of unmanaged forests will it be possible to maintain viable populations of bird species such as the White-backed Woodpecker.

Table 8. Recommended deadwood quantities for birds in managed forests (following Müller and Bütler (2010)) across the whole forest surface.

Forest type	**Dead wood m^3/ha**
Lowland beech-oak forest	30–50
Montane mixed beech-fir-spruce forest	30–60
Alpine-boreal spruce-pine forest	20–50

For securing future forest bird species diversity in Europe, the following recommendations for forest management can be made:

1. In all managed forests,
    a. there is always an equilibrium between middle-aged stands with rather closed canopy, ready for harvesting timber, and open, young stands with a well-developed shrub layer;
    b. quantities of deadwood per hectare are as recommended in Table 8; and
    c. selection of tree species follows the natural vegetation, i.e. conifer plantations in lowland forests where the natural vegetation would primarily consist of broadleaved species are reduced to a minimum.
2. Alongside all managed forests, there is a well-connected system of unmanaged large forest reserves across the whole landscape.

Nevertheless, there is an urgent need for studies quantifying thresholds of specific habitat elements for specialised bird species. Likewise, threshold values for overall avian diversity in different forest types should be established.

References

Baguette, M., Deceuninck, B. and Muller, Y. 1994. *Effect of spruce afforestation on bird community dynamics in a native broadleaved forest area. Acta Oecol. 15:275–288.*

Brenot, J.F., Catusse, M. and Ménoni, E. 1996. *Effets de la station de ski de fond du plateau de Beille (Ariège) sur une importante population de Grand Tétras* Tetrao urogallus. *Alauda 64:249–260.*

Czeszczewik, D. and Walankiewicz, W. 2006. *Logging affects the white-backed woodpecker* Dendrocopos leucotos *distribution in the Białowieża Forest. Ann. Zool. Fenn. 43:221–227.*

Du Bus de Warnaffe, G. and Deconchat, M. 2008. *Impact of four silvicultural systems on birds in the Belgian Ardenne: implications for biodiversity in plantation forests. Biodivers. Conserv. 17:1041–1055.*

Fuller, R.J., Smith, K.W. and Hinsley, S.A. 2012 *Temperate western European woodland as a dynamic habitat for birds: a resource-based view. In: Fuller, R.J. (ed.): Birds and habitat: Relationships in changing landscapes. Cambridge University Press, Cambridge, UK. Pp. 352–380*

Mosimann, P., Naef-Daenzer, B. and Blattner, M. 1987. *Die Zusammensetzung der Avifauna in typischen Waldgesellschaften der Schweiz. Ornithol. Beob. 84:275–299.*

Müller, J. and Bütler, R. 2010. *A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. Forest Res. 129: 981–992.*

Scherzinger, W. 2011. *Der Wald als Lebensraum der Vogelwelt. In: Wallner, R. (ed.): Wald – Biotop und Mythos. Grüne Reihe des Lebensministeriums, Band 23. Böhlau Verlag, Wien, Köln, Weimar. Pp. 27–154*

Thiel, D., Jenni-Eiermann, S., Palme, R. and Jenni, L. 2011. *Winter tourism increases stress hormone levels in the Capercaillie* Tetrao urogallus. *Ibis 153:122–133.*

Virkkala, R., Alanko, T., Laine, T. and Tiainen, J. 1993. *Population contraction of the white-backed woodpecker* Dendrocopos leucotos *in Finland as a consequence of habitat alteration. Biol. Conserv. 66:47–53.*

3.2 Forest insects and their habitat requirements

Beat Wermelinger, Thibault Lachat, and Jörg Müller

Among insects, some well-known groups such as beetles, ants, butterflies, and moths are very suitable as indicators of biodiversity, ecological integrity, and management of forests

Insects form a hyperdiverse taxonomic category contributing to more than half of terrestrial species diversity. As a rough estimate, some 30,000 insect species live in European forests. They respond to the structural complexity of forests at different temporal and spatial scales and are markedly influenced by natural and anthropogenic disturbances such as windthrow, logging, and fragmentation. Insects are considered good indicators for the overall biodiversity and integrity of forests because they meet many of the requirements defined for ecological indicators: Many are relatively easy and cost-efficient to assess with standardized methods, measurements are reliable due to the high abundance of insects, and they cover a wide range of life histories, habitat requirements, and functional groups with important roles in forest ecosystems (Ferris and Humphrey 1999; Maleque et al. 2006). Due to their short turnover cycles, they are sensitive to and react rapidly to changes in their environment.

With few exceptions, taxonomic or functional groups rather than single species have been used as indicators in forests. These include ants (Formicidae), butterflies and moths (Lepidoptera), hover flies (Syrphidae), parasitic wasps (Terebrantes), and most of all beetles, in particular ground beetles (Carabidae), longhorned beetles (Cerambycidae), saproxylic beetles in general, and dung beetles (part of Scarabaeidae). Among the numerous environmental factors known to affect species diversity, such as breeding substrate, food supply, or canopy openness/insolation, the amount and quality of deadwood is the most important prerequisite for saproxylic insects and has therefore been the most investigated. There is hardly any quantitative information for other habitat requirements of forest insects.

Deadwood is a vital resource for thousands of saproxylic (wood-inhabiting) organisms. Beetles alone comprise more than 1,400 saproxylic species in Central Europe and are good indicators of biodiversity. Depending on the forest type, deadwood volumes from 20 to 80 m^3/ha are recommended to support a rich assemblage of saproxylic species

Deadwood is widely acknowledged as a crucial resource for many species and as an indicator for forest naturalness. Saproxylic insects exploiting this resource are very susceptible to the type and intensity of forest management and its effect on the quantity and quality of deadwood. Saproxylic organisms depend, at least during some part of their life cycle, on dead or dying wood or on organisms associated with these substrates (Speight 1989). Among the saproxylic insects, the requirements of beetles have been most extensively studied (Figure 45). They are considered excellent indicators of woodland biodiversity in general and have been found to represent different habitat qualities. Most obviously, deadwood is a prime prerequisite. The amount of deadwood and/or its diversity are positively correlated to the species richness of saproxylic beetles. Longhorned beetles, a readily identified group, are particularly good indicators not only for deadwood volume, but also for forest openness and flower supply (Müller et al. 2008). This is because most of these species depend on different qualities of bark and wood as a food resource during their larval development, but in their adult stage feed on pollen of flowering plants to complete their maturation. The latter resource is mainly available in insolated, open forest habitats or in forests with many gaps and borders. Open forests not only harbour more longhorned beetles, but also more indicator species of beetles in general (Lehnert et al. 2013). Stag beetles (Lucanidae) are considered to be a suitable indicator group representing habitats with high amounts of deadwood in different climate conditions (Lachat et al. 2012).

Figure 45. The lesser stag beetle (*Dorcus parallelipipedus*) is a good indicator for warm beech forests with medium and high amounts of deadwood. Photo by B. Fecker.

Stipulating a single threshold value for deadwood does not capture the complexity of this multifaceted substrate and its colonisers. This resource encompasses different tree species, positions, decomposition stages, and diameters, and each insect species depends on specific deadwood qualities. Generally, an increase in the total volume of deadwood coincides with an increase in the diversity of this substrate (Similä et al. 2003).

A comprehensive meta-analysis of literature data by Müller and Bütler (2010) provides a set of thresholds for different forest types in Europe (see Box 26). Since these figures are based on various systematic groups such as fungi, plants, insects, and birds, the threshold ranges for the saproxylic beetles alone are narrower. Saproxylic beetles tend to have a requirement for higher deadwood volumes than other groups of organisms. The required amount of deadwood ranges from 40 to 70 m^3/ha for lowland beech-oak forests, 35 to 140 m^3/ha for montane-mixed forests (beech-fir-spruce), and 24 to 70 m^3/ha for boreo-alpine spruce-pine forests. The upper end of these ranges is particularly significant for threatened species (Müller et al. 2008). From these findings, recommendations for minimal deadwood volumes can be derived (see Box 26).

In particular, large dimensions of deadwood are generally scarce and therefore need to be fostered. However, small diameter-limbs, due to their large variation of qualities, are also a valuable substrate for beetle and fly fauna (Schiegg 2001). There are distinct indicator groups for early or late successional stages in the forest development. For example, bark beetles (Curc.: Scolytinae) and jewel beetles (Buprestidae) colonise fresh bark and wood, while longhorned beetles utilize a large range of deadwood conditions (Wermelinger et al. 2002). Towards the end of the decomposition process, rose chafers (Cetoniidae) colonise the soft and rotten wood.

Box 26. Recommended deadwood volumes for saproxylic beetles

Saproxylic beetles are one of the best-investigated indicator groups for forest biodiversity. Their requirements for deadwood volumes were compiled by Müller and Bütler (2010). Based on these values and considering their applicability in managed forests, the following volumes of deadwood are suggested as guidelines for sustaining a rich saproxylic beetle fauna:

	Dead wood volumes
Lowland beech-oak forests	30–50 m^3/ha
Montane-mixed forests (beech-fir-spruce)	40–80 m^3/ha
Boreo-alpine spruce-pine forests	20–50 m^3/ha

Habitat trees offering microhabitats such as dead branches, woodpecker cavities, bark losses, or polypore fruiting bodies are vital for a wide range of specialised saproxylic beetles. The number of such trees and their microhabitats is lower in managed forests than in old growth forests (Brunet and Isacsson 2010; Müller et al. 2008). In particular, hollow trees harbour many red-listed insect species with low dispersal capacities such as the hermit beetle (*Osmoderma eremita*), one of the best-investigated saproxylic species and an excellent single species indicator. Formerly distributed all over Europe, its populations are now very fragmented. This species depends on hollow trees, mostly oak, and lives for generations in suitable single trees. Modelling revealed that 20 stands with at least 10 hollow trees within a distance of 250 m are needed to form a viable metapopulation (Ranius and Hedin 2004).

Another very important resource for a large number of fungicolous species are polypore fungi. Many species are indicators for forests with a long deadwood tradition and high conservation value. In a recently compiled list of "Urwald relict beetle species" (i.e. species that have only relict records, high deadwood requirements, declining populations, and are tied to habitat tradition), 16 % are fungivores (Müller et al. 2005).

Large amounts of total deadwood volumes do not guarantee the long-term existence of any species. The levels may still be too low for particular species, specific microhabitats may be too scarce, or the connectivity of suitable habitats may be limiting. In managed forests, late-decay stages of large dimension logs and microhabitats such as rot holes harbouring many red-listed beetle species are lacking. Also, the dynamics of saproxylic populations at the landscape level needs further research.

Bees, wasps, hover flies, butterflies, and moths are similar in that they are potential pollinators but otherwise have a very broad range of ecologies. These indicators not only reflect the differing food demands for their larval development, but also the supply of flowers providing nectar and pollen to the adult insects and thus represent the openness of a stand

Besides many pollen-feeding beetle species, bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera), and hover flies (Syrphidae) are the most relevant pollinators (Figure 46). They pollinate herbaceous plants rather than forest trees, which are mostly wind-pollinated in Europe. Hover flies represent a wide range of different ecologies and thus have different requirements and functional roles. Their species diversity reflects the diversity of their habitats. While their larvae have quite diverse biologies, most adult hover flies consume nectar or pollen and pollinate flowers. Many syrphid species as well as bees and wasps are good indicators for the openness or gappiness of forests (Lehnert et al. 2013; Bouget and Duelli 2004).

Figure 46. Hover flies (here *Episyrphus balteatus*) are important pollinators of forest ground vegetation. Their abundance is an indicator for the canopy openness of forests. Photo by B. Wermelinger.

Likewise, most butterflies and moths, as adults, feed on nectar provided by flowers. Therefore, they are reliable indicators for open and recently disturbed forests, former and present management regimes, and forest fragmentation (Freese et al. 2006; Maleque et al. 2009). For example, the density of the wood white (*Leptidea sinapis*) (a butterfly) varies with the amount of shading (Warren 1985). Some species are typical for, and thus depend on, early successional forest stages (coppicing) with understorey vegetation, such as the endangered butterflies *Euphydryas maturna* and *Lopinga achine* (Freese at al. 2006; Streitberger et al. 2012). In North American deciduous forests, families of moths (Arctiidae and Notodontidae) have proven to be good indicators for general moth species richness (Summerville et al. 2004).

Insect predators and parasitoids consume mostly herbivorous insects. They represent the different ecologies of their prey. Therefore, a high species richness of these natural enemies indicates rich prey diversity

Predatory insects feed on other animal species, most often herbivores or detritivores. Representing a higher trophic level, they integrate extensive ecological information of other communities (Ferris and Humphrey 1999). Old growth forests usually have a higher diversity and abundance of predators and detritivores (Schowalter 1995). Among the predators, ground beetles, tiger beetles (Cicindelidae), and epigeic rove beetles (Staphylinidae) are considered to be a good reflection of forest management intensity (Osawa et al. 2005; Pearson and Cassola 1992; Pontégnie et al. 2004). Other predatory groups such as ants can also serve as indicators for forest management and resulting canopy structure (Dolek et al. 2009).

Box 27. Indicator species

Indicator species or species groups are characteristic for specific habitat features and are often of high conservation value. Thus, for enhancing the quality of forest biodiversity, management should aim at improving habitat quality in order to sustain or increase the number of indicators rather than maximizing species number. In this way, a broad range of ecological requirements and functional types of insects are favoured, which is likely to also benefit rare specialists.

References

Bouget, C. and Duelli, P. 2004. *The effects of windthrow on forest insect communities: a literature review. Biol. Conserv. 118:281–299.*

Brunet, J. and Isacsson, G. 2010. *A comparison of the saproxylic beetle fauna between lowland and upland beech forests in southern Sweden. Ecol. Bull. 53:131–139.*

Dolek, M., Freese-Hager, A., Bussler, H., Floren, A., Liegl, A. and Schmidl, J. 2009. *Ants on oaks: effects of forest structure on species composition. J. Insect Conserv. 13:367–375.*

Ferris, R. and Humphrey, J.W. 1999. *A review of potential biodiversity indicators for application in British forests. Forestry 72:313–328.*

Freese, A., Benes, J., Bolz, R., Cizek, O., Dolek, M., Geyer, A., Gros, P., Konvicka, M., Liegl, A. and Stettmer, C. 2006. *Habitat use of the endangered butterfly* Euphydryas maturna *and forestry in Central Europe. Anim. Conserv. 9:388–397.*

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G. and Müller, J. 2012. *Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecol. Indicators 23:323–331.*

Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J. and Müller, J. 2013. *Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages. J. Nature Conserv. 21:97–104.*

Maleque, M.A., Ishii, H.T. and Maeto, K. 2006. *The use of arthropods as indicators of ecosystem integrity in forest management. J. For. 104:113–117.*

Maleque, M.A., Maeto, K. and Ishii, H.T. 2009. *Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Appl. Entomol. Zool. 44:1–11.*

Müller, J., Bussler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J. and Zabransky, P. 2005. *Urwald relict species – saproxylic beetles indicating structural qualities and habitat tradition. waldökologie online 2:106–113.*

Müller, J., Bussler, H. and Kneib, T. 2008. *Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. J. Insect Conserv. 12: 107-124.*

Müller, J. and Bütler, R. 2010. *A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129:981–992.*

Osawa, N., Terai, A., Hirata, K., Nakanishi, A., Makino, A., Sakai, S. and Sibata, S. 2005. *Logging impacts on forest carabid assemblages in Japan. Can. J. For. Res. 35:2698–2708.*

Pearson, D.L. and Cassola, F. 1992. *World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): Indicator taxon for biodiversity and conservation studies. Conserv. Biol. 6:376–391.*

Pontégnie, M., du Bus de Warnaffe, G. and Lebrun, P. 2004. *On the interest of litter-dwelling invertebrates to assess silvicultural impact on forest biodiversity. In Marchetti, M. (ed). Monitoring and indicators of forest biodiversity in Europe – From ideas to operationality. EFI Proceedings 51. European Fores Institute. Pp. 259–269.*

Ranius, T. and Hedin, J. 2004. *Hermit beetle* (Osmoderma eremita) *in a fragmented landscape. In Akçakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S. and McCarthy, M.A. (eds.). Species conservation and management: Case studies. Oxford University Press, Oxford. Pp. 162–170.*

Schiegg, K. 2001. *Saproxylic insect diversity of beech: limbs are richer than trunks. For. Ecol. Manage. 149:295–304.*

Schowalter, T.D. 1995. *Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. For. Ecol. Manage. 78:115–125.*

Similä, M., Kouki, J. and Martikainen, P. 2003. *Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. For. Ecol. Manage. 174:365–381.*

Speight, M.C.D. 1989. *Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.*

Streitberger, M., Hermann, G., Kraus, W. and Fartmann, T. 2012. *Modern forest management and the decline of the Woodland Brown* (Lopinga achine) *in Central Europe. For. Ecol. Manage. 269:239–248.*

Summerville, K.S., Ritter, L.M. and Crist, T.O. 2004. *Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. Biol. Conserv. 116:9–18.*

Warren, M.S. 1985. *The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white* Leptidea sinapis. *Biol. Conserv. 33:147–164.*

Wermelinger, B., Duelli, P. and Obrist, M.K. 2002. *Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. For. Snow Landsc. Res. 77:133–148.*

3.3 Forest-specific diversity of vascular plants, bryophytes, and lichens

Wolf-Ulrich Kriebitzsch, Helga Bültmann, Goddert von Oheimb, Marcus Schmidt, Hjalmar Thiel and Jörg Ewald

In temperate forests, a great diversity of vascular plants, bryophytes, and lichens exists

These organisms make up the different forest strata (the tree, shrub, herb, and moss layer) and can be classified according to the substrate they live on as epigeic (in/on the soil), epiphytic (on another living plant), epixylic (on deadwood), or epilithic (on rock surfaces). The tree layer makes up the forest's structure, constitutes most of the biomass in the forest, and controls many important ecosystem functions and services. Furthermore, the structure, composition, and diversity of the overstorey exert substantial influence on the understorey and epiphytes by determining light availability, soil conditions, bark pH, microclimate, and forest floor quality (Braun-Blanquet 1964, Ellenberg and Leuschner 2010).

The understorey, and most notably the herb layer, hosts the greatest diversity of vascular plants, both in terms of species richness and phenological, structural, and functional differentiation (Gilliam 2007). Understorey vegetation also contributes to energy flow and element cycling and offers habitat and food for many organisms. Juvenile woody plants (seedlings, sprouts and saplings) are a transient part of the herb layer, whence they either grow into higher strata or die off. Understorey dynamics may therefore exert an important influence on forest regeneration and dynamics.

Epiphytic and epixylic bryophytes and lichens represent another highly significant component of overall forest diversity, whose richness outnumbers that of vascular plants in many forest types

Instead of rooting in soil, epiphytes obtain moisture and nutrients from the atmosphere. This enables them to grow on otherwise uninhabitable surfaces and to use a wide range of habitat conditions that can be very different from those of the forest floor (Rose and

Coppins 2002). Due to low growth rates epiphytes depend on perennial plant structures such as the bark of stem bases, trunks, branches, and, rarely, leaves of evergreen trees. The surface areas of these structures normally exceed the ground area of forests, greatly extending the space colonisable by plants. Dead and decaying wood provides substrate for epixylic bryophytes and lichens. Its quality changes with ongoing decay. This process is driven by fungi, insects, and other animals and is accompanied by a succession of epixylic vegetation. Coarse woody debris and the dead parts of old living trees are especially important in providing a particularly suitable physical and chemical environment for numerous epixylics.

Many vascular plants, bryophytes, and lichens in forests occupy highly specific realized ecological niches along certain environmental gradients. These species therefore lend themselves as indicator plants for resource availability or old-growth forest sites

Forest plant diversity is highly variable across climatic, geographic, topographic, edaphic, and light gradients (Ellenberg and Leuschner 2010). Besides these factors, diversity may be affected by historical land use and current forest management (Verheyen et al. 2003), dispersal limitation, herbivory, and chronic resource alterations caused by global change (e.g. nitrogen deposition, climate change). Epiphytic, epixylic, and epilithic cryptogams are particularly responsive to microclimatic as well as physical and chemical substrate properties, which directly depend on tree age and diameter, bark texture, or decay stages of deadwood (Rose and Coppins 2002). In addition, ubiquitous plant species and even species from open habitats such as grasslands occur in forests, which may result in high species richness of disturbed forests. Therefore, in evaluating diversity, completeness, typical development, and naturalness, it is necessary to distinguish forest plant species according to how closely they are associated with forests. The most promising approach for this is an extensive expert system based on a consistent methodology.

Vascular plants have the lowest and lichens the highest proportion of extinct and threatened species in Central Europe

For vascular plants and bryophytes, the larger share of red-listed species is typical for open land, whereas the reverse is true for lichens, of which the majority of threatened species depend on forest habitats (Hauck et al. 2013, Schmidt et al. 2011). Thus, with 58 % threatened and 33 % extinct or threatened by extinction, epiphytic lichens are top-runners on red lists. Many red-listed epiphytic forest bryophytes and lichens have not fully recovered from heavy air pollution (smoke damage by SO_2 and NO_x caused by unfiltered burning of fossil fuels), which has been largely controlled since the 1990s (Bobbink et al. 1998).

Lichens, which comprise a large number of old-growth and deadwood specialists, are particularly sensitive to human intervention

Plant species are threatened through a range of factors, the most important being habitat fragmentation and destruction, change of management practices, eutrophication, amelioration, and drainage (Verheyen et al. 2003). The largest group of threatened forest vascular plants and bryophytes, as well as soil-dwelling reindeer lichens, requires a combination of oligotrophic soils and open canopies as found in pine and oak forests. These stress-tolerant strategists, which also include several rare tree species, are easily overgrown by nitrophytic and shade-tolerant competitors. Broad-scale nutrient enrichment tends to level out species composition to the disadvantage of rare and threatened species, resulting in homogenized landscapes (Bobbink et al. 1998). Once widespread in pre-industrial multiple-use woodlands and natural oligotrophic early successional forest stages, stress-tolerant strategists survive in forest openings and fringes, often remnants of coppicing and forest pasture, but decline due to nitrogen emissions, self-amelioration, and canopy closure.

While continuous cover forestry is obviously detrimental to stress-tolerant plants, it is doubtful whether intensification of modern timber harvesting alone can benefit this species group without simultaneously favouring ubiquitous ruderals and even invasive plants

In Central Europe, oligotrophic habitats are naturally bound to early stages of successions on immature, skeletal, and sandy soils, as induced by morphodynamics such as river (sandbanks, gravel plains, undercut slopes), slope (rockfalls, landslides) and wind erosion (dunes), and peat bogs fed by rainwater (Figure 49). Such habitats have been largely destroyed by regulation, amelioration, and draining. Many normal forest sites were degraded by exporting biomass through fuel extraction, forest pasture, and litter raking in pre-modern times, creating secondary oligotrophic habitats (Ellenberg and Leuschner 2010).

Under modern emission regimes, driven by agriculture and combustion, restoration of oligotrophic sites requires profound disruptions of the nitrogen cycle such as topsoil removal, which are unusual in forests. Thus, the survival of these species depends on continued or reinstalled historic uses and primary succession after soil removal, as may occur in abandoned sandpits or quarries (Flinn and Vellend 2005).

Box 28. A comprehensive list of forest species of vascular plants, bryophytes, and lichens for Germany

For the first time, Schmidt et al. (2011) provided a comprehensive list of forest species of vascular plants, bryophytes, and lichens for Germany. As an extension of the concept of fidelity, lists of forest species categorize plants according to their affinity to forest vs. open land habitats. Regional differences in species behaviour are accounted for by separate evaluation within three major physiographic regions of Germany ((1) Northern Lowlands, (2) Hillsides and Low Mountains, and (3) Alps). The list of forest plants is differentiated into four groups of species that depend on forest habitats.

Fidelity classes:

1 restricted to forest habitats
  1.1 largely restricted to closed forest
  1.2 prefers forest edges and clearings

2 occurring in forest and open land
  2.1 occurs in forests as well as in open land
  2.2 may occur in forests, but prefers open land

The lists for bryophytes and lichens mention the substrates on which the species regularly dwell regardless of physiographic region. While some bryophytes and lichens are restricted to one single substrate (Ellenberg et alal. 2001), many have a broader ecological amplitude and are found on several substrate types (Figure 47).

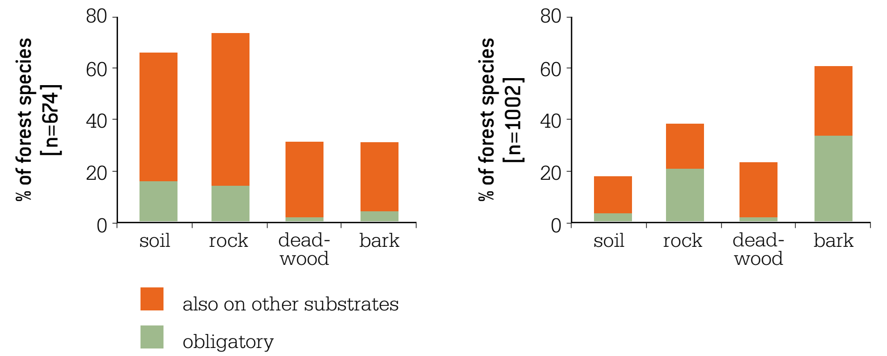


Figure 47. Forest bryophytes (left) and lichens (right) and their substrates: an analysis of the list of forest plants shows that a high proportion of bryophytes and lichens is confined to bark, deadwood, and rocks. Species growing on these substrates require specific conservation measures. Their assessment should complement monitoring of soil vegetation.

In their present form, the lists of forest species for the whole of Germany enumerate 1,216 vascular plants, 674 bryophytes, and 1,002 lichens. The list of vascular plants contains 76 trees, 4 epiphytes, 116 shrubs, and 1,020 herbaceous species.

In total, the three lists comprise 41 % of the vascular plant species, 58 % of the bryophyte species, and 51 % of the lichen species listed in the respective reference lists for Germany. Thanks to the higher ecological heterogeneity, forest species pools of the hillside and low mountain region are distinctly larger than those of the Northern Lowlands. Considering the small surface area, the pools of forest species in the Alps are also remarkable.

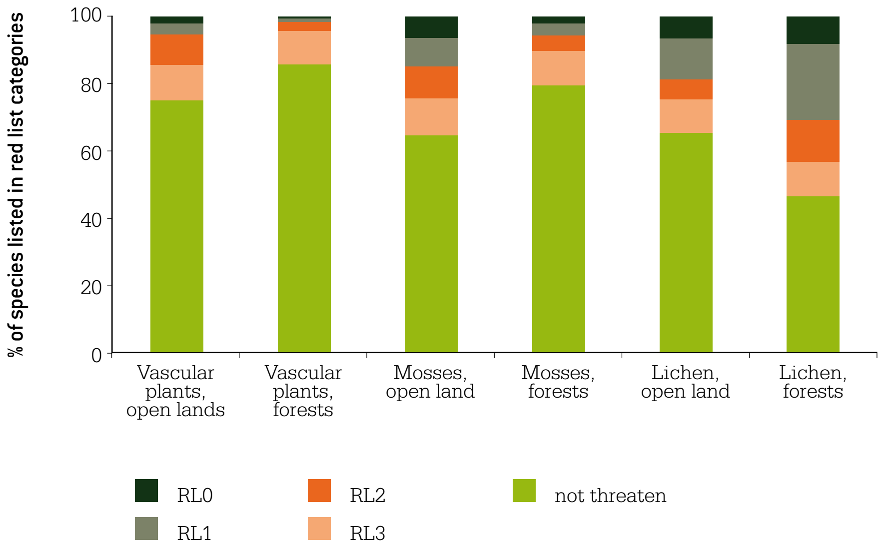


Figure 48. Comparison of red list status of forest plant species (categories 1.1, 1.2 and 2.1) and species of the open land (categories 2.2 and 0) in Germany. RL0: extinct or possibly extinct; RL1: critically endangered; RL2: endangered; RL3: vulnerable. Category “not threatened” subsumes unlisted species as well as all other red list categories.

Draining of wetlands and damming of floodplains have exerted broad-scale effects on forest sites, often leading to improved production, but severe habitat loss for specialised plants

Figure 49. Recurrent morphodynamics of wild alpine rivers initiate primary successions with oligotrophic sites and semi-open successional forests. Photo by J. Ewald.

Figure 50. Oligotrophic Scots pine forest on a raised bog in Upper Bavaria. Photo by J. Ewald.

Another important part of endangered vascular plants and bryophytes depend on wet forest habitats. Forest wetland plants are highly diversified according to nutrient supply, including oligotrophic raised bogs (Figure 50), minerotrophic fens, and alluvial forests. As long as the hydrology is left intact and adapted harvesting technology is employed, sustainable forestry and wetland conservation are compatible or even synergistic (i.e. by favouring oaks and rare tree species). Allowing and re-initialising natural geomorphodynamics may also restore oligotrophic sites in river floodplains, steep mountain slopes, and along coasts.

Epiphytic and epixylic diversity of forest plants in Central Europe has declined in the past 100–150 years due to removal of old trees and deadwood from managed forests

Old, crooked, damaged, and dead trees offer a wealth of microhabitats. Their removal results in a decline of biodiversity. Specialist species depend on such trees (Figure 51; Liira and Sepp 2009). Thus, certain lichen communities require deep furrows of thick, water-retaining bark and other cavities that are sheltered from rain. Bark chemistry on old and damaged trees is often more variable. Stemflow from rot holes in old beech trees raises bark pH locally and thereby supports epiphyte diversity and rare species. Many extinct or red-listed epiphytic bryophytes and lichens are sensitive to air pollution, especially sulphur dioxide and nitrogen oxides (Bobbink et al. 1998, Hauck et al. 2013). Air quality has improved during the last decades, but sensitive species are returning extremely slowly due to dispersal limitation.

Figure 51. Specialist species are solely restricted to old, crooked, damaged, and dead trees. *Lobaria pulmonaria*, Vosges, France. Photo by H. Bültmann.

Figure 52. Rocks are refugia of endangered cryptogams in forested areas, Sauerland, North Rhine-Westphalia. Photo by H. Bültmann.

The hardness, structure, and chemistry of deadwood not only depend on tree species, but also on the size of the deadwood element. In particular, coarse woody debris can retain considerable amounts of water, providing a constantly moist substrate and sustaining a high diversity of epixylics. Species numbers, especially of liverworts, are often particularly high in a microclimate of constant high air humidity. In contrast to vascular plants, which usually profit from enhanced light levels, opening the tree canopy can reduce humidity, damage shade-tolerant species, and may result in a decline of epixylic growth (Rose and Coppins 2002).

A considerable proportion of threatened forest vascular plants, bryophytes, and lichens are bound to special habitats in forests

Biotopes such as springs, streamlets, fens, stones, rocks, or boulder slopes are a characteristic part of many forests (Figure 52). Such sites have ecological conditions that differ from those of the surrounding forest. Their vegetation is specific and adds disproportionally to the diversity of species. Although tree cover or location in a forest is not essential for their existence, these communities depend on shading and a microclimate typically found in forests. Bryophytes and lichens growing on rocks can serve as an example: According to the list of forest plants in Germany (Schmidt et al. 2011), 73 % of forest bryophytes and 39 % of forest lichens use this substrate (Figure 47). These special habitats are protected by law and must be respected by forestry. Shaded and exposed rocks can carry very different assemblages of rare bryophytes and lichens. Both may suffer from changes in meso- and microclimate, as induced by felling (shaded rocks) or dense coniferous thickets (open rocks). Sensitive special habitats require special protection, e.g. against depositing slash.

Figure 53. Ancient deciduous woodland site in the Northern Lowlands near Uelzen (Lower Saxony) with some ancient forest species such as *Anemone nemorosa* and *Melica uniflora*. Photo by M. Schmidt.

Land-use history and habitat continuity has substantial impacts on ecological processes and plant species composition in forest ecosystems

In many parts of Europe, forests have undergone cycles of deforestation and conversion to agricultural land followed by forest recovery, resulting in considerable differences in the composition of understory vegetation between ancient (Figure 53) and recent forests. Former agricultural use impacts species composition directly (local elimination of plants and propagules of forest species) or indirectly (altered environmental conditions, fertilization, and eutrophication, often persisting for centuries; Flinn and Vellend 2005). Because of the direct effects, recent forests have to be recolonised by forest plants. However, ancient forest species are mostly long-lived perennials with the capacity to reproduce clonally, but unfit for long-distance seed dispersal (Verheyen et al. 2003). Like vascular plants, epiphytic bryophytes and lichens differ widely in their ability to recolonise. Some slow dispersers are very specific indicators of forest continuity. Restoration of recent forests is therefore a question of time, spatial arrangement, and connectivity.

As forest cover and history differ between regions, the indicator value of ancient forest species requires accounting for regional differentiation

In the northwestern lowlands of Germany, overall forest cover is low (10 to 25 %), and only one quarter of these forests are classified as ancient (Figure 54). In contrast, the northeastern lowlands have ca. 50 %, and the mountain regions of Germany, where total forest cover is considerably higher than in the lowlands, have some 90 % of ancient forests.

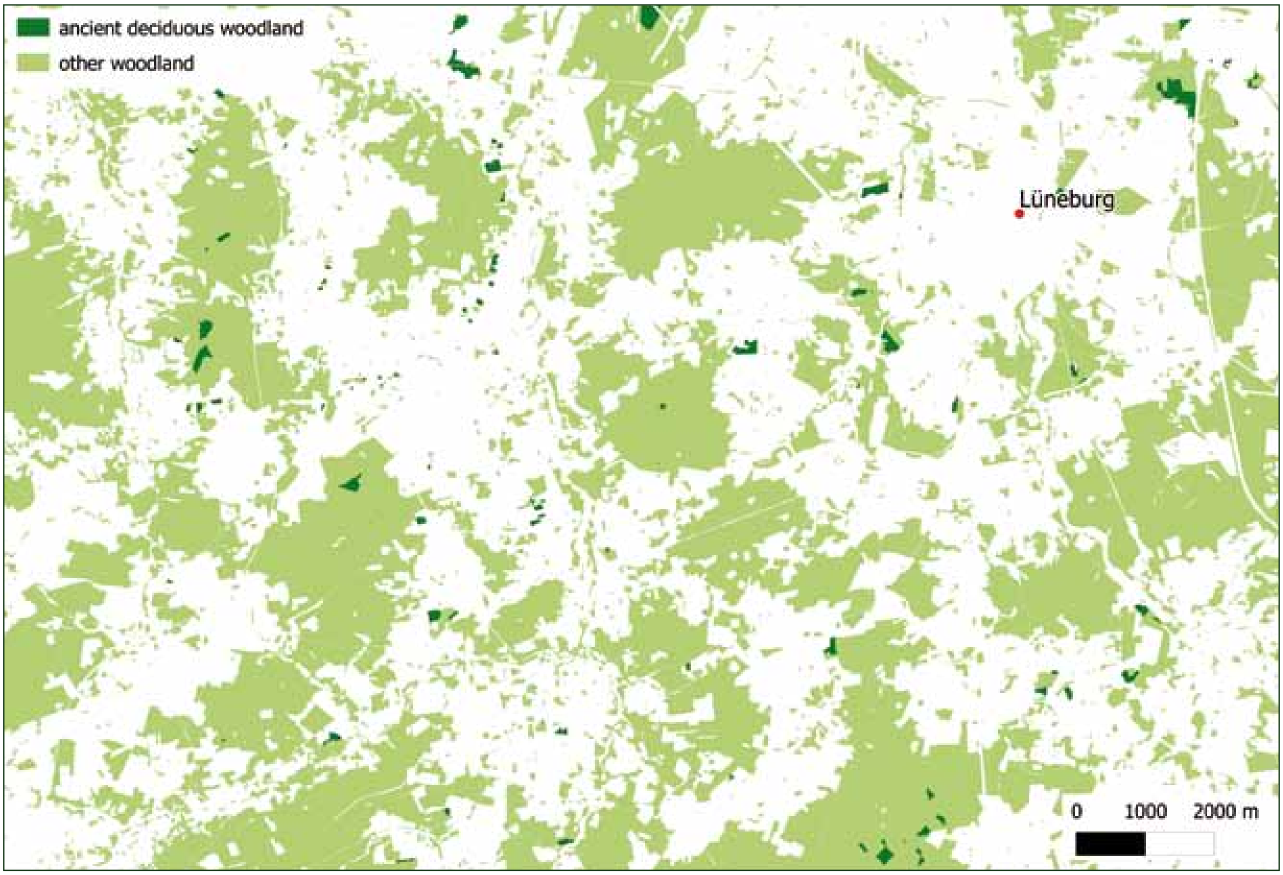


Figure 54. Example for the distribution of ancient deciduous woodland and other woodland in the Northern Lowlands.

Box 29. Recommendations for management

Managing for plant biodiversity must take account of the different requirements of this large number of forest plants. Considering the diversity of life forms and realized ecological niches, there cannot be a single recipe to protect all forest plants. Nevertheless, some general principles can be recommended:

1. Close-to-nature forestry

Forest management should prefer native tree species, and it should aim to retain and emulate elements of natural forest communities. Thus, naturally regenerating native tree species, both of site-specific climax stages and pioneer phases, should be allowed their place in managed forests. Game populations should allow regeneration of all native tree species. Roads and skidding lines should be spaced at distances that leave sufficient area of untouched forest floor for a typical understorey to develop.

2. Respect ecological gradients and habitat diversity

Natural gradients of moisture, pH, and nutrients, as depicted in site maps, offer niches for many different forest plants. Special habitats are protected by EU or regional law if they conform to the respective legal requirements. These special habitats often harbour a large number of rare or endangered species, and, thus, maintaining and restoring these sites has a disproportionally large effect on biodiversity. Special habitats and their surroundings should be excluded from commercial forestry use but managed under a conservation regime. Furthermore, all stages of forest development in proportions corresponding to the natural disturbance regime should be maintained. Thus, the continuous cover strategy may have to be supplemented by concepts to preserve all native tree species and forest community types.

3. Respect old growth structures, deadwood, and groups of large trees with epiphytes

Management should leave and create niches for epiphytic and epixylic bryophytes and lichens that require old trees, deadwood, and certain key tree species. Shade and humidity should be maintained by selective logging and retention. As continuity of microclimate is important for bryophytes and many lichens, it is also essential to retain large groups of trees without harvesting.

4. Respect forest continuity and counteract fragmentation

In agricultural landscapes, especially in Central European lowlands, the value of forest islands for plant conservation depends on historical continuity. Here, conservation management should be focused on ancient forest remnants and their reconnection by habitat corridors. In regions with a low proportion of ancient forest sites, the remaining ancient deciduous forests should not be converted to coniferous or deciduous-coniferous forests for economic reasons.

5. Respect and continue traditional forest management

Traditional forest uses such as forest pasture, coppicing, and coppice-with-standards have almost become extinct in Central Europe and persist only in a few localized regions. Yet many of the older stands still bear legacy features of these practices that can be of high conservation value. Thus, wooded pastures are hotspots of threatened old-growth and deadwood specialists such as beetles and moths, cavity-breeding birds, and saproxylic fungi. Coppicing favours light-demanding organisms, such as rare tree and shrub species with high capacity to resprout, flowering plants, butterflies, and photophytic epiphytes.

> *High proportions of forest species in the total floras of the three plant groups underpin the great responsibility that forestry holds for preserving biodiversity in Central Europe*

All members of the lists of forest species should be treated first and foremost as forest plants, even when they occur in, or even prefer, open land. In the practice of forest conservation, specialists restricted to forest habitats will often be the main focus. However, in the face of increasing pressures on open land habitats (land-use intensification, eutrophication, urbanization), forests are gaining importance as refuges for threatened plants of broader amplitude (Box 28, groups 2.1, 2.2).

References

Bobbink, R., Hornung, M. and Roelofs, J. G. M. 1998. *The effects of air-borne pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86:717–738.*

Braun-Blanquet, J. 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde. 3. Aufl., Berlin, Wien, New York. 865 p.*

Ellenberg, H. and Leuschner, Ch. 2010. *Vegetation Mitteleuropas mit den Alpen. 6. Aufl., Ulmer-Verlag, Stuttgart. 1334 p.*

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. 2001. *Zeigerwerte von Pflanzen in Mitteleuropa. 3. Aufl. Scripta Geobotanica 18:1–262.*

Flinn, K.M. and Vellend, M. 2005. *Recovery of forest plant communities in post-agricultural landscapes. Frontier in Ecology and the Environment 3:243–250.*

Gilliam, F.S. 2007. *The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845–858.*

Hauck, M., de Bruyn, U. and Leuschner, Ch. 2013. *Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. Biological Conservation 157:136–145.*

Liira, J. and Sepp, T. 2009. *Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46:308–325.*

Rose, F. and Coppins, A.M. 2002. *Site assessment of epiphytic habitats using lichen indices. In: Nimis, P.L., Scheidegger, C. and Wolseley, P.A. (eds.) Monitoring with Lichens – Monitoring Lichens. [NATO Science Series IV. Earth and Environmental Sciences Vol. 7]. Kluwer Academic Publishers, Dordrecht, Boston, London. Pp 343–348.*

Schmidt, M., Kriebitzsch, W.-U. and Ewald, J. (eds.) 2011. *Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. BfN-Skripten 299:1–111 p.*

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. and Foster, D.R. 2003. *Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91:563–577.*

3.4 Biodiversity of mycorrhizal fungi as a crucial player in forest ecosystem functioning

Martina Peter, Marc Buée and Simon Egli

More than 6,000 mycorrhizal fungi live in forest ecosystems worldwide, fulfilling important functions in nutrient and water mobilisation. A high diversity of these fungi in forests is important for the functioning and resilience of forest ecosystems, allowing them to adapt to changing environmental conditions

Fungi are important components of forest ecosystems. As saprotrophic degraders, they are essential players in the nutrient turnover of litter and wood, and as parasites, they enhance forest dynamics. Fungi also have a fundamental role as symbiotic partners of forest trees through the so-called mycorrhizal symbiosis (see Box 30). In this chapter we focus on the biodiversity of these symbiotic fungi, the role they play in forest resistance and resilience, and what factors impact this diversity.

Box 30. Mycorrhizal symbiosis

The mycorrhizal symbiosis is a mutualistic interaction between a fungus (Greek "myco") and the fine roots (Greek "rhiza") of a vascular plant. The fungus colonises the roots of the host plant by penetrating either into the cells as in arbuscular mycorrhizal fungi, or between the cells and forming a fungal sheath around the roots as in ectomycorrhizal fungi. At the interface between the two partners, sugars delivered from the plant are exchanged for water and mineral nutrients provided by the fungus. Fungal hyphae are much smaller in diameter than root hairs and proliferate farther away from the roots, which gives the roots access to nutrients and water from a bigger soil volume than they would be able to access alone. By secreting enzymes, fungi can acquire nutrients from organic matter, and by secreting antibiotic substances, they protect tree roots from pathogenic organisms. In temperate and boreal forests, ectomycorrhizal symbiosis is the dominant form (Figure 55). Almost all tree species in this region form ectomycorrhizas, and non-colonised root tips are rarely observed in nature because this association is obligate in many cases. Most mycorrhizal fungi are not able to grow and complete their life cycle without plants, and many plants cannot acquire enough soil resources to prosper and reproduce under natural conditions without their fungal symbionts. Each tree can be associated with more than a hundred different ectomycorrhizal fungal species. The hyphal networks of these fungi interconnect different trees within a forest, which can be seen as a wood-wide web. Recommended reading: Smith and Read (2008).

Figure 55. Mycorrhizal association between a young Norway spruce and the mycorrhizal fungus Hebeloma mesophaeum, which forms a bright mantle around the fine roots and produces a yellowish external mycelium that colonises the surrounding soil. Photo by S. Egli.

Most edible forest fungi such as the boletes, the truffles, and the chanterelles are obligate symbionts of forest trees. Some of them are generalist species that can associate with different tree species, and some of them are specialists such as the Larch bolete, which can only live in association with larch. There are at least 6,000 fungal species that have been shown to live in symbiosis with tree species, but estimates of species that form this association go up to 25,000 species worldwide (Tedersoo et al. 2010). The diversity within forest stands is usually high. It varies with forest structure and site conditions, increases with tree species diversity, and even goes up to more than 100 mycorrhizal fungal species in monoculture forests (Horton and Bruns 2001). A single tree can live in symbiosis with hundreds of different fungal species, which form mycorrhizas in close vicinity to each other on the fine roots (Figure 56), and this community is very dynamic in space and time (Bahram et al. 2011; Coince et al. 2013). The diverse fungal species associated with a single tree or multiple trees can occupy different habitat niches. For example, a pronounced vertical distribution of fungal species has been detected in diverse forest and soil types (e.g. Coince et al. 2013). This indicates that different mycorrhizal fungal species may have complementary functional abilities that together allow them to optimally exploit the available soil resources.

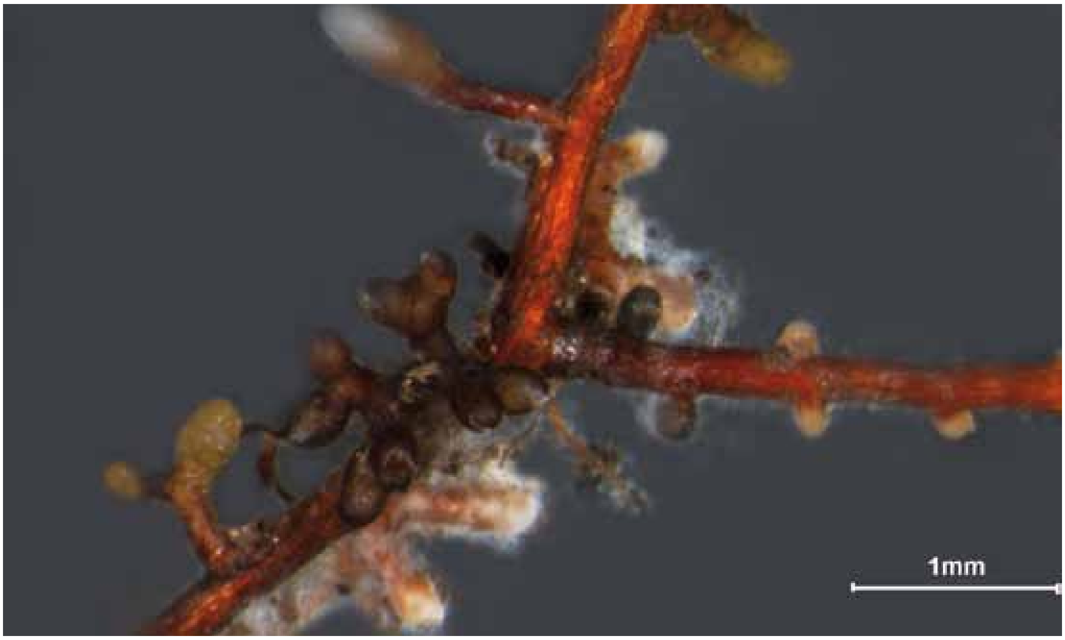


Figure 56. A short piece of the fine roots of Scots pine colonised by several mycorrhizal fungi that show diverse morphological characteristics. Photo by S. Hutter.

Mycorrhizal fungi secrete extracellular enzymes involved in the decomposition of organic matter. The activities of these enzymes can be measured and help describe the functional role of mycorrhizal fungi

New emerging techniques allow to study the functional diversity of mycorrhizal fungi under natural conditions in forests (Courty et al. 2010). One of the most important functions of these fungi is the enhanced nutrient uptake of forest trees. Therefore, the functional abilities of nutrient mobilisation from organic material were tested in several forest ecosystems and under diverse environmental conditions (Pritsch and Garbaye 2011). These studies show that species do have different functional abilities in enzymatic activities, e.g. for nitrogen acquisition by degrading proteins in the soil or in lignin degradation (see Figure 57, Hutter et al. in prep). Whereas some mycorrhizal species complement each other, some are redundant in these functions but are sometimes adapted to other soil conditions and might be complementary in additional functions such as water uptake (Buée et al. 2007, Jones et al. 2010, Rineau and Courty 2011). Therefore, on the one hand, high diversity in the mycorrhizal fungal community is of great importance for forest trees to optimally exploit soil resources through the different functional abilities of single species. On the other hand, a high diversity allows the mycorrhizal community to respond to changing environmental conditions and disturbances by modifying the community towards better-adapted species that maintain important ecosystem functions.

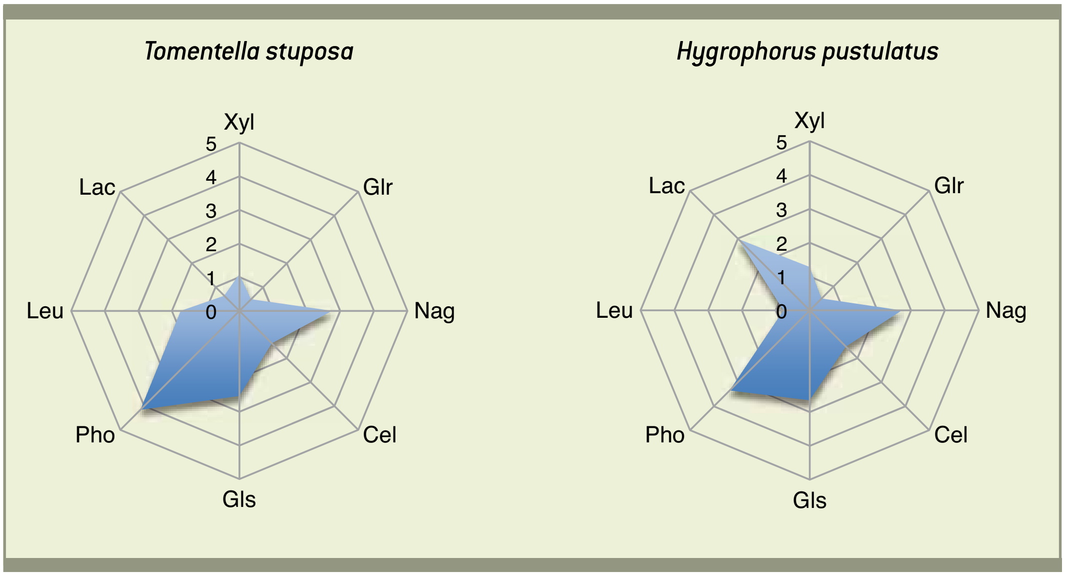


Figure 57. Different mycorrhizal species have different functions in a forest ecosystem. Activity profiles of eight enzymes involved in organic matter degradation from two abundant mycorrhizal species in a subalpine Norway spruce stand. Xyl = Xylosidase, Glr = Glucuronidase, Nag = Chitinase, Cel = Cellobiohydrolase, Gls = Glucosidase, Pho = Phosphatase, Leu = Leucine aminopeptidase, Lac = Laccase. Values are activities in ln pmol/min/mm^2. Source: own data, unpublished.

> *Mycorrhizal fungi form underground hyphal networks that link trees to each other and allow nutrients, water, and carbon to be transferred. They facilitate the regeneration of seedlings, particularly in harsh environments such as those that prevail after windthrow or during drought. The importance of these networks will become more critical to the stability of forest ecosystems under the predicted climate change scenarios*

A tree is associated with many fungal species, and a single mycorrhizal fungal mycelium can link the roots of several plants of one or more species in a mycorrhizal network (Simard et al. 2012). This network can transfer carbon, nutrients, and water between the plants and is particularly important for colonising new seedlings and enhancing regeneration. Recently, it has been shown that this mycorrhizal network can also act as an underground messaging system between plants that allows neighbouring plants to invoke herbivore defences before being attacked (Babikova et al. 2013). The facilitating effect of regeneration is more important where tree seedlings are establishing under high abiotic stress such as drought and where fungal inoculum is low. This has been shown in diverse growth chamber and field studies using mesh bags with different pore sizes that control the passage of roots and/or mycelia. With climate warming, it is expected that the severity and duration of drought will increase, and therefore the maintenance of intact mycorrhizal networks will become more critical to the stability of forest ecosystems (Simard and Austin 2010).

By facilitating the regeneration of plants that have access to the network, mycorrhizal fungi can impact plant community dynamics. They may change the competitive ability of plants that can or cannot link to the network or to some of the fungal species present in them (Simard et al. 2012). Furthermore, it has been shown that mycorrhizal fungal diversity affects plant diversity and productivity. At least for arbuscular mycorrhizal systems in grasslands, we have clear evidence for this (van der Heijden et al. 1998). In addition, experiments with tree seedlings show that the composition and number of mycorrhizal fungi impacts seedling productivity. This can be explained by the more efficient use of available resources by different mycorrhizal species as outlined above but also by the greater chance of a fungal species being present that particularly promotes plant growth (Kipfer et al. 2012).

Mycorrhizal diversity usually increases with forest diversity and successional stage. After disturbances such as clear-cut, wild fire, or windthrow, mycorrhizal diversity is higher in the initial stand stages when vital remnants of trees and tree seedlings are left over

Whereas mycorrhizal species may affect the growth and composition of tree species in a forest, the opposite is also true. That is, both the species composition and successional stage of the forest impacts mycorrhizal diversity and community composition. Generally, the number of fungal species increases with stand age, most pronouncedly until canopy closure, and the fungal community composition stabilizes in the stand reinitiation stage (Dahlberg 2001; Twieg et al. 2007). The different colonisation strategies, resource use, and competitive abilities of fungi help explain these patterns. Some fungi are able to rapidly colonise a site after disturbance by spores or resistant propagules, whereas others need an intact mycorrhizal network that connects them to another tree for colonisation. Early stage fungi generally persist on the root system and are later augmented by additional fungi that have different colonisation strategies and resource uses. After disturbances such as clear-cut, wildfire, or windthrow, these patterns are most pronounced when no stumps and vital roots are left over from which mycorrhizal fungi can recolonise new roots. When such vital remnants are present, the mycorrhizal fungal diversity is already much higher in the initial stand stages.

Mycorrhizal diversity can be assessed by fruitbody monitoring or by molecular analysis of soil or root samples

Since the diversity of mycorrhizal fungi is crucial for the functioning and resilience of forest ecosystems, it is important to have tools to assess it and to understand which factors can impact it. Traditionally, the diversity of mycorrhizal fungi has been surveyed by monitoring fruitbodies above ground. Although these surveys often do not reflect the functionally important composition of mycorrhizas below ground on the root system of trees and in the soil, it is the part of the fungi that we perceive and appreciate for recreation and as a non-wood forest product. They are of course also very important in producing spores that colonise disturbed sites and ensure genetic regeneration. It is the belowground fungal structures, however, that provide direct functions for forest ecosystems. Molecular techniques have revolutionized mycorrhizal ecology because they provide the means to accurately assess this huge hidden fungal species composition where the morphological characteristics of mycelia or mycorrhizas are limited. Molecular studies have revealed that many functionally important and abundant mycorrhizal species do not form large conspicuous fruitbodies and are therefore overlooked in above ground surveys (Horton and Bruns 2001). On the other hand, because mycorrhizal species are spatially very heterogeneously distributed in the soil, belowground root or soil sampling may provide an incomplete picture of the real diversity, and rare species may be overlooked even though they are present as fruitbodies.

Generally, the mycorrhizal community consists of a few abundant species and a long list of rare species (Dahlberg 2001). Several factors, such as natural disturbances, forest management, and anthropogenic pollution, impact this diversity and structure, in most cases by changing the competitiveness and dominance of the species present. Under severe disturbances, species richness is impacted, lowering the potential resistance to additional stresses or even reducing ecological function. In the following section we will outline the most prominent factors that affect the mycorrhizal community and how management could help maintain forest stability in this regard.

> *Nitrogen fertilization of forests through atmospheric deposition or direct fertilizer inputs reduces the fruitbody production of mycorrhizal fungi and decreases mycorrhizal diversity. A strong reduction of the mycorrhizal species pool increases the vulnerability of the forest ecosystem to additional stresses since appropriate adaptation of the mycorrhizal community and the maintenance of its functions may no longer be guaranteed*

In the last decades, nitrogen (N) deposition has strongly increased through the combustion of fossil fuels and industrial fixation of N for intensive agricultural activities. Ectomycorrhizal symbiosis is generally regarded as an adaptation to the N-limited conditions that prevail in temperate and boreal forest ecosystems. The higher availability of this nutrient is therefore expected to have a large impact on the mycorrhizal community. Several field studies along gradients or in fertilization experiments show a significant decline in mycorrhizal diversity (Cox et al. 2010; Lilleskov et al. 2011). Whereas fruit body production is drastically and persistently reduced shortly after nitrogen supply, the belowground species diversity significantly changes over the long term. At higher N levels, plants invest less carbon in roots and mycorrhizal partners but allocate more in aboveground biomass. Our own studies of a fertilization experiment in a subalpine spruce forest shows that not only did species abundance of fruitbodies and at the root system change prominently, but also that species richness was significantly reduced due to nitrogen addition (Gillet et al. 2010, Peter et al. 2001). We investigated the functional meaning of such a community change by looking at extracellular enzyme activities. The functions of the most abundant species were complementary within but redundant between treatment plots. The analyses revealed that although mycorrhizal fungi show species-specific

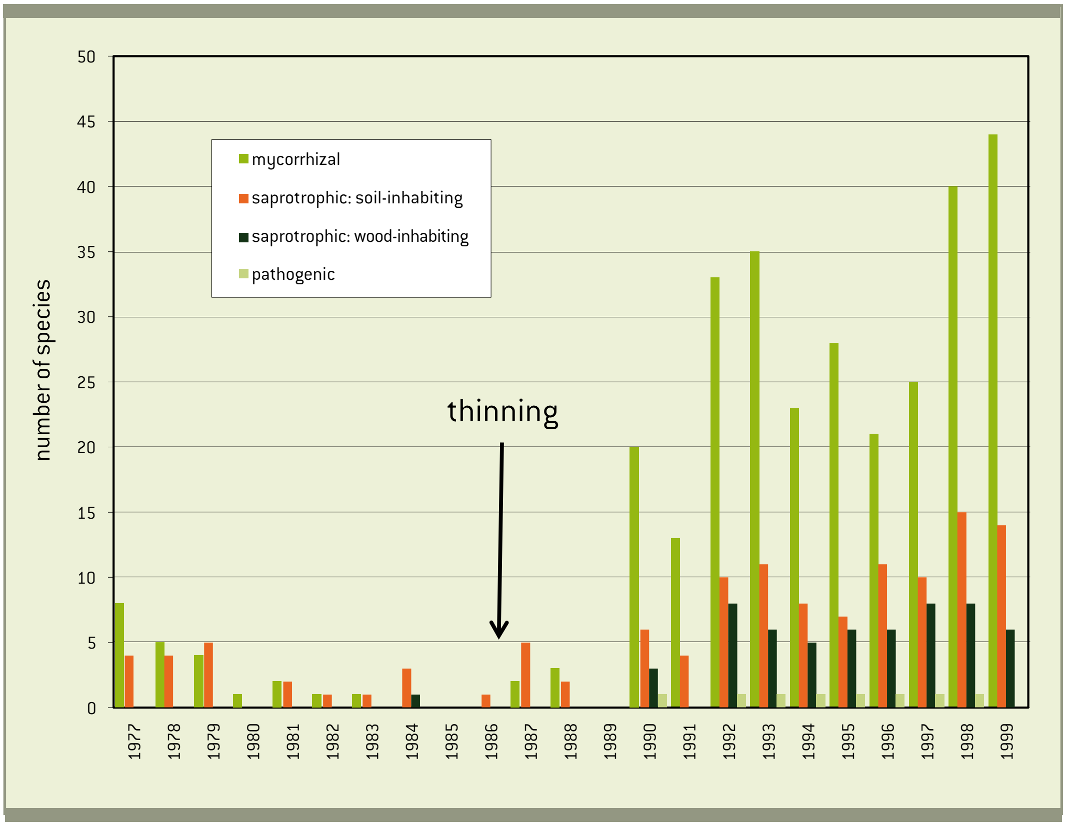


Figure 58. Positive effect of an increment thinning on fruitbody production of fungi (mycorrhizal, saprotrophic, and pathogenic species). The thinning comprised a 46% reduction of the overstory trees in a dense old-growth beech forest in Switzerland. Source: Modified from Egli et al. 2010.

enzymatic profiles, the overall enzyme activity per mm2 root surface remained constant in the fertilization and control plots. The functions were taken over by redundant but better-adapted species. Similar reactions of an ectomycorrhizal community to fertilization were observed by Jones et al. (2012). This indicates that forest ecosystems were resilient to fertilization stress in regard to the tested functions. However, since mycorrhizal species richness is significantly reduced by nitrogen fertilization, the ecosystem may be more vulnerable to additional stresses when the available species pool no longer allows an appropriate adaptation.

Climate change factors, such as increased CO_2 levels, drought, and soil warming, show less clear and inconsistent effects (review in Pickles et al. 2012). Generally, enhanced CO_2 levels and soil temperatures are expected to increase plant productivity and with it their mycorrhizal partners since more carbon will be allocated to the roots to meet nutrient and water demands. Likewise, reduced precipitation should promote plants to invest more in roots to scavenge for water. Field studies show both increasing and decreasing mycorrhizal diversity at the root level, but in most cases a community change. The production of fruitbodies generally increases under higher CO_2 levels and temperature (Büntgen et al. 2013). This will impact spore dispersal and community composition and, of course, is of interest in terms of the economic value of mushrooms as non-wood forest products.

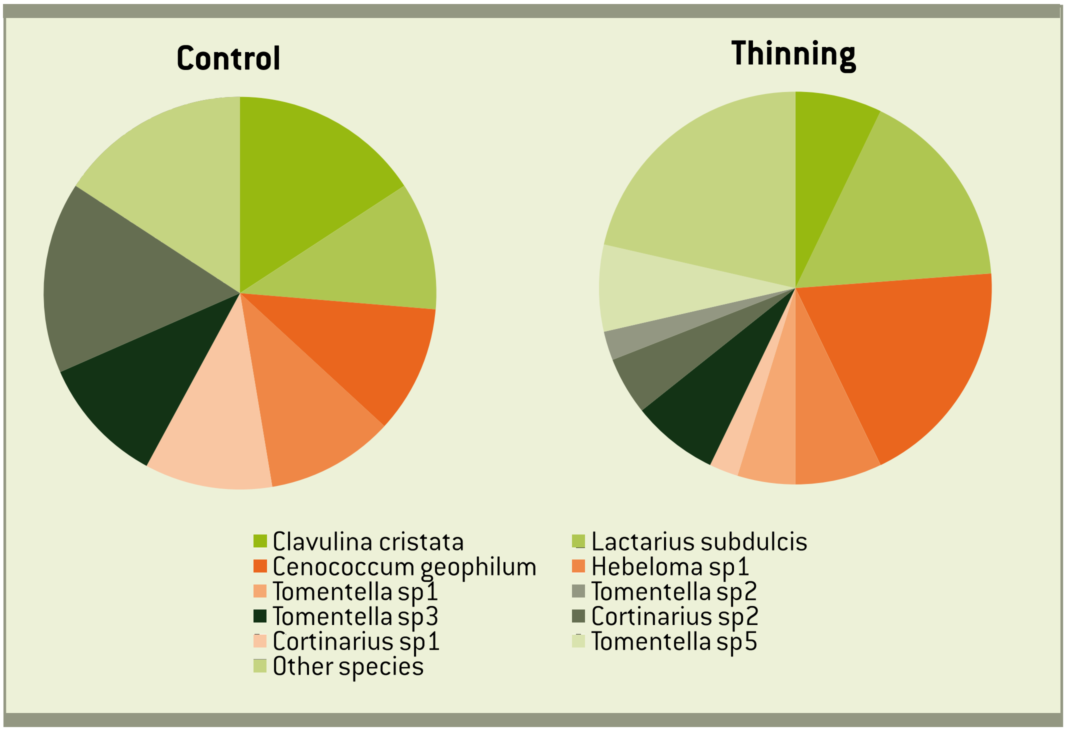


Figure 59. Thinning impacts the mycorrhizal species composition on the root system and slightly increases its species richness. The silvicultural treatment resulted in a 76% reduction of the trees in an 80-year-old beech forest in France. Source: Modified from Buée et al. 2005.

Although the effect of climate change factors and their interaction on mycorrhizal communities is complex and difficult to predict, it is likely that these communities will help stabilize forest ecosystems under the predicted climatic scenarios (Simard and Austin 2010). Management practices should therefore consider the functional importance of mycorrhizal fungi and their networks in the natural regeneration and resilience of forests. The effect of thinning on mycorrhizal communities has been studied in several forest ecosystems. After an increment thinning in a Swiss mixed beech forest, our studies showed a significant increase in above ground species richness and the number of fruitbodies produced, particularly of mycorrhizal fungi (see Figure 58). In a French beech forest, we observed a less prominent increase in species richness belowground and a significant shift in the mycorrhizal community composition (see Figure 59), which was also observed in a *Pinus contorta* stand in Canada (Teste et al. 2012).

Thinning on the one hand enhances tree growth and probably below ground carbon allocation and on the other hand alters the light and soil water conditions, which can explain the response of the mycorrhizal community. Extensive studies in Douglas-fir stands in British Columbia, however, showed that targeted removal of old and large trees with patches of smaller trees left over for seed dispersal clearly decreased the success of seedling establishment. The seedlings showed lower mycorrhizal diversity and received less nutrients and water than those that had access to a mycorrhizal network connected to an old tree (Simard and Austin 2010). Therefore, moderate thinning with some old trees left over seems to be optimal for both the mycorrhizal community as well as the success of natural forest regeneration.

Box 31. Recommendations for management

- Moderate thinning of dense forests with some old trees left over may increase biodiversity and fruitbody production of mycorrhizal fungi.
- Clearcutting should be avoided.
- Strong thinning should leave old residual trees to guarantee rapid establishment of the mycorrhizal network and its diversity. This enhances the success of seedling establishment and natural regeneration.
- Similarly, care should be given to residual trees and seedlings after windthrow as refuges to re-establish mycorrhizal networks.
- Diversity of tree species and tree age classes in a forest increases the diversity of mycorrhizal fungi.
- Nitrogen fertilization in forests should be minimized.

References

Babikova, Z., Gilbert, L., Bruce, T.J.A., Birkett, M., Caulfield, J.C., Woodcock, C., Pickett, J.A. and Johnson, D. 2013. *Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. Ecology Letters 16(7): 835–843.*

Bahram, M., Põlme, S., Kõljalg, U. and Tedersoo, L. 2011. *A single European aspen (Populus tremula) tree individual may potentially harbour dozens of Cenococcum geophilum ITS genotypes and hundreds of species of ectomycorrhizal fungi. Fems Microbiology Ecology 75:313–320.*

Buée, M., Courty, P.E., Mignot, D. and Garbaye, J. 2007. *Soil niche effect on species diversity and catabolic activities in an ectomycorrhizal fungal community. Soil Biology and Biochemistry 39:1947–1955.*

Buée, M., Vairelles, D. and Garbaye, J. 2005. *Year-round monitoring of diversity and potential metabolic activity of the ectomycorrhizal community in a beech (Fagus silvatica) forest subjected to two thinning regimes. Mycorrhiza 15:235–245.*

Büntgen, U., Peter, M., Kauserud, H. and Egli, S. 2013. *Unraveling environmental drivers of a recent increase in Swiss fungi fruiting. Global Change Biology 19(9):2609–2928.*

Coince, A., Caël, O., Bach, C., Lengellé, J., Cruaud, C., Gavory, F., Morin, E., Murat, C., Marçais, B. and Buée, M. 2013. *Below-ground fine-scale distribution and soil versus fine root detection of fungal and soil oomycete communities in a French beech forest. Fungal Ecology 6:223–235.*

Courty, P.-E., Buée, M., Diedhiou, A.G., Frey-Klett, P., Le Tacon, F., Rineau, F., Turpault, M.-P., Uroz, S. and Garbaye, J. 2010. *The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and emerging concepts. Soil Biology and Biochemistry 42:679–698.*

Cox, F., Barsoum, N., Lilleskov, E.A. and Bidartondo, M.I. 2010. *Letter: Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. Ecology Letters 13:1103–1113.*

Dahlberg, A. 2001. *Community ecology of ectomycorrhizal fungi: an advancing interdisciplinary field. New Phytologist 150:555–562.*

Egli, S., Ayer, F., Peter, M., Eilmann, B. and Rigling, A. 2010. *Is forest mushroom productivity driven by tree growth? Results from a thinning experiment. Annals of Forest Science 67.*

Gillet, F., Peter, M., Ayer, F., Bütler, R. and Egli, S. 2010. *Long-term dynamics of aboveground fungal communities in a subalpine Norway spruce forest under elevated nitrogen input. Oecologia 164:499–510.*

Horton, T. and Bruns, T.D. 2001. *The molecular revolution in the ectomycorrhizal ecology: peeking into the black-box. Molecular Ecology 10:1855–1871.*

Hutter S., Egli S., Maire R., Garbaye J., Peter M. *In prep. Enzyme activities show a stronger dependency on ectomycorrhizal fungal types than on long-term nitrogen addition and season in a spruce forest.*

Jones, M.D., Phillips, L.A., Treu, R., Ward, V. and Berch, S.M. 2012. *Functional responses of ectomycorrhizal fungal communities to long-term fertilization of lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm.) stands in central British Columbia. Applied Soil Ecology 60:29–40.*

Jones, M.D., Twieg, B.D., Ward, V., Barker, J., Durall, D.M. and Simard, S.W. 2010. *Functional complementarity of Douglas-fir ectomycorrhizas for extracellular enzyme activity after wildfire or clearcut logging. Functional Ecology 24:1139–1151.*

Kipfer, T., Wohlgemuth, T., Van Der Heijden, M.G.A., Ghazoul, J. and Egli, S. 2012. *Growth response of drought-stressed* Pinus sylvestris *seedlings to single- and multi-species inoculation with ectomycorrhizal fungi. PLoS ONE 7, e35275.*

Lilleskov, E.A., Hobbie, E.A. and Horton, T.R. 2011. *Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. Fungal Ecology 4:174–183.*

Peter, M., Ayer, F. and Egli, S. 2001. *Nitrogen addition in a Norway spruce stand altered macromycete sporocarp production and below-ground ectomycorrhizal species composition. New Phytologist 149:311–325.*

Pickles, B.J., Egger, K.N., Massicotte, H.B. and Green, D.S. 2012. *Ectomycorrhizas and climate change. Fungal Ecology 5:73–84.*

Pritsch, K. and Garbaye, J. 2011. *Enzyme secretion by ECM fungi and exploitation of mineral nutrients from soil organic matter. Annals of Forest Science 68:25–32.*

Rineau, F. and Courty, P.-E. 2011. *Secreted enzymatic activities of ectomycorrhizal fungi as a case study of functional diversity and functional redundancy. Annals of Forest Science 68:69–80.*

Simard, S. and Austin, M. 2010. *The role of mycorrhizas in forest soil stability with climate change. In: Simard, S. (ed.) Climate change and variability.http://www.intechopen.com/books/climate-change-and-variability/the-role-of-mycorrhizas-in-forest-soilstability-with-climate-change.*

Simard, S.W., Beiler, K.J., Bingham, M.A., Deslippe, J.R., Philip, L.J. and Teste, F.P. 2012. *Mycorrhizal networks: Mechanisms, ecology and modelling. Fungal Biology Reviews 26:39–60.*

Smith, S.E. and Read, D.J. 2008 *Mycorrhizal symbiosis, London, Academic press.*

Tedersoo, L., May, T. and Smith, M. 2010. *Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20:217–263.*

Teste, F., Lieffers, V. and Strelkov, S. 2012. *Ectomycorrhizal community responses to intensive forest management: thinning alters impacts of fertilization. Plant and Soil 360:333–347.*

Twieg, B.D., Durall, D.M. and Simard, S.W. 2007. *Ectomycorrhizal fungal succession in mixed temperate forests. New Phytologist 176:437–447.*

Van Der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. and Sanders, I.R. 1998. *Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72.*

3.5 Lichens: sensitive indicators of changes in the forest environment

Juri Nascimbene, Anna-Liisa Ylisirniö, Juha Pykälä and Paolo Giordani

Lichens are a species-rich component of the forest biota that contributes to forest functioning

Lichens are composite organisms consisting of a symbiotic association of a fungus with a photosynthetic partner, which is either a green alga or cyanobacterium. They are a species-rich component of the forest biota, occurring on many substrates, including trees, bare rocks, and exposed soil surfaces. Epiphytic lichens growing on tree trunks and branches play an important role in forest ecosystem functioning (Ellis 2012). They affect water cycling by retaining precipitation in the canopy, and cyanobacterial lichens influence nutrient cycling by fixing atmospheric nitrogen. They are a crucial component in forest food webs, increasing microhabitat complexity and the diversity of forest invertebrate fauna, which in turn serve as food for a variety of passerine bird species.

The physiology of lichens is closely coupled to ambient moisture, temperature, and light conditions such that their geographical distribution is expected to be associated with climatic gradients. Many lichens are habitat specialists with exact micro- and macrohabitat requirements. Most epiphytic lichens prefer half-shady conditions (natural old-growth forests tend to be less shady than managed forests), and many of them are sensitive to abrupt changes in light conditions. Some epiphytes require shady habitats and are very sensitive to direct sunlight. Most lichens are also sensitive to air pollution (sulphur dioxide and nitrogen deposition), which shapes forest lichen richness and composition. Recently, the diversity of functional groups of sensitive epiphytic lichens was used to set critical loads of nitrogen deposition in forest ecosystems of Europe and North America. However, along with climate and air pollution, forest management is a key direct control of epiphytic lichen diversity in forest ecosystems (Aragón et al. 2010; Johansson 2008; Nascimbene et al. 2013). Epiphyte diversity is related to forest structure and dynamics, and several environmental factors relevant to their dispersal, establishment, and maintenance are affected by forest management. Studies on lichen diversity clearly demonstrate dramatic losses of species caused by forest management in European temperate and boreal forests (e.g. Hauck et al. 2013). The main negative effects of forestry are related to the lack of old trees, short rotation cycles, excessive canopy cover, or excessive exposure to direct light in the final part of the rotation cycle, lack of substrate, particularly for dead-wood dwelling species, decrease of structural diversity, lack of forest continuity and forest fragmentation (Nascimbene et al. 2013). Additional negative impacts are caused by the edge effect (i.e. changes in environmental conditions of a forest stand due to cutting of a bordering stand) and large-scale drainage that decreases air humidity and moisture of tree bases and logs (Hauck et al. 2013).

Figure 60. *Lobaria pulmonaria* is an easily identifiable epiphytic macrolichen mainly associated with broad-leaved tree species. The occurrence of this species indicates high epiphytic lichen diversity of a stand. Photo by J. Nascimbene.

Figure 61. The thallus of *Lobaria pulmonaria* can grow 20–30 cm in diameter. Photo by J. Nascimbene.

> *Tree age, stand continuity, and tree species composition are among the main factors influencing the patterns of forest lichen diversity*

Epiphytic lichens are slowly growing organisms that under natural conditions are adapted to the disturbance regime of forests. Their diversity is enhanced by increasing tree age, which especially benefits rare, threatened (red-listed), and late successional species (Ellis 2012). In natural conditions, disturbances such as fires and storms create a mosaic of stands in different regeneration phases, and the stand structures are variable, with trees of different ages and tree species. In managed forests, forest age often overlaps with tree age, and the fixed rotation period prevents establishment of old and large trees, decreasing microhabitat quality and heterogeneity, substrate availability, and forest continuity, all of which are important attributes for diverse lichen flora. Old trees provide different and highly variable bark structure as well as other microhabitats such as rot holes, growth anomalies, and moss cover. Large old trees also favour the establishment of dispersal-limited species that have more time for colonisation, higher surface availability, and more stable substrate conditions. Moreover, old-growth forests have a more diverse structure and provide different types of substrates for specialised lichens, such as deadwood, which is usually scarce in production forests.

Many lichens exclusively occur on deadwood, with different ecological requirements for the decay stage and deadwood type. The retention of logs and snags in production forests is therefore the most effective management improvement for deadwood-dwelling lichens. Epiphytic lichens strongly depend on host tree species (although rather few are restricted to one host tree species), this effect being mainly related to species-specific differences in the chemical (e.g. pH) and physical (e.g. texture) traits of the bark. The importance of host tree species is reflected by the fact that tree species composition strongly influences patterns of lichen diversity at the forest scale. As a consequence, the maintenance of native tree species diversity in mixed stands is one of the most common management recommendations for improving lichen diversity (see Box 32).

Past forest management and landscape context influence large-scale regional processes of epiphytic lichen metapopulations

At a local scale, species persistence is the result of extinction-colonisation dynamics, which are influenced by the availability of lichen propagules (reproductive particles) in the surrounding landscape and by habitat connectivity. Moreover, studies that evaluated the role of past management provide evidence for an extinction debt for epiphytic lichens, i.e. species may exhibit a time-delayed extinction after habitat deterioration. This perspective highlights the importance of past management in explaining current patterns of lichen diversity, and indicates habitat loss and fragmentation as the most detrimental factors. Therefore, increasing the extent of woodland around species-rich sites and decreasing forest fragmentation with the creation of a network of set-aside stands are among the main suggestions to improve lichen conservation in productive forest landscapes (see Box 32).

Figure 62. A forest stand with high diversity of epiphytic lichens and mosses. Photo by J. Nascimbene.

Box 32. Recommendations for management

- Identification and protection of woodland key habitats or forest reserves (patches identified with red-listed and indicator species and structural elements). The studies indicate a minimum effective patch size of one to tens of hectares for a woodland key habitat.
- Improving woodland quality for lichens by creating a network of set-asides around woodland key habitats and other valuable habitats.
- Maintenance of large old trees/habitat trees in production forests.
- Maintenance and restoration of mixed tree species composition in production forests.
- Mimicking the natural disturbance regime during forest management. For example, in temperate forests, continuous forest cover forestry (e.g. selective logging) should be preferred over clear cutting and shelterwood management.
- Extension of rotation periods (100–300 years).
- Making canopy openings for light-demanding species, including maintenance and restoration of wooded pastures.
- Leaving groups of live retention trees in production forests to ensure substrate continuity. Retention groups are found to maintain better lichen diversity over solitary trees.
- Leaving deadwood as logs, snags, and retention trees for deadwood dwelling species.
- Avoidance of forest drainage and restoration of wetland forests.
- Minimizing fragmentation of stands.
- Softening edges by creating buffer zones around forest compartments.
- Using landscape-level planning of forestry with old-growth patches and ancient/habitat trees to ensure maintenance of species pools, and corridors and stepping stones to aid dispersal of species.

> *Selective cutting should be preferred over the shelterwood system or clear cutting*

In general, higher lichen diversity is related to lower management intensity, even though in some cases non-intensively managed forests may provide better conditions for epiphytic lichens than recently abandoned forest. Several studies suggest that selective cutting is less detrimental to forest lichens than the shelterwood system or clear cutting (Nascimbene et al. 2013). However, this depends on how selective cutting is performed, i.e. if old trees are selected, selective cutting may be as detrimental as clear cutting. The benefit of selective cutting is apparently related to the long-term permanence of the canopy cover and occurrence of old trees. However, most lichens of European temperate forests have an optimum under intermediate light conditions and avoid both direct solar radiation and deep shade, indicating that excessive canopy closure should also be avoided. In the framework of the shelterwood silviculture system, the prolongation of rotation periods and the retention of groups of mature trees are suggested to mitigate the negative effects of intensive forestry.

Valuable woodland key habitats should be identified and preserved

However, many lichens do not persist even in non-intensively managed forests with prolonged rotation periods. Several studies stress the need to conserve old-growth remnants as well as to decrease forest fragmentation around these remnants by restoring a network of set-aside areas acting as refugia and propagation sources for forest species. Unfortunately, restoration without effective conservation of forests with existing high nature value may fail to succeed since suitable habitat conditions for red-listed lichens are often formed after very long time periods (even hundreds of years). Secondly, some species may be not able to re-establish in suitable habitats that are available after a period of logging abandonment due to their historical large-scale decline that eliminated any source of propagules over large geographical areas (Hauck et al. 2013). Thirdly, air pollution may restrict the successful establishment of lichens to newly available habitats. For these reasons, the identification and protection of stands with high conservation priority (e.g. stands hosting red-listed species and rich lichen communities) that could act as sources of propagules to the surrounding forests should be urgently encouraged among forest managers. Studies have shown that red-listed and rare lichens are strongly concentrated in particular habitat types and structural forest elements ("hot spots"). The identification of such kinds of woodland key habitats could also be achieved using selected indicator species such as the large foliose lichen *Lobaria pulmonaria* (Nascimbene et al. 2010; see Box 33).

Box 33. *Lobaria pulmonaria*, an indicator species of valuable forest habitats

Lobaria pulmonaria is a macrolichen with green algae as the main photobiont and nitrogen-fixing cyanobacteria within its internal cephalodia. The thallus is foliose, large-lobed, and often exceeds 20–30 cm in diameter. Reproductive strategies mainly involve vegetative lichenized structures, while the fruiting bodies of the mycobiont are rarely formed. It has an estimated generation time of ca. 30 years. Lobaria pulmonaria can be found in several forest types, mainly beech-, oak- and chestnut-dominated forests, being mainly associated with broad-leaved trees such as beech, ash, aspen, oak, and chestnut, and more rarely with conifers such as silver fir. It has suffered a general decline throughout Europe as a consequence of air pollution and intensive forest management and is currently red-listed in several European countries. Several studies support its suitability as an indicator of lichen diversity and of sites hosting sensitive and rare species that share similar ecological requirements, such as many cyanolichens. The use of this easily identifiable lichen occurring in different forest types throughout Europe should be tested among forest managers for a rapid assessment to identify sites worthy of lichen conservation.

Several methods have been proposed for mitigating the negative effects of forestry on lichens (Box 32.). These can be divided into two main groups. The first group includes methods for conserving and restoring patches of high habitat quality for lichens (e.g. woodland key habitats). The second group includes forestry methods that are less detrimental or improve the habitat quality of lichens in production forests, such as selective logging or extension of rotation periods, leaving retention trees, or making canopy openings for light-demanding species.

References

Aragón, G., Martínez, I., Izquierdo, P., Belinchón, R. and Escudero, A. 2010. *Effects of forest management on epiphytic lichen diversity in Mediterranean forests. Applied Vegetation Science 13:183–194.*

Hauck, M., de Bruyn, U. and Leuschner, C. 2013. *Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. Biological Conservation 157:136–145.*

Johansson, P. 2008. *Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. Biological Conservation 141:1933–1944.*

Ellis, C.J. 2012. *Lichen epiphyte diversity: A species, community and trait-based review. Perspectives in Plant Ecology, Evolution and Systematics 14:131–152.*

Nascimbene, J., Brunialti, G., Ravera, S., Frati, L. and Caniglia, G. 2010. *Testing Lobaria pulmonaria (L.) Hoffm. as an indicator of lichen conservation importance of Italian forests. Ecological Indicators 10:353–360.*

Nascimbene, J., Thor, G. and Nimis, P.L. 2013. *Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe – A review. Forest Ecology and Management 298:27–38.*

3.6 Spiders in forest ecosystems

Anne Oxbrough and Tim Ziesche

Spiders are a key component of forest ecosystems, occupying a unique position in food webs as both predators and prey

Spiders are a key component of forest ecosystems, occupying a unique position in food webs. As predators, they are important in the regulation of invertebrate populations, which include pest species, and as prey they provide food for other invertebrates and birds. This is notwithstanding the contribution they make to ecosystems in their own right. Currently, the known German spider fauna stands at 992 species from 38 families, which is approximately 25 % of the European count (van Helsdingen 2012). Additionally, almost half of these species are associated with forested habitats (Blick et al. 2013), demonstrating the significant role individual trees and whole forests play in supporting these important animals.

Spiders are influenced by changing environmental conditions and can be used as indicators of habitat quality (Wise 1993). They are one of the most abundant groups of terrestrial predators, relatively easily sampled through methods like pitfall trapping (small plastic cups placed in the ground), and taxonomically well known in Europe compared to other invertebrate groups. In forested ecosystems, spiders have the added advantage of inhabiting all layers from the litter to the canopy, allowing comparisons of the fauna across the vertical strata of the forest. Furthermore, spiders are ecologically well studied and can be classified into guilds determined by their hunting strategy (e.g. active hunters, ambush predators, various types of web builders), which gives additional information on species habitat use.

Spider diversity is strongly influenced by variation in habitat structure in litter and vegetation layers from the ground to the canopy

The spider fauna associated with a particular habitat is greatly influenced by variation in small "microhabitat" features, such as ground vegetation and litter layers, deadwood, and bark, though processes influencing spider diversity in the canopy are less well known (Box 34). Spiders are also influenced by variation in sunlight, temperature, air humidity, and water content of soil and litter, which are interlinked with these microhabitats. For instance, in the litter layers, thickness, structure, and composition are important for spiders (Bultman and Uetz 1984) because they influence humidity, pH, structural components, and prey availability. Many spider species live inside the litter layer, using the space to build small horizontal webs or to escape predation.

Box 34. The unknown frontier: spiders in the forest canopy

Canopies are extremely diverse, supporting up to 50 % of all living organisms (Didham and Fagan 2004). Despite this, the canopy is among the least commonly investigated components of forests due to the difficulty in accessing this habitat. Few studies of spiders in the canopy of Central European forests have been conducted, though several authors have shown that a diverse fauna exists in other temperate and boreal forests. For example, canopies of coniferous stands predominantly support hunting spiders, whereas in deciduous canopies web building families are more frequent (Albert 1982). Spiders are known to use both the canopy and the tree trunk for hunting (Pinzón and Spence 2010). Nonetheless, the ecological role of spiders in the canopy and their specific habitat requirements are poorly understood, creating a challenge for monitoring biodiversity in typical forest management units. This is a clear knowledge gap which must be addressed.

Spiders are also influenced by variation in microhabitats among the vegetation layers (Ziesche and Roth 2008). Indeed, McNett and Rypstra (2000) have found that higher plant diversity is generally associated with enhanced diversity of spiders, which is probably related to the resulting greater structural complexity and its suitability to meet spatial requirements for web arrangement, microclimatic conditions, and an increase in prey items and diversity.

Spider fauna changes markedly over the growth cycle of a forest and is influenced by canopy tree species

The spider fauna changes markedly over the growth cycle of a forest. This cycle begins following a management activity such as felling, or through a natural process such as windthrow, disease, or fire. Following this, young trees establish but have not yet achieved a closed canopy and the stand is characterised by high light levels and warm conditions with the sun reaching the ground. Under these conditions, a structurally complex ground and herb layer vegetation flourishes, and spider species associated with more open habitats are able to colonise the young forest (Oxbrough et al. 2005, 2010). Spiders may colonise from surrounding open areas directly by moving along the ground, or they can disperse aerially using a process called ballooning, by which they can travel much greater distances (Box 35). At this early stage, ground and herb layer vegetation increases to the benefit of a range of species, particularly web builders. Active hunters, such as those from the Lycosidae family (wolf spiders), are also able to take advantage of the warm and sunny conditions.

As the trees grow and the canopy closes, the conditions become darker and the herb layer vegetation is shaded out, affecting plant species composition and cover. In addition, the litter layers begin to accumulate, influencing the humus content of the upper organic soil layers. At this stage, the open habitat species begin to decline, but overall diversity in the spider fauna is maintained as forest-associated species colonise (Oxbrough et al. 2005, 2010) from

Box 35. Spider dispersal by ballooning

Spiders can colonise new habitats by ballooning. This process involves the spider climbing up vegetation to the highest point they can reach, pointing their abdomen towards the sky so that their spinnerets (silk producing appendages at the end of the abdomen) are directed upwards, and letting out a strand of silk which gets caught by the wind. This is a passive method of dispersal determined by the local wind conditions, with the spiders having no ability to select where they land. Nevertheless, spiders can disperse tens or hundreds of metres using ballooning; they have been found in the middle of the ocean using this method and are often the first colonisers of volcanic islands and other newly disturbed habitats. A wide range of species utilise ballooning as a dispersal mechanism when juvenile, but many species from the family Linyphiidae also balloon as adults. Linyphiidae are small spiders, typically 1–4 mm in length, but are very diverse, accounting for more than 37 % of the German spider fauna (van Helsdingen 2012).

nearby patches or by ballooning. Species can take advantage of the structure provided by the developing litter layers (Bultman and Uetz 1982) and ground vegetation (Pearce et al. 2004). At the later stages of the forest cycle, the canopy and understory vegetation develops. Forest spiders that can build webs in the canopy and active hunters on the bark colonise (Buddle et al. 2006; Pinzón and Spence 2010), and spider diversity, particularly of forest specialists, generally increases with forest age (Oxbrough et al. 2005; Buddle et al. 2006). Diversity may decline again in very old stands (Begon et al. 1998); however, gap formation in the canopy can allow open habitat species to recolonise (Oxbrough et al. 2006; Paradis and Work 2011).

Canopy type has a major impact on the spider assemblages, particularly when we look at the characteristics of conifer and broadleaved forests (Oxbrough et al. 2005; Ziesche and Roth 2008). For instance, the leafy litter layers of broadleaved forests are structurally very different from the needle litter of conifers and such differences in litter complexity will influence spider diversity and the abundance of potential prey (Uetz 1991). Similarly, canopy conditions will influence ground vegetation on the forest floor. For example, conifer forests have a canopy all year and often support different plant communities in the ground and herb layer than deciduous stands. Such differences in habitat complexity between conifer and deciduous stands are known to influence spider diversity (Oxbrough et al. 2005).

Mature undisturbed forest stands, including those of old-growth, are increasingly rare. They are generally considered significant centres of biodiversity and are important for the conservation of characteristic forest flora and fauna (Meyer et al. 2011). Such stands may act as recolonisation sources for nearby disturbed areas, facilitating the maintenance of spider diversity in surrounding managed forests (Ziesche et al. 2011). Although the majority of forest-associated spider species can be found in a range of common forest types and are tolerant to some level of management or disturbance (e.g. selective felling under continuous cover forestry), some species exhibit a preference for undisturbed forest types (Willett 2001), and species associated with undisturbed, typically old forests, are negatively impacted by selective felling practices (Halaj et al. 2008; Pinzón et al. 2012).

Figure 63. Small-scale structural diversity from the forest floor to the canopy enhances spider species diversity. Photos by T. Ziesche.

Spiders are affected by processes acting at stand and landscape scales as well as at very small scales (e.g. among microhabitats)

Extensive forest management decreases variation in habitat structure at small scales (e.g. among microhabitat features) to large scales (e.g. reduction in age classes or canopy species diversity). As spiders are influenced by processes acting across a range of scales, it is important that efforts in forest management aim to enhance habitat variability both within and between stands as well as across landscapes (Box 36).

At a small scale within a stand, spiders are positively influenced by variation in microhabitats in the litter and vegetation layers (Figure 63) between stems (Ziesche and Roth 2013). Small-scale variations in habitat conditions can be encouraged in managed forests by creating small gaps to open up the canopy of single aged stands, particularly monocultures. This will alter the lower vegetation and allow a greater variety of species to coexist. In managed forests these may be created during the process of continuous cover forestry, through the selective felling process, or when harvesting trails are made. However, uniformity in canopy gaps across a stand should be avoided as this will not be of benefit to species associated with closed canopy or undisturbed conditions.

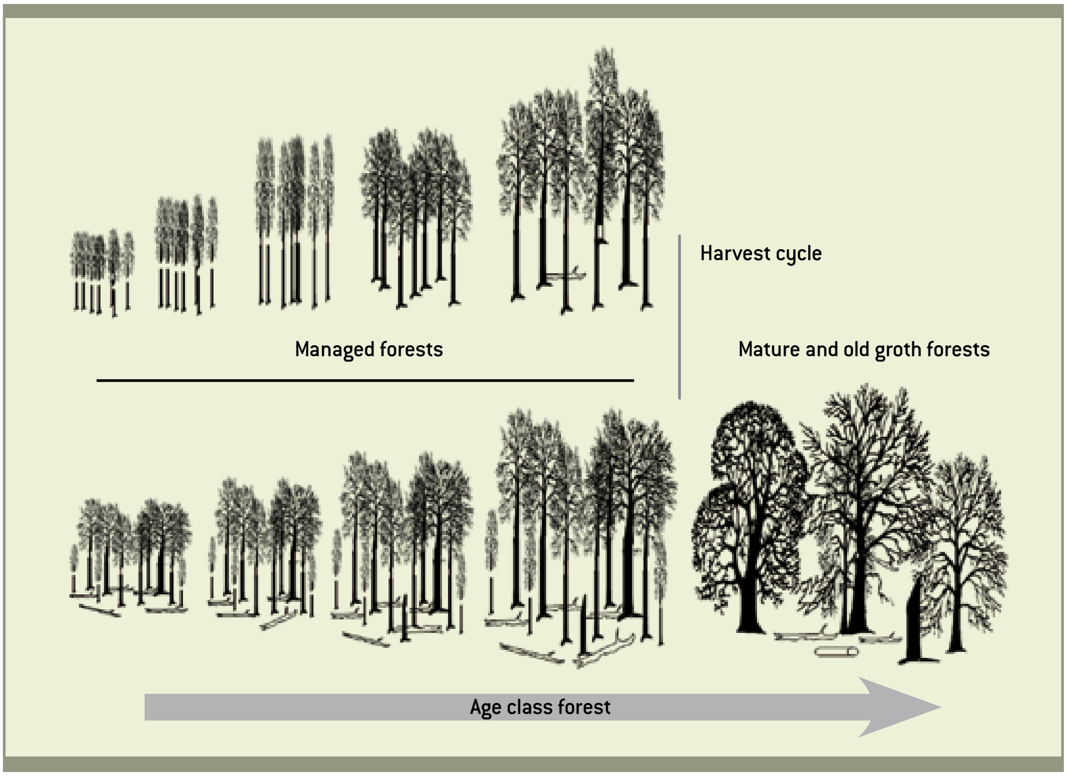


Figure 64. Enhancing structural and tree species diversity from the stand to the landscape scale is an efficient strategy to benefit spider diversity within managed forests.

Encouragement of the growth of mixed species stands where site conditions are suitable will enhance diversity in the litter layers at a small scale and likely lead to a greater diversity of prey and vegetation structure to the benefit of the spider fauna. Diversity of spider communities can be promoted by the inclusion of a variety of tree species since broadleaf and conifer stands support different suites of species (Oxbrough et al. 2005). However, this should only be encouraged for the range of tree species naturally found in the region. As generalist predators, spiders may be more tolerant than other invertebrate groups to the planting of non-native species. Nonetheless, the potential of spiders to occupy an important position in terrestrial food webs as predators, particularly of pest species, may be negatively affected by the wide scale establishment of non-native tree species, through the loss of specialist spider fauna (Ziesche et al. 2004).

Insecticide application within a stand may have a negative impact on beneficial organisms such as spiders, as has been shown in agricultural environments (Rezac et al. 2010), though the effect of insecticides on forest-dwelling spiders is largely unknown and will likely depend on the method and frequency of application. Furthermore, the potential role of spiders as biological control agents in forests requires more research, particularly given the significant impact they are known to have in non-forest agro-ecosystems (Chatterjee et al. 2009).

Box 36. Recommendations for maintaining and enhancing spider diversity in managed forest ecosystems

Management recommendation	Biodiversity benefit	Implementation in practice
Small scale (within-stand)		
Canopy gaps	Species associated with more developed vegetation	CCF[1] thinning operations unevenly distributed within the stand
Closed canopy areas	Forest species associated with deeper litter layers	
Forest species associated with deeper litter layers	Species associated with a certain tree species or canopy type (e.g. conifer or broadleaved)	Stand initiation and growth phase
Deadwood retention	Provides structure for web building species and potential prey items	CCF thinning operations leave a range of deadwood in-situ
Stand scale (between stands)		
Variety of natural tree species	Species associated with common local/native tree species	At forest planning phase Tree initiation phase
Retain old-growth stands and mature stands, older than the rotation cycle	Mature stand and old-growth associated species	Select during CCF thinning phase
Structural complexity in canopy to promote heterogeneous stand conditions	Species associated with microclimate and structural parameter	Species associated with microclimate and structural parameter
Limit and optimise insecticide application	Beneficial predatory spiders on the forest floor and in the canopy	When insect outbreak occurs
Landscape scale		
Stand type patchiness incorporating a near natural range of tree species	Species with high stand type specificity	At forest planning phase (including harvesting plans) consider spatial arrangement and proximity of stands within the natural range for the region
Range of age classes from young to overmature	Species associated with specific stages of forest succession	
Connectivity among patches of similar type	Species with poor dispersal abilities and high habitat specificity	

[1] Continuous cover forestry

Naturalness at a landscape scale can be promoted by providing the range of forested habitats expected in nature. This includes a range of successional stages in the forest cycle and the appropriate range of tree species diversity which can be assumed to grow under natural conditions for a particular region and climate. The natural forest dynamics of a region will include overmature patches and young stands of trees which have previously been subject to a disturbance such as disease or windthrow. Where possible, management should allow for this range of variation across the landscape (Figure 64).

Although spiders can colonise by ballooning, many species rely solely on movement along the ground to disperse among patches. For these species proximity to suitable habitat is key to their survival. Whilst continuous cover forestry systems are able to support many forest-associated species, it is likely that some species associated with old-growth or undisturbed stands will benefit from connectivity among patches or proximity to suitable areas which act as sources of specialist species. This is particularly important given that species associated with undisturbed areas are negatively affected by 40–75 % levels of selection harvest (Halaj et al. 2008; Pinzón et al. 2012). In this case, the forested landscape as a whole should be considered when formulating management plans (Box 36). This will benefit species particularly sensitive to management activities such as selective felling under continuous cover forestry.

References

Albert, R. 1982. *Untersuchungen zur Struktur und Dynamik von Spinnengesellschaften verschiedener Vegetationstypen im Hoch-Solling 16, Freiburg (Hochschul-Verlag). 135 p.*

Begon, M.E., Townsend, C.R. and Harper, J.L. 1998. *Ökologie. Spektrum Akademischer Verlag, Heidelberg. Pp. 329–355*

Blick, T., Finch, O., Harms, K., Kiechle, J., Kielhorn, K., Kreuels, M., Malten, A., Martin, D., Muster, C., Nährig, D., Platen, R., Rödel, I., Scheidler, M., Staudt, A.H.S. and Tolke, D. 2013. *Rote Liste der Spinnen Deutschlands (Araneae). Naturschutz und Biologische Vielfalt.*

Buddle, C.M., Langor, D.W., Pohl, G.R. and Spence, J. R. 2006. *Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation 128:346–357.*

Bultman, T.L. and Uetz, G.W. 1982. *Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55:34–41.*

Bultman, T.L. and Uetz, G.W. 1984. *Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. American Midland Naturalist 111:165–172.*

Chatterjee, S., Isaia, M. and Venturino, E. 2009. *Spiders as biological controllers in the agroecosystem. Journal of Theoretical Biology 258:352–362.*

Didham, R.K. and Fagan, L.L. 2004. *Forest Canopies In: Burley, J., Evans, J. & Youngquist, J. (eds.) Encyclopedia of Forest Sciences. Academic Press. Pp. 68–80.*

Halaj, J., Halpern, C.B. and Yi, H. 2008. *Responses of litter-dwelling spiders and carabid beetles to varying levels and patterns of green-tree retention. Forest Ecology and Management 255:887–900.*

Meyer, P., Schmidt, Mar., Blick, T., Brunet, J., Dorwo, W, Hakes, W., Härdtle, W., Heinken, T., Hertel, D., Knapp, H.D., Leuschner, C., Oheimb, G. v., Otte, V. and Schmidt, W. 2011. *Stellungnahme zu Walentowski H. et al. 2010. Sind die deutschen Waldnaturschutzkonzepte adäquat für die Erhaltung der buchenwaldtypischen Flora und Fauna? Eine kritische Bewertung basierend auf der Herkunft der Waldarten des mitteleuropäischen Tief- und Hügellandes. Forstarchiv 81, 195-217. Forstarchiv 82. Jg.. Pp. 62–66.*

McNett, B. and Rypstra, A. 2000. *Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. Ecological Entomology 25:423–432.*

Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P.S. and Smith, G.F. 2005. *Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212:171–183.*

Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P.S. and Kelly, T. C. 2006. *The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237:404–417.*

Oxbrough A., Irwin, S., Kelly, T. C. and O'Halloran, J. 2010. *Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259:2111–2121.*

Paradis, S. and Work, T.T. 2011. *Partial cutting does not maintain spider assemblages within the observed range of natural variability in Eastern Canadian black spruce forests. Forest Ecology and Management 262:2079–2093.*

Pearce, J.L., Venier, L.A., Eccles, G., Pedlar, J. and McKenney, D. 2004. *Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. Biodiversity and Conservation 13:1305–1334.*

Pinzón, J. and Spence, J. 2010. *Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. Journal of Insect Conservation 14:439–458.*

Pinzón, J., Spence, J.R. and Langor, D.W. 2012. *Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. Forest Ecology and Management 266:42–53.*

Rezac, M., Peka, S. and Stara, J. 2010. *The negative effect of some selective insecticides on the functional response of a potential biological control agent, the spider* Philodromus cespitum. *Biocontrol 55:503–110.*

Uetz, G. 1991. *Habitat structure and spider foraging In: Bell, S., McCoy, E. and Mushinsky, H. (eds.) Habitat structure. The physical arrangement of objects in space. London: Chapman and Hall.*

van Helsdingen, P. J. 2012. *Araneae. In: Fauna Europaea Database (Version 2012.2).*

Willett, T.R. 2001. *Spiders and other arthropods as indicators in old-growth versus logged redwood stands. Restoration Ecology 9:410–420.*

Wise, D.H. 1993. *Spiders in Ecological Webs. Cambridge University Press.*

Ziesche, T.M., Förster G. and Roth, M. 2004. *Die Lebensraumfunktion von Wäldern für Gliederfüßer (Arthropoda): Einfluss der Baumarten und des Bestandesalters. – (Weilheim) Verlag B. Felbermeier, In: Mosandl, R. and Felbermeier, B. (eds). Ökosystem Management 1:27–37.*

Ziesche, T.M. and Roth, M. 2008. *Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat?' Forest Ecology and Management 255:738–752.*

Ziesche, T.M., Kätzel, R. and Schmidt, S. 2011. *Erarbeitung von naturschutzfachlichen Empfehlungen zur Bewirtschaftung von stabilen, artenreichen, naturnahen Eichenwäldern im Nordostdeutschen Tiefland. BfN-Schriftenreihe; Naturschutz und Biologische Vielfalt. 204 p.*

Ziesche, T.M and Roth, M. 2013. *Microhabitat heterogeneity in temperate forests: is distance to stems affecting ground-dwelling spider communities? Community Ecology 14(1):8–17.*

3.7 Snails and slugs as indicators of sustainable forest management

Heike Kappes

True forest gastropods are a substitute indicator group for a vast number of forest floor biota

The slow active dispersal of gastropods, combined with their specific demands on habitat, food quality, and microclimate, make them a potentially suitable indicator group for analyzing and monitoring the effects of forest use on leaf-litter decomposing biota and ecosystem integrity, stability, and functioning. The results are also likely to hold true for other forest floor biota, including fungi, bacteria, protozoans, nematodes, earthworms, tardigrades, millipedes, centipedes, woodlice, spiders, collembolans, and beetles (e.g. Dunger and Fiedler 1997 and references therein; Topp et al. 2006a, 2006b) as well as many mosses, ferns, and bryophytes (Wiklund 2004; López-Barrera et al. 2007 and references therein).

However, it needs to be pointed out that the demands of true forest gastropods often contrast those of many forest-associated insects that need warmer, and prefer drier, climatic conditions. The latter may occasionally survive in small patches or even single habitat trees, whereas true forest floor species need spatio-temporal continuity of the forest floor with its typical soil characteristics and microclimatic properties. Different strategies are therefore needed for the protection of these two contrasting groups of conservation interest. Our focus here is on true forest species.

The following mainly applies to the widespread forest type of (oak-)beech forests on mesic to acidic soils. Where appropriate, differences between the Atlantic Biogeographic region and the Central European Biogeographic region are highlighted.

Closed canopies create a forest microclimate and foster forest species

Terrestrial gastropods, amongst others, are sensitive to soil and leaf litter quality and microclimatic amplitudes. On a large spatial scale, soil quality is the most important factor for snail species richness and assemblage turnover, but within a given forest, tree species and microclimatic amplitudes seem to play a more important role for gastropods (e.g. Hotopp 2002; Martin and Sommer 2004; Kappes 2006). Tree canopy cover ensures a balanced microclimate, promotes the formation of a typical humic soil layer, and facilitates detritivores and true forest species (Figure 65). Clearings and forest edges increase the microclimatic amplitude and allow a substantial diversity of herbs to grow on the forest floor, allowing the occurrence of euryecious and invasive species that do not depend on forests or even would not survive below a closed canopy (Kappes 2006; Kappes et al 2009a).

One of the species that profit from disturbances is the non-native invasive slug *Arion lusitanicus* auct. non Mabille (syn. *A. vulgaris*) (Kappes 2006; Kappes et al. 2009a), which is related to the decline of the native *Arion rufus* (Wiese 1985; Noble and Jones 1996). However, the slug assemblages from Central European low mountain range forests are relatively resilient: when forests mature, and/or human disturbances decrease, the proportion of specialist species increases (Kappes 2006). Thus, prolonged rotation intervals accompanied by single-tree or small-group felling are recommended. When stands age and canopies close, species that are typical for open habitats, such as *Deroceras reticulatum* and *Arion 'lusitanicus'*, do not survive (Kappes 2006). The resilience of biota in lowland forests is expected to be considerably lower because of the ambient climatic conditions and extreme fragmentation, as will be discussed later.

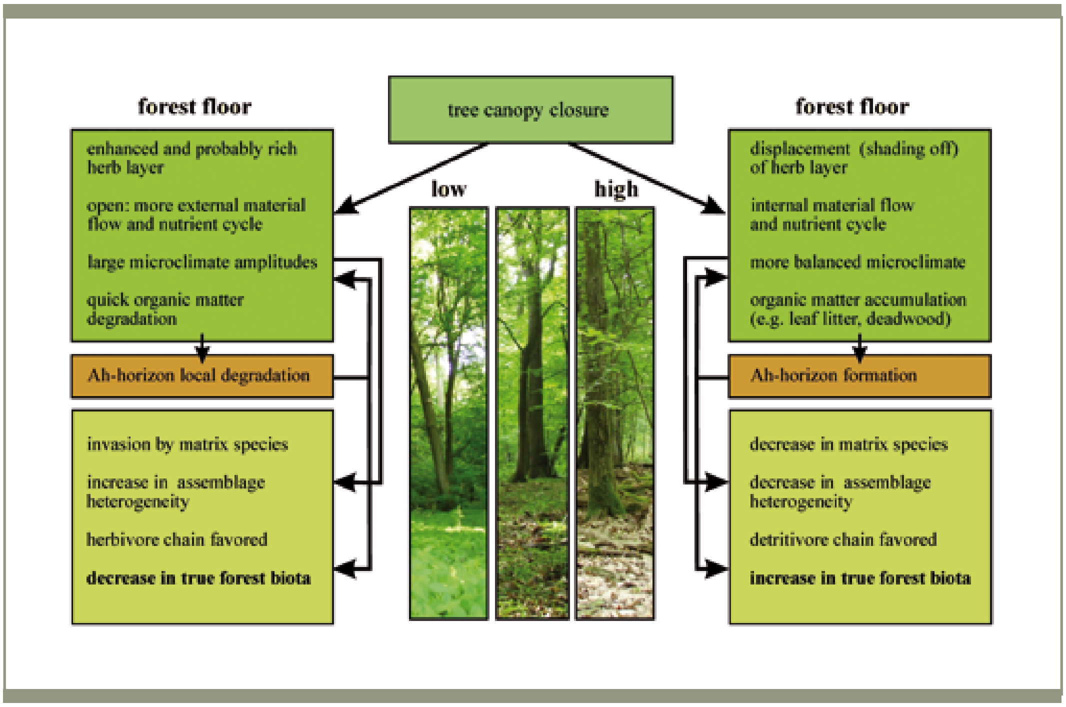


Figure 65. Highly simplified conceptual model of causes, changes, and effects of canopy closure and organic matter accumulation on forest floor fauna. Photos by H. Kappes.

Microhabitat requirements for specialist conservation are an estimated minimum amount of 20-50 m³ of coarse woody debris per ha in managed forests and rigorous restrictions for deadwood removal from still pristine systems

In contrast, favourable microclimatic conditions are created by upwelling ground water (Martin and Sommer 2004) or by structures associated with organic matter accumulation such as coarse woody debris or small hollows (Kappes et al. 2012, and references therein). In these conditions, gastropods find suitable microsites for reproduction. Additional hard substrates such as outcrops (if the parent material is not too acidic) can substantially broaden the resource spectrum in the lower mountain ranges, and limestone outcrops are key structures for (protecting) snail diversity (Kappes et al. 2012).

Coarse woody debris improves soil quality. It is associated with higher pH values and increased calcium and magnesium availability. Moreover, soil microbial biomass, density of detritivores, and species richness of snails, slugs, and millipedes have been found to be higher close to coarse woody debris (e.g., Jabin et al. 2004; Kappes 2005; Kappes et al. 2007). The results indicate that coarse woody debris influences nutrient fluxes and locally decreases the acidification-related risk of tree damage (Kappes et al. 2007).

Large amounts of coarse woody debris increase habitat availability and the connectivity of the resources provided by coarse woody debris, which, in turn, stabilizes the habitat for specialists (Kappes et al. 2009c). The amount of woody debris is positively related to overall gastropod species richness in laurel forests on Tenerife (Kappes et al. 2009d) and to the proportion of true forest slugs in oak-beech forests in Western Germany (Kappes 2006). The estimated minimum amount of deadwood for gastropod conservation is 20–50 m³ of coarse woody debris per ha (Müller et al. 2005; Kappes et al. 2009c). Kappes et al. (2009b) conclude that below this threshold, the habitat is perceived as being fragmented, assemblages become heterogeneous, and the extinction risk of specialist species increases. Specialists that depend on coarse woody debris, such as representatives of the Clausiliidae (Kappes et al. 2009c) and some Coleoptera (Kappes and Topp 2004; Buse 2012), seem to have gone extinct in some managed forests.

Tree composition influences gastropod assemblages though leaf litter quality. Trees such as maple and lime provide high quality resources, whereas conifers provide those of low quality

In closed-canopy forests, the leaf litter provides a substantial part of the habitat structure and food resources. Leaf litter can be beneficial for gastropod abundance and species richness, if it provides the following: structural refuges and good digestability, or a high calcium content (Hotopp 2002). Here, maple (*Acer*) and lime (*Tilia*) provide more accessible resources than beech (*Fagus*) or oak (*Quercus*) (Hotopp 2002). It may be hypothesized that interspersing these trees in beech or oak stands would be beneficial to forest floor fauna. In contrast, gastropod richness and densities are substantially reduced in conifer plantations that produce a thick, almost impenetrable layer of acidic needles (Kappes 2011).

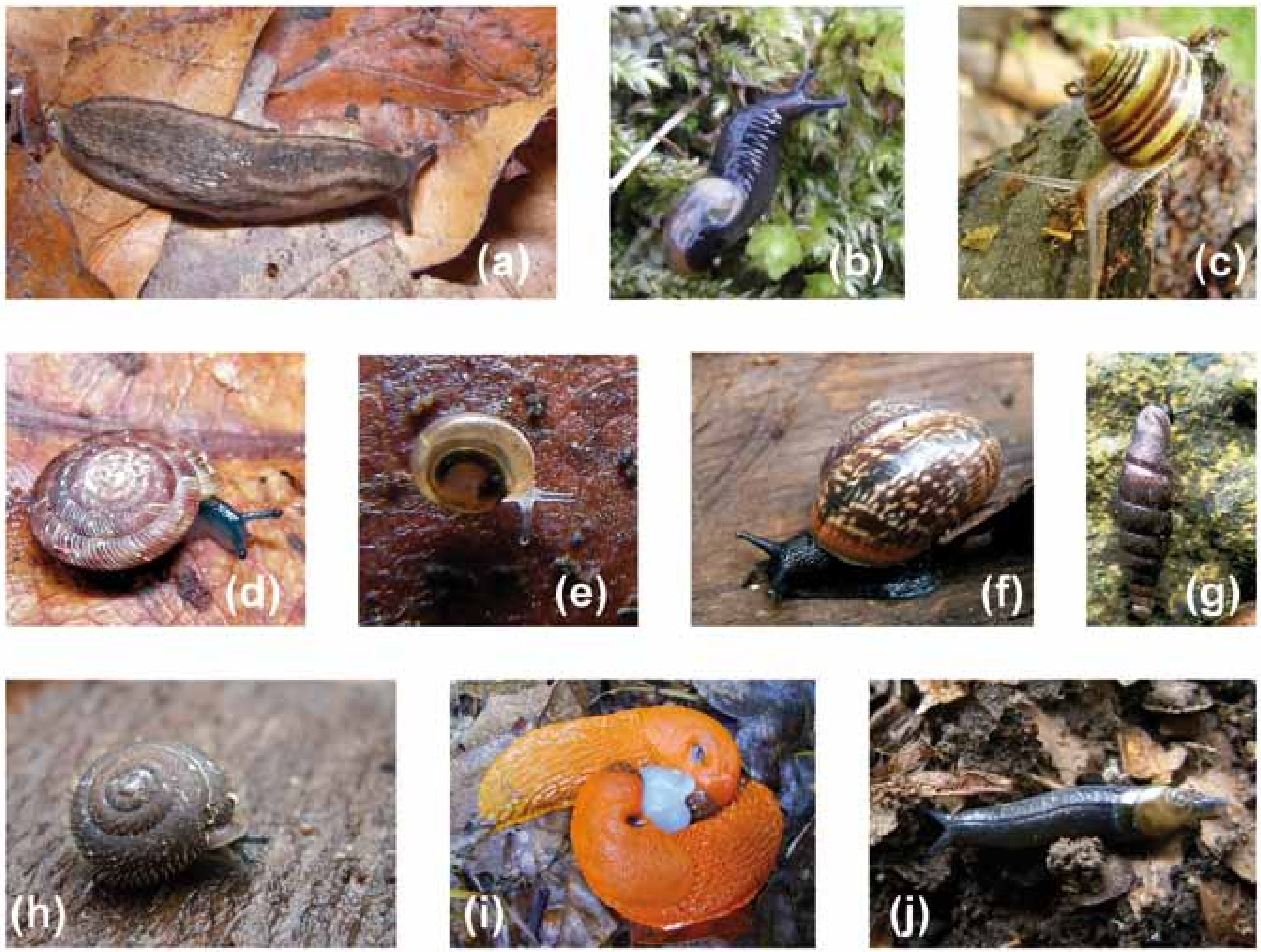


Figure 66. Examples for gastropods in forests. (a) The Forest Arion (*Arion silvaticus*) is a typical leaf-litter dweller; (b) The Ear-Shaped Glass Snail (*Eucobresia diaphana*) is a semislug that usually occurs in cool and moist places; (c) the White Lipped Snail (*Cepaea hortensis*) is a focus species of the Citizen Science Project ‘Evolution MegaLab’ that maps shell color and banding across Europe (here: ’5-banded, yellow‘); (d) the flat shell of the Rotund Disc (*Discus rotundatus*) facilitates crawling between fallen leaves and under the loose bark of dead wood; (e) close-up of the mircodetritivorous Dwarf Snail (*Punctum pygmaeum*) that is the smallest European terrestrial snail (adult shell diameter < 1.5 mm); (f) the brownish shell pattern of the Copse Snail (*Arianta arbustorum*) provides camouflage in woodlands; (g) Door Trap Snails such as this *Clausilia* species are highly sensitive to hard substrate (*rocks, deadwood*) removal; (h) the haired Mask Snail (*Isognomostoma isognomostomos*) is an indicator for well-structured and deadwood-rich forests of the Central European Biogeographic region; (i) a mating couple of the Large Red Slug (*Arion rufus*); (j) the predacious semislug *Daudebardia rufa*. Photos by H. Kappes.

Fragmentation induces edge effects that significantly reduce the core habitat area in warm climatic conditions

There are mounting concerns over forest integrity in the Atlantic Biogeographic Region of Europe, where only fragments of ancient woods and old-growth forests remain. These fragments are surrounded by hostile agriculture or by densely populated areas. Edge effects are strong under these conditions, and the distance to disturbances (external edges, internal edges such as roads) strongly affects gastropod species and assemblage characteristics (Kappes et al. 2009a).

Forest edges create a gradient in light, temperature, humidity, vapor pressure deficit, and litter moisture (Matlack 1993). The immediate response of species assemblages is often more strongly related to changes in microclimate than to changes in structure or vegetation, as was shown, for example, for beetles (Grimbacher et al. 2006). Environmental changes associated with the forest edge are said to be typically restricted to the first 40–60 m into a forest (Davies-Colley et al. 2000). However, the richness of generalist snail species was found to increase up to 250 m into the forest in the Atlantic Biogeographic Region close to Cologne, Germany (Kappes et al. 2009a). This strong edge effect could result from the lack of a protective mantle of shrubs and small trees, along with the highly contrasting agricultural matrix in one of the warmest regions of Germany.

Thus, fragmentation substantially decreases the core habitat for true forest species: taking a forest square of 1km × 1km (1 km^2) as an example, traditional assumptions of edge effects maximally protruding 75 m into the forest leave a core area of about 0.73 km^2, whereas edge effects of up to 250 m reduce the core area to 1/4th of the forest (0.25 km^2). Several biotic interactions are likely to be modified in between the obvious minimum (75 m) and snail-indicated maximum (250 m) edge effect. Among these effects could be those from the invasive alien slug *Arion lusitanicus* auct. non Mabille (syn. *A. vulgaris*), the occurrence of which coincides with the recession of the native sibling species *Arion rufus* (Wiese 1985; Noble and Jones 1996).

The remnant size and the species extinction debt: (inappropriate) management increases the forest fragment size needed for survival

The surroundings strongly affect remnant fragments: In the Central European Biogeographic region, snail assemblages in a forest plot are correlated to land use within a radius of one kilometer (Kappes et al. 2011). In the Atlantic Biogeographic Region, forest remnant size determines the species composition of the plots sampled therein (Kappes et al. 2009a). A prominent example for species loss through shrinking habitat size is the true forest slug *Limax cinereoniger*. This species currently has a highly isolated distribution in the Atlantic Biogeographic Region and needs forests of > 1000 ha to have an occurrence probability above

50% around Cologne, Germany (Kappes et al. 2009a, Figure 67). This is probably due to the different, incompatible uses integrated into forest remnants.

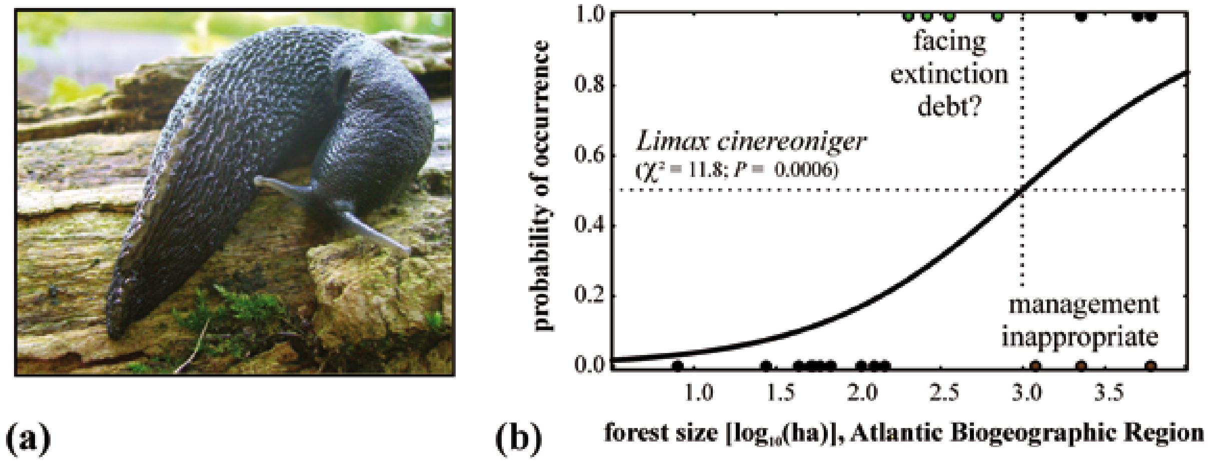


Figure 67. (a) The true forest slug *Limax cinereoniger* (photo: H. Kappes). (b) The species does not occur in small old-growth forest fragments in the lowlands around Cologne, Germany. The smallest forests that harbor the species have only been fragmented in the last 60–80 years and are thus likely under the so-called extinction debt, and a lack of the species in large forests occurred in locations that had signs of severe recent or historical disturbances/clearcuts. Source: Modified from Kappes et al. 2009a.

Forest turnover is accompanied by a loss of specialist species and cryptic effects in recolonizing populations. Reforestation is thus not an alternative to forest protection and sustainable management

A strong reason for protecting old-growth forests is that they cannot be substituted. New forests show substantial deviations from the species composition of old-growth forests, as they do not harbor forest specialists (e.g. Kappes 2006; Topp et al. 2010; Buse 2012). There are also differences in terms of phenotypic or genetic composition, as evidenced in the euryecious snail *Discus rotundatus* (Kappes et al. 2009b). Habitat gain, accomplished by afforestation, is associated with seemingly persistent changes in genetic composition, indicating an introduction of individuals, along with altered shell characters, such as shell height and aperture size (Kappes et al. 2009b).

Thus, some species may recolonize afforested areas, but populations inhabiting restored habitats may not necessarily reflect their original features. Most, if not all, historical

Box 37. Recommendations for management.

At the stand level, the conservation of true forest species warrants a tree canopy that should not be artificially opened, thus ensuring a balanced microclimate, especially in warmer conditions. Conifer plantations should be converted to mixed or broad-leaved forests. In tree species-poor broadleaved forests, the fauna might profit from interspersing more broadleaved tree species such as maple or lime. An estimated minimum amount of 20–50m^3 of coarse woody debris per hectare should be (permanently) retained in managed forests and rigorous restrictions should be applied for deadwood removal from still (almost) pristine systems.

Generally speaking, disturbances and edge effects (fragmentation) should be minimized. Single-tree or small-group felling can reduce the effects of harvesting on forest microclimate. Long rotation intervals help specialist species to establish and give them time to disperse. Natural regeneration can be favored over planting because planting new trees can introduce atypical species or genotypes.

Protection of true forest floor biota is **usually compatible** with forest protection areas, freshwater and soil protection forests, old-growth habitat islands, low-intensity recreation, deadwood retention, and CO_2 retention. Integration of groundwater extraction must be limited, especially where specific or rare forest types are interspersed, such as alder forests, wet floodplain softwoods, or swamp forests that are highly sensitive to decreases in the water table.

In the low mountain ranges (Central European Biogeographic Region), protection of true forest floor biota is **incompatible** with fragmentation, fuel extraction, any sort of forest loss, (conversion to) conifer plantations, forest pasture, and intensive recreation pressure. It may be hypothesized that over the landscape scale, mosaics of forest use may buffer negative effects at the stand level, but the details need further research.

In the highly fragmented forests of the Atlantic Biogeographic Region, protection of true forest floor biota is **highly incompatible** with any sort of forest habitat loss, further fragmentation, fuel extraction, (conversion to) conifer plantations, forest pasture, intensive recreation pressure, etc., even at the landscape level. Here, each of the few remaining fragments deserves full attention, as it can be important for biodiversity conservation (on the species and population genetic level) and should be protected against loss. These fragments should only be managed extensively and sustainably and should be enlarged and connected.

phylogeographic information and local characteristics, including adaptations, get lost along with the deforestation event. Some concerns may be raised if new forests planted as a substitute for old-growth forests will ever equal the old-growth forests of the region because old-growth forests harbor assemblages and genotypes from historical times, and colonization and exchange conditions have changed along with soil acidification, climate, biotic interactions, connectivity, and the regional species and gene pool.

This result underpins the importance of nature-oriented management should as single-tree or small-group felling, with natural regeneration instead of afforestation. Kappes (2006) and Moning and Müller (2009) suggest increasing logging intervals above the typical 110–140 years, at least in patches. Nature-oriented management should be supported by long-term protection of all old-growth forests. Any further loss of deciduous forest area to mining, military areas, or agriculture, or degradation because of an inappropriate large-scale felling regime or conversion to conifer stands, is expected to cause permanent erosion of biodiversity and a loss of species and genotypes, regional (biological and cultural) identity, and environmental quality.

References

Buse, J. 2012. *"Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. Journal of Insect Conservation 16:93–102.*

Davies-Colley, R.J., Payne, G.W. and van Elswijk, M. 2000. *Microclimate gradients across a forest edge. New Zealand Journal of Ecology 24:111–121.*

Dunger, W. and Fiedler, H.J. 1997. *Methoden der Bodenbiologie. Fischer, Jena. 432 p.*

Grimbacher, P.S., Catterall, C.P. and Kitching, R.L. 2006. *Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest. Australian Ecology 31:458–470.*

Hotopp, K.O. 2002. *Land snails and soil calcium in central Appalachian mountain forests. Southeastern Naturalist 1:27–44.*

Jabin, M., Mohr, D., Kappes, H. and Topp, W. 2004. *Influence of deadwood on soil macro-arthropods in an oak-beech forest. Forest Ecology and Management 194:61-–69.*

Kappes, H. 2005. *Influence of coarse woody debris on the gastropod community (Mollusca: Gastropoda) in a managed calcareous beech forest in Western Europe. Journal of Molluscan Studies 71:85–91.*

Kappes, H. 2006. *Relations between forest management and slug assemblages (Gastropoda) of deciduous regrowth forests. Forest Ecology and Management 237:450–457.*

Kappes, H. 2011. *Schnecken als Gütesiegel für Waldökosysteme? Scenckenberg natur forschung museum 141:230–239.*

Kappes, H. and Topp, W. 2004. *Coleoptera from deadwood in a managed broadleaved forest in Central Europe. Biodiversity and Conservation 13:1905–1924.*

Kappes, H., Catalano, C. and Topp, W. 2007. *Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. Applied Soil Ecology 36:190–198.*

Kappes, H., Jordaens, K., Hendrickx, F., Maelfait, J.-P., Lens, L. and Backeljau, T. 2009a. *Response of snails and slugs to fragmentation of lowland forests in NW Germany. Landscape Ecology 24:685–697.*

Kappes, H., Jordaens, K., Van Houtte, N., Hendrickx, F., Maelfait, J.-P., Lens, L. and Backeljau, T. 2009b. *A land snail's view of a fragmented landscape. Biological Journal of the Linnean Society 98:839–850.*

Kappes, H., Jabin, M., Kulfan, J., Zach, P. and Topp, W. 2009c. *Spatial patterns of litter-dwelling taxa in relation to the amounts of coarse woody debris in European temperate deciduous forests. Forest Ecology and Management 257:1255–1260.*

Kappes, H., Delgado, J.D., Alonso, M.R. and Ibáñez, M. 2009d. *Native and introduced gastropods in laurel forests on Tenerife, Canary Islands. Acta Oecologia 35:581–589.*

Kappes, H., Sundermann, A. and Haase, P. 2011. *Distant land use affects terrestrial and aquatic habitats of high naturalness. Biodiversity and Conservation 20:2297–2309.*

Kappes, H., Clausius, A. and W. Topp 2012. *Historical small scale surface structures as a model for post-mining land reclamation. Restoration Ecology 20:322–330.*

López-Barrera, F., Armesto, J.J., Williams-Linera, G., Smith-Ramírez, C. and Manson, R.H. 2007. *Fragmentation and edge effects on plant–animal interactions, ecological processes and biodiversity. In: Newton, A.C. (ed.) Biodiversity loss and conservation in fragmented forest landscapes: the forests of montane Mexico and temperate South America. CAB International, Wallingford. Pp 69–101.*

Martin, K. and Sommer, M. 2004. *Relationships between land snail assemblage patterns and soil properties in temperate-humid forests. Journal of Biogeography 31:531–545.*

Matlack, G.R. 1993. *Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185–194.*

Moning, C. and Müller, J. 2009. *Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. Ecological Indicators 9:922–932.*

Müller, J., Strätz, C. and Hothorn, T. 2005. *Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. European Journal of Forest Research 124:233–242.*

Noble, L.R. and Jones, C.S. 1996. *A molecular and ecological investigation of the large arionid slugs of North-West Europe: the potential for new pests. In: Symondson, W.O.C. and Liddell, J.E. (eds.) The ecology of agricultural pests. Chapman & Hall, London. Pp 93–131.*

Topp, W., Kappes, H., Kulfan, J. and Zach, P. 2006a. *Distribution pattern of woodlice (Isopoda) and millipedes (Diplopoda) in four primeval forests of the Western Carpathians (Central Slovacia). Soil Biology and Biochemistry 38:43–50.*

Topp, W., Kappes, H., Kulfan, J. and Zach, P. 2006b. *Litter-dwelling beetles in primeval forests of Central Europe: does deadwood matter? Journal of Insect Conservation 10:229–239.*

Topp, W., Thelen, K. and Kappes, H. 2010. *Soil dumping techniques and afforestation drive ground-dwelling beetle assemblages in a 25 year-old open cast mining reclamation area. Ecological Engineering 36:751-756.*

Wiese, V. 1985. *Zur Verbreitungssituation der Land-Nacktschnecken in Schleswig-Holstein (Gastropoda: Arionidae, Milacidae, Limacidae, Agriolimacidae, Boettgerillidae). Faunistisch-Ökologische Mitteilungen 5:305–311.*

Wiklund, K. 2004. *Establishment, growth and population dynamics in two mosses of old-growth forests. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 996. Uppsala. 47 p.*

4. Key challenges

Chapter 4 highlights important topics with relevance for future challenges for the integration of biodiversity conservation into forest management. Climate change and invasive species are two main challenges for the future of forest management. Consequences of these issues on species assemblages may be drastic but are generally difficult to predict – although there are trends and models that allow forest managers to be better prepared. Functional diversity as a rather recent discipline is gaining increasing attention because it focuses on functional traits rather than on particular species. Genetic diversity is another important topic that is currently on the rise and will become more important in the future. Monitoring systems for biodiversity constitute a very important feedback to biodiversity management and will be crucial in assessing changes in species composition and its causes. The chapter is structured into five sections:

4.1 Biodiversity conservation and forest management in European forest ecosystems under a changing climate

4.2 The functional role of biodiversity in forests

4.3 Invasive neobiota in forest ecosystems: opportunity or threat?

4.4 Genetic diversity of forest trees

4.5 Monitoring forest biodiversity in Europe: state of the art, challenges and opportunities

4.1 Biodiversity conservation and forest management in European forest ecosystems under changing climate

Marcus Lindner, Frank Krumm and Gert-Jan Nabuurs

> *Climate is changing, but many uncertainties remain about the likely impacts of climatic changes on forest ecosystems, species distributions, and the implications for biodiversity conservation*

Climate change scenario projections and forest ecosystem models provide us with the expected directions of changes in climate and outline possible impacts. Even though concrete and reliable information about future developments cannot be made, it is still possible to derive some general conclusions regarding forest management and biodiversity conservation. The current biodiversity conservation strategies are not designed to cope with changing environmental conditions, and it is urgent to include likely impacts of climate change in adaptive forest management strategies.

Climate change is already evident and affects forest ecosystems in Europe. For example, Scots pine has declined in areas close to its dry distribution limit (Rigling et al. 2013), beech forests recently showed growth depressions in Belgium (Kint et al. 2012) and lost habitats in mountainous forests in Spain (Penuelas et al. 2007), whereas the species expands its range following storm disturbances at its Northern range margin (Bolte et al. 2013). Projections indicate that climate change will continue its gradual warming trend, whereas changes in average precipitation sums will be quite variable regionally. It is likely that Northern Europe will receive more precipitation on average, while the Mediterranean forests will become significantly drier, especially during the summer months. In addition, it is expected that the climate will become more variable and that forests will more often be subject to extreme events such as extended drought periods and devastating wildfires or storms.

> *Future conservation efforts should be fully aware that the distribution of biodiversity, and species of concern, will be dramatically altered by climate change and that increased extinction risk is one of the possible outcomes. Conserving biodiversity will require approaches above and beyond those that are currently implemented in Europe*

Figure 68. A windstorm event (2005) followed by a drought period (2006) and a subsequent insect outbreak (2007) have triggered species replacement in an old-growth forest reserve (Siggaboda) in southern Sweden: when the spruce overstorey died due to bark beetle attacks, the beech understorey was vitalized and became the dominant species (Bolte et al. 2013). Photo by A. Bolte.

All these changes will affect species distributions. Species at the rear edge of their distribution range will become more vulnerable and subject to increased mortality. On the other hand species are likely to expand their distribution towards higher elevations and northern latitudes.

In Southern and continental parts of Europe the frequency of years with devastating fire seasons as well as the intensity of fires is projected to increase. Fire susceptibility of forests depends on fuel loads and the flammability of the vegetation, which is predicted to increase due to increasing drought frequency. Drought events already have longer durations, and it is foreseen that precipitation will further decrease and air temperature will increase in certain areas or periods and will lead to more intensive drought periods (Allen et al. 2010). Combined with extreme heat waves such as in Greece 2007 or in Russia 2010 there is a large risk for mega-fires (Coumou and Robinson 2013; San-Miguel-Ayanz et al. 2013). An analysis of the mega-fires in Greece 2007 showed that the fires extended into forest types at higher elevations, damaging forests that were previously not considered to be at risk (Koutsias et al. 2012). Fire risk will also increase in other regions of Europe as climate variability increases, and extended summer droughts may occur even in regions that become more humid on average.

Other disturbances, including storms and pests, are also affected by climate change. Since 1990, severe storm events have frequently caused widespread damage across Europe. While the overall storm frequency in Europe is expected to decline, the return-time of high intensity storm events is very likely to become shorter under climate change (Gardiner et al. 2010).

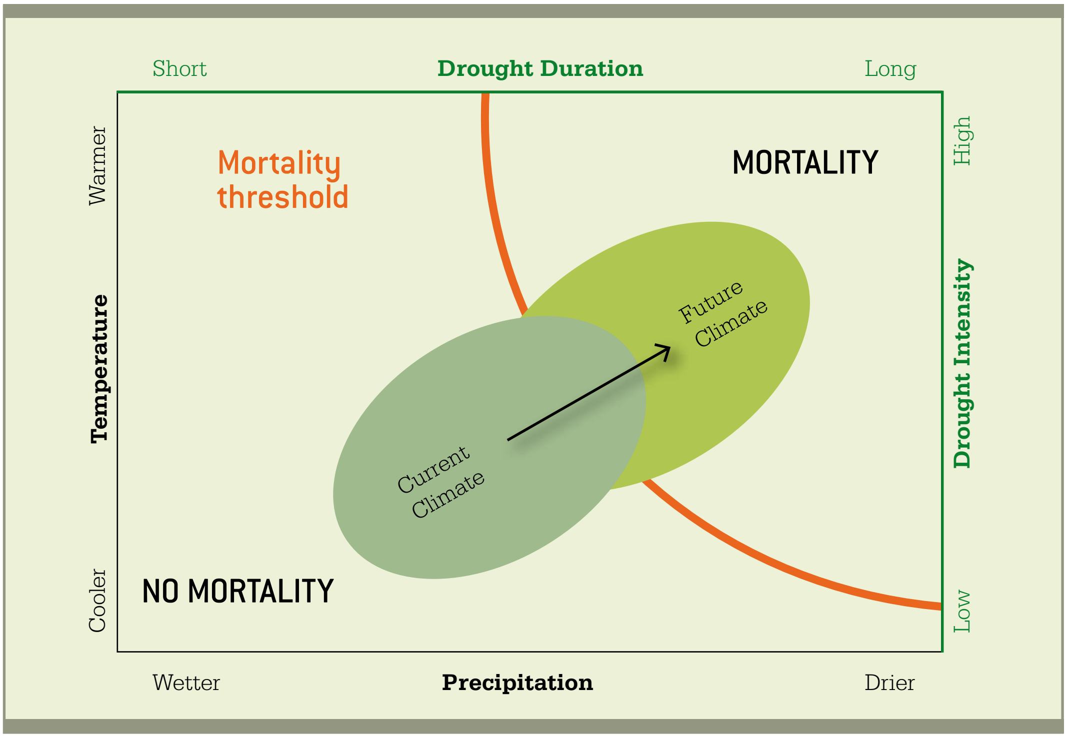


Figure 69. Conceptual figure describing the effect of climate change on species mortality risks due to more intense and longer drought events. Source: Modified from Allen et al. (2010).

The European spruce bark beetle benefits from disturbance calamities and will react to warmer temperatures with more reproduction cycles. The borderlines for pests and diseases in general will also shift, and bark beetle outbreaks may occur in higher altitudes than in the past (Netherer and Schopf 2010).

Forests and forest related species will not only have to adapt to long-term changes in climate but also to increased variability with more extreme weather events, such as prolonged drought, devastating storms and floods. Additionally, combinations of direct climate stresses (e.g. heat waves) and indirect climate-induced pressures (e.g. pest outbreaks) will exacerbate the situation

Changes in species composition will evidently have implications for biodiversity conservation. In this context the literature refers to potential “winners” and “losers” of climate change. Winners are species that gain climatic suitability under the changing climate, whereas for losers climatic suitability declines. While climate change improves climatic suitability for many reptile species, other species groups generally show more losers than winners under climate change (Araújo et al. 2011). Araújo et al. (2011) studied also the effectiveness of conservation efforts on changes in climatic suitability of four different species groups in Natura 2000 and other protected areas. The results showed that Natura 2000 areas rarely provided better climatic suitability to the EU habitat directive species compared to randomly selected unprotected sites. Other protected areas performed better in retaining climatic suitability for the modelled species in these areas compared to unprotected sites. Araújo et al. (2011) explained the variable performance as being partially related to topography. Whereas most nationally designated protected areas are in mountains or rugged environments, Natura 2000 also prioritizes farmland located in lower and flatter areas. Natura 2000 conservation areas are thus more vulnerable to climate change because proportional range losses arising from climate change are usually more pronounced in flatlands than in rugged terrain (Loarie et al. 2009).

Figure 70. High severity forest fires are increasing especially in the Mediterranean basin and may have drastic consequences for forest ecosystems and ecosystem services. Photo by D. Kraus.

Up to now, biodiversity conservation focused strongly on the protection of flagship species (e.g. *Tetrao urogallus, Rosalia alpina*). Protected areas were often established to conserve species that depended on traditional landscape features and that became threatened by intensive or changing land use practices. Many prominent species with high conservation value would not survive without management interventions because they do not belong to the natural climax vegetation of the region. Over the past decades, the share of unmanaged strictly protected areas has increased. But active conservation management has also remained a common strategy in biodiversity conservation. With the changing climatic conditions, many flagship species are likely to lose their habitats. Conservation management will have to consider that target conservation species not only require specific management intensities, but that they may additionally be suffering from declining climatic suitability.

Under the prospect that many species will lose suitable habitats under the future climate, a new important question arises: Which should be the target species for biodiversity conservation under climate change?

- Currently present rare species?
- Immigrating rare species that lose their current habitats?
- Or even currently common species that might become threatened in the future?

Possible effects of climate change on species diversity can be demonstrated with Denmark as an example. Denmark, a small country with very scarce natural areas, lies in three different climatic zones (boreal, continental, and atlantic). If the range margins of any of these particular climate zones moves, it might have drastic consequences for the ecosystems in Denmark with its approximately 30,000 species. Certain species will disappear, others might enter. Strange et al. (2011) studied implications for conservation policy for Denmark and presented two different options:

A Native Species Focus

- Should conservation policy focus efforts on protecting species native to a geopolitical area and fight to protect them in spite of climate change pressures?
- How should the issue that species may change habitats within the area be addressed?

An All Species Focus

- Should conservation policy instead give equal weight to the protection of immigrating species – climate refugees – as well as native ones?
- How should the issue that these species may be in need of protected habitats different from those the current native biodiversity depends on be addressed?

Choosing between these options can create a conservation management dilemma. Nature conservation actors and the public often prefer the native species focus – reflecting that established conservation policies are by nature conservative, focusing on preserving existing species and ecosystems, or even restoring what has been (Strange et al. 2011). Under climate change, however, it is questionable how long this strategy could be maintained. It appears much more promising to adapt conservation policies by also including immigrating threatened species and a possible rezoning of protected areas to react to the changing climatic conditions.

Under climatic change not all of a species' historic range remains suitable habitat. Plans and assumptions about protected areas will have to be reconsidered

There is a multitude of forest management measures available that support adaptation of forests to better cope with climate change (Kolström et al. 2011). Many of these measures can be combined, but some are incompatible with each other (or in strong conflict with other management objectives). In general, these adaptive measures can either aim to reduce

Table 9. Examples of forest management measures that support the adaptation of forests to climate change (partly based on Bolte et al. 2009; and Kolström et al. 2011).

Stand level	*Forest regeneration*	the manipulation of species and stand composition enhancing the genetic diversity using natural regeneration using artificial regeneration if and where needed. favouring mixed stands of suitable tree species diverse tree composition and ground vegetation
	Harvesting	small scale harvesting interventions systems which support natural regeneration diverse harvesting practices
Landscape level	*Management Planning*	reduced rotation length in response to increased growth rates and to lower the risk of financial losses from disturbances diverse combination of forest types and management systems at the landscape level
Policy level	*Investment in infrastructure*	the provision of infrastructure including a dense forest road network to support small scale thinning and harvesting practices and facilities for salvage timber storage to mitigate impacts of large scale disturbances
	Seed production and nurseries	support provision of climatically suitable seeds and plants by nurseries and forest tree breeding
	Adaptation options in risk management to fight pests and fire	Removal of forest residues Wind throw clearings Sanitation felling

negative climate change impacts or they can aim to increase the adaptability of the forests to the changing conditions. Increasing species diversity at the stand level as well as more diverse combinations of management systems at the landscape level are particularly useful approaches to increase the adaptive capacity of the forests and simultaneously support conservation management objectives.

> *Conservation management should be adapted to better respond to the challenges of climate change*

This can be done with a focus on establishing core areas, buffer zones, and corridors to develop improved protected area networks (Lewis 2009, Figure 71). Core protected areas should be designed to be large enough since extended areas are more likely to contain viable populations of species, and the species are less affected by fragmentation (Hannah 2008; Virkkala et al. 2008). Large latitudinal or longitudinal coverage and/or topographic diversity within the protected area will provide local variation in climatic, edaphic, and hydrologic habitat features, thus increasing the likelihood of species to find suitable habitats under changing conditions (Halpin 1997). High habitat diversity therefore enhances resilience of forest biodiversity (Graham 1988). Within such core protected areas it should be possible to restore populations of threatened and endangered species and/or to increase population size and genetic diversity. Core protected areas may also serve to manage and reduce future stressors such as invasive species, pests, and diseases. The reduction of browsing pressure would also be important in these areas as browsing prevents plant species from shifting their ranges and migrating to higher latitudes (Hulme 2005).

Within the buffer zones close to nature forestry should be applied to allow species to expand their range outside the protected forest area into the buffer zone (Hannah et al. 2002). Finally, continental scale corridors could aid in species range shifts. Corridors should therefore run parallel to longitudinal, altitudinal, and coastal inland gradients (Graham 1988).

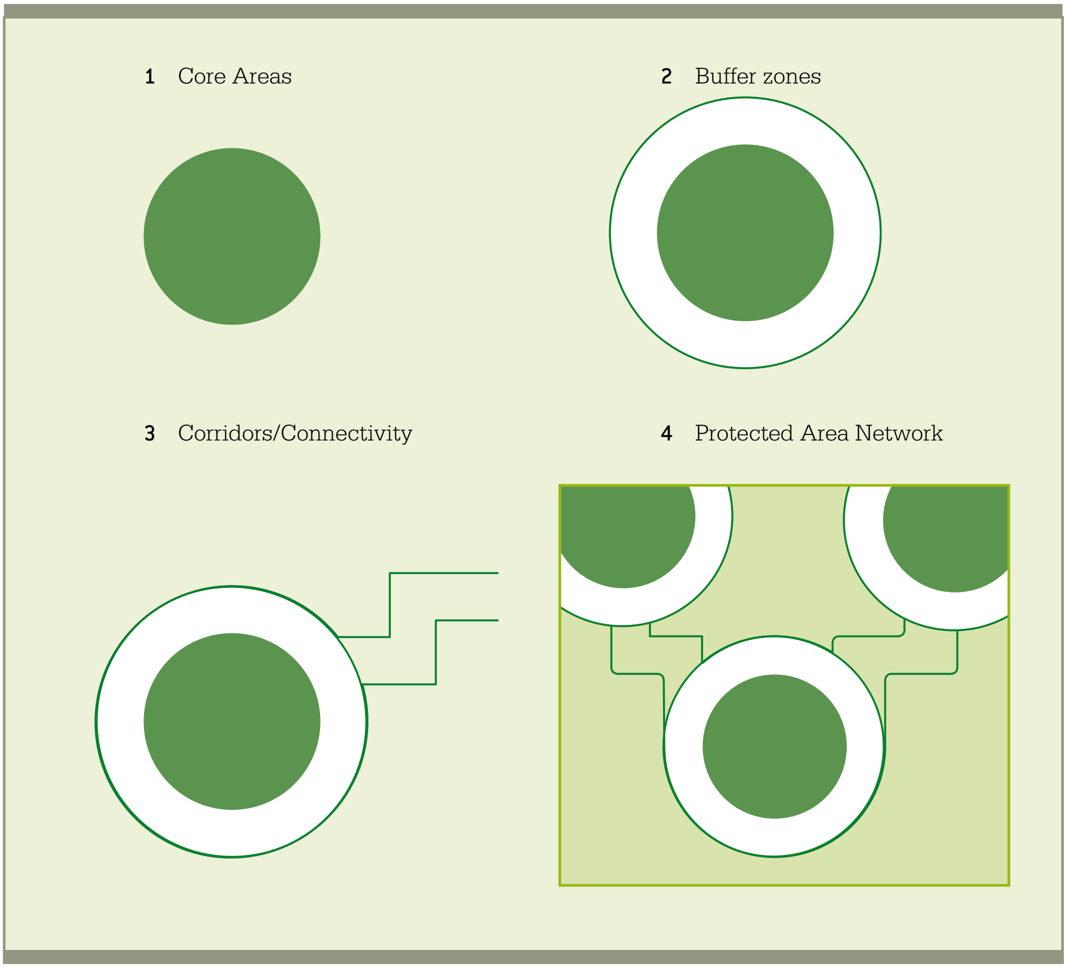


Figure 71. Idealized scheme to display the establishment of a protected area network. Core areas (green circles) surrounded by buffer zones (2 ff), corridors (3 ff) that secure the connectivity of the core areas, and finally a schematic protected area network (4). Source: Modified from Lewis (2009).

Landscapes with supporting habitat networks characterised by high spatial cohesion are crucial as sources of recolonisation. Gaps and fragmentations in species distributions following weather perturbations may cause permanent retraction in highly fragmented landscapes. Less fragmented regions support increased oscillations in occupancy and abundance (Opdam and Wascher 2004). During periods of favourable weather conditions, low quality habitats can be colonised again from high diversity source landscapes.

> *It is important to quantify how much extra area, patches, or connecting elements are needed for habitat cohesion considering the regional circumstances*

The corridors should also consider sessile species and should offer functional and physical diversity. However, it is clear that corridors are unlikely to secure the dispersal of the most slowly migrating species (Pearson and Dawson 2005). Therefore, another option for forest management could be to assist migration of species with slow dispersal rates (Honnay et al. 2002). The implementation of assisted migration could build on active ecological restoration of appropriate sites for species in new locations (Harris et al. 2006; Ibanez et al. 2006). On a European scale an increased number of protected areas would help to prevent the extinction of certain species (Hannah et al. 2007) and would also provide higher altitudinal and latitudinal/longitudinal variation within protected area networks (Halpin 1997).

> *Traditional conservation policies are not suitable under changing environmental condition, thus there is a need for a paradigm shift in conservation management*

Consequently, future biodiversity protection policy needs to be adapted and planned across borders. Conservation management under climate change should reclassify existing conservation areas to improve conservation outcomes (Fuller et al. 2010). It is likely that new conservation areas will be needed and the facilitation of species movements will require an improved integrated management of landscapes to support biodiversity conservation under changing climate (Araújo et al. 2011).

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. and Cobb, N. 2010. *A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.*

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. and Thuiller, W. 2011. *Climate change threatens European conservation areas. Ecology Letters 14:484–492.*

Bolte, A., Ammer, C., Löff, A., Madsen, P., Nabuurs, G.J., Schalm P., Spathelf, P. and Rock, J. 2009. *Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. Scandinavian Journal of Forest Research 24:473–482.*

Bolte, A., Hilbrig, L., Grundmann, B. and Roloff, A. 2013. *Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest – the Siggaboda case study. Annals of Forest Science 10.1007/s13595-013-0283-y.*

Coumou, D. and Robinson, A. 2013. *Historic and future increase in the global land area affected by monthly heat extremes. Environmental Research Letters 8.*

Fuller, R.A., McDonald-Madden, E., Wilson, K.A., Carwardine, J., Grantham, H.S., Watson, J.E.M., Klein, C.J., Green, D.C., and Possingham, H.P. 2010. *Replacing underperforming protected areas achieves better conservation outcomes. Nature 466(7304):365–367.*

Gardiner, B., Blennow, K., Carnus, J-M., Fleischer, P., Ingemarson, F., Landmann, G., Lindner, M., Marzano, M., Nicoll, B., Orazio, C., Peyron, J-L., Reviron, M-P., Schelhaas, M-J., Schuck, A., Spielmann, M., and Usbeck, T. 2010. *Destructive Storms in European Forests: Past and Forthcoming Impacts. Final Report to EC DG Environment.*

Graham, R.W. 1988. *The role of climatic-change in the design of biological reserves – the paleoecological perspective for conservation biology. Conservation Biology 2:391–394.*

Halpin, P.N. 1997. *Global climate change and natural-area protection: management responses and research directions. Ecological Applications 7:828–843.*

Hannah, L. 2008. *Protected Areas and Climate Change. Annals of the New York Academy of Science 1134(1):201–212.*

Hannah, L., Lovejoy, T, Midgley, G., Bond, W., Bush, M., Lovett, J., Scott, D. and Woodward, I. 2002 *Conservation of Biodiversity in a Changing Climate. Conservation Biology 16:11–17.*

Hannah, L., Midgley, G., Andelman, S., Araujo, M., Martinez-Meyer, E., Pearson, R. and Williams, P. 2007. *Protected Area Needs in a Changing Climate. Frontiers in Ecology and the Environment 5(3):131–138*

Harris, J.A., Hobbs, R.J., Higgs, E. and Aronson, J. 2006. *Ecological restoration and global climate change. Restoration Ecology 14:170–176.*

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. and Hermy, M. 2002. *Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters 5:525–530.*

Hulme, P.E. 2005. *Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42:784–794.*

Ibanez I, Clark JS, Dietze MC et al. 2006. *Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. Ecology, 87, 1896–1906.*

Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A. and Muys, B. 2012. *Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. Climatic Change 115:343–363.*

Kolström, M., Lindner, M., Vilén, T., Maroschek, M., Seidl, R., Lexer, M.J., Netherer, S., Kremer, A., Delzon, S., Barbati, A., Marchetti, M. and Corona, P. 2011. *Reviewing the science and implementation of climate change adaptation measures in European forestry. Forests 2:961–982.*

Koutsias, N., Arianoutsou, M., Kallimanis, A.S., Mallinis, G., Halley, J.M. and Dimopoulos, P. 2012. *Where did the fires burn in Peloponnisos, Greece the summer of 2007 Evidence for a synergy of fuel and weather. Agric. For. Meteorol. 156:41–53.*

Lewis, S., 2009. *Climate Change and Biodiversity in European Protected Forests: Policies for Adaptation. MSc thesis, Imperial College London. 93p.*

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. and Ackerly, D.D. 2009. *The velocity of climate change. Nature 462:1052–1055.*

McCarty, J.P. 2001. *Ecological consequences of recent climate change. Conservation Biology 15: 320–331.*

Netherer, S; Schopf,A. 2010. *Potential effects of climate change on insect herbivores in European forests-General aspects and the pine processionary moth as specific example. Forest Ecology and Management 259:831–838.*

Opdam, P. and Wascher, D. 2004. *Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117: 285–297.*

Pearson, R.G. and Dawson, T.P. 2005. *Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123:389–401.*

Penuelas, J., Ogaya, R., Boada, M. and Jump, A.S. 2007. *Migration, invasion and decline: changes in recruitment and forest structure in a warming – linked shift of European beech forest in Catalonia (NE Spain). Ecography 30:829–837.*

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R. and Dobbertin, M. 2013. *Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Global Change Biology 19:229–240.*

San-Miguel-Ayanz, J., Moreno, J.M. and Camia, A. 2013. *Analysis of large fires in European Mediterranean landscapes: Lessons learned and perspectives. Forest Ecology and Management 294:11–22.*

Strange, N., Thorsen, B.J., Bladt, J., Wilson, K.A. and Rahbek, C. 2011. *Conservation policies and planning under climate change. Biological Conservation 144:2968–2977.*

Virkkala, R., Heikkinen, R.K., Leikola, N. and Luoto, M. 2008. *Projected large-scale range reductions of northern-boreal land bird species due to climate change. Biol. Conserv. 141:1343–1353.*

4.2 The functional role of biodiversity in forests

Michael Scherer-Lorenzen

European forests cover a large gradient of compositional, structural, and functional diversity

A large variety of different forest types can be found in Europe, resulting from the stratification of paleo-climates of the past two million years and from the large climatic, geological, and geographical gradients across the European continent. These forests exhibit a large compositional, structural, and functional diversity. Human-induced disturbances such as logging, grazing, burning, and forest clearing to create space for agriculture have left an important anthropogenic footprint in forests. However, historical and recent management has also created sharp gradients in forest biodiversity, sometimes over relatively short geographical distances. Logging and replanting of single fast-growing species has created forest types of rather low species and structural diversity, while selective logging and favouring of natural regeneration has resulted in coexisting species growing in several different strata (e.g. "selection forest"), possibly beyond natural levels of species and structural diversity. In addition, recent forest policies aim to support the conversion of production-orientated monocultures to multifunctional and diverse forests. Ongoing climate change will also affect forests and the organisms living in them. It is clear that forest biodiversity is changing and will continue to change in the near future. We must therefore face the question whether and how changes in forest biodiversity will affect the functioning and stability of ecosystems and the services humans derive from forests.

Changing biodiversity has several consequences for ecosystems

Single tree species with their specific functional characteristics, or traits, have clear impacts on ecosystem properties, such as biomass production, nutrient cycling, or the presence and abundance of other organisms. For example, Reich et al. (2005) showed in a replicated experiment with 14 gymnosperm and angiosperm tree species that, 30 years after establishment of single-species plots, differences in litter calcium concentrations resulted in profound changes of soil chemistry and fertility. In addition, earthworm abundance and diversity were higher in those stands where tree species rich in calcium were grown. Hence, there are direct links between vegetation, soil organisms, and soil biogeochemistry. A change of the dominant tree species within a forest patch, e.g. due to management or changing climate, will therefore have cascading effects on certain ecosystem functions and services. Such phenomena are also known as “species identity effects”.

In contrast to such rather well known identity effects, the question of how changes in tree diversity will affect a multitude of ecosystem processes simultaneously is still rather equivocal. The challenge of understanding the influence of biodiversity on ecosystem functioning has initiated a new interdisciplinary research area that emerged in the early 1990s. Since then, a new ecological framework has evolved that underscores the active role of the biota and its diversity in governing environmental conditions within ecosystems, with cascading effects on the delivery of ecosystem services and human well-being. For logistical reasons, this functional diversity research focused mainly on species richness and primary productivity, using model communities of laboratory organisms or grasslands (Cardinale et al. 2011).

Box 38. Ecosystem properties, processes, functions, and services

The terms ecosystem (or ecological) processes and properties, functions or functioning, and services are central for the concepts of functional biodiversity research. They are used in the following sense (compiled from Naeem et al. 2002; Hooper et al. 2005; MA 2005; de Groot et al. 2009):

Ecosystem processes: the physical, chemical, and biological actions or events that link organisms and their environment, e.g. biomass production, litter decomposition, nutrient cycling.

Ecosystem properties: the size of compartments e.g. pools of material such as carbon or soil organic matter.

Ecosystem functions: the capacity of ecosystems to provide services – directly and indirectly – underpinned by biophysical structures and processes. They can be seen as intermediates between processes and services.

Ecosystem functioning: activities, processes, or properties of ecosystems that are influenced by its biota.

Ecosystem services: benefits people obtain from ecosystems, including provisioning services (e.g. food, fibre, genetic resources), regulating services (e.g. erosion control, climate regulation, pollination), cultural services (e.g. spiritual and religious, recreational, educational), and supporting services (e.g. soil formation, primary production, nutrient cycling).

Functional traits of species determine the underlying biological mechanisms for mixture effects

Existing studies of forest diversity effects on ecosystem functioning fall into four groups: (1) forest yield studies of monocultures and two-species mixtures using permanent sample plots or silvicultural trials, (2) observational approaches along natural gradients of forest diversity, (3) analyses of national or regional inventory databases, and (4) tree diversity experiments establishing forests stands differing in tree diversity by planting.

Forest yield studies suggest an idiosyncratic relationship between diversity and productivity, with the difference between monocultures and mixtures depending on species composition and environmental conditions. Similar idiosyncratic effects are reported for nutrient cycling, resistance to storm damage, and other ecosystem processes. There is some indication that mixes of complementary functional types, i.e. species with similar performance or effects on ecological processes (e.g. shade-tolerant and intolerant, early- and late-successional, nitrogen-fixing and non-fixing species) yield higher productivity. Although these findings are restricted to the lowest end of the diversity scale (1 versus 2 species) and mainly to few commercial timber species, they illustrate two key issues: the importance of functional traits, and the occurrence of niche complementarity and facilitation as underlying biological mechanisms for mixture effects (see Box 39).

Box 39. Underlying mechanisms of biodiversity effects on ecosystems

"It is not possible to make general statements that mixed-species stands are better or worse than monocultures for all purposes. The nature of the interactions among species controls the differences in production and other ecological processes between mixtures and monocultures of the component species. It is not helpful to ascribe positive aspects of mixtures to a vaguely defined synergism; it is necessary to understand competition and other interactions among species, relative to local site conditions, in order to apply results of studies to management situation in an appropriate way" (quoted from Kelty and Cameron, 1995, p. 322).

This quote clearly shows that we need a profound knowledge about the biological mechanisms of interactions among coexisting tree species in order to understand the nature of mixing effects and to design tree species mixtures that can fulfil multiple purposes and functions. In general, diversity effects on ecosystem processes are the result of four main mechanisms: **Niche complementarity** occurs where a more diverse community, composed of a mixture of specialised species differing in structure and function, is able to exploit the available resources better than any given monoculture, leading to higher productivity and/or lower levels of unconsumed resources. **Facilitation**, i.e. the positive effect of one species on the performance of another (e.g. as so-called nurse plants, or through the additional input of nutrients via symbiotic nitrogen-fixation) can also result in higher resource use and hence productivity. The **selection effect** recognises that more diverse communities are more likely to contain high-performing species, which dominate the community and its effects on ecosystem processes. The concept of **ecological insurance** stresses that, when subject to unpredictable perturbations, more diverse communities are more likely to contain species that can cope with the new conditions.

Species richness is among the major determinants of ecological processes in ecosystems

Observational and comparative studies along larger gradients of tree diversity are surprisingly scarce, although they offer the advantage of comparing complex communities under natural conditions. More importantly, there was no systematic establishment of observational studies allowing the quantification of the biodiversity-ecosystem functioning relationship in European forests (but see Box 40). Results from the first study in Central European beech forests in the German Hainich National Park show that increasing the number of tree species from pure beech to 5-species mixtures has variable effects on different ecosystem functions. For example, total standing aboveground biomass was negatively related to tree diversity (Jacob et al. 2010), while positive associations with tree diversity were found for herb-layer diversity (Mölder et al. 2008), or beetle diversity (Sobek et al. 2009). It became clear that the identity and abundance of the tree species present are the major determinants of the processes under study, associated with a "dilution" of beech with increasing species richness. In addition, covariation of some soil properties with tree diversity makes it difficult to distinguish direct diversity effects on processes from those mediated by the environment. In sum, these findings from observational studies have shown that tree diversity explains some variation in several ecosystem functions and processes, together with environmental factors and tree species identity.

Recent inventory-based diversity-functioning studies reported positive relationships between tree species diversity and productivity

A very recent study by Gamfeldt et al. (2013) could show that multiple ecosystem services, such as production of tree biomass, soil carbon storage, berry production, game production, understory plant species richness, and presence of deadwood were all positive to positively hump-shaped related to tree species richness in Swedish production forests. Such inventory analyses can capitalize on the huge number of permanent monitoring plots existing in many countries. However, the large number of co-variables introducing "noise" in the diversity-function relationship is problematic, and their effects must be statistically accounted for. In addition, tree diversity is only a "by-product" because the selection of plots has not been based on a diversity criterion, but rather on representativeness of forest types or on grid-based sampling schemes. Hence, most inventory plots do only cover the lower end of the diversity gradient. Nevertheless, there is increasing evidence from such studies that tree diversity does indeed positively influence ecosystem functioning and services.

Similar to the highly successful application in grassland biodiversity research, the experimental manipulation of tree diversity aims to decouple the effect of the environment from biodiversity effects by establishing experimental communities differing in certain aspects of diversity, but growing in the same environmental conditions. Only by adopting this "synthetic community approach" can within-habitat effects of diversity be detected unequivocally, allowing us to test causal relationships between diversity and function. This approach has been followed within the network of tree diversity experiments (TreeDiv-Net; www.treedivnet.ugent.be). The first results from these experiments show that tree diversity can indeed have significant effects on tree growth and biomass production, litter production, herbivory, and nutrient budgets of trees, while decomposition of litter remained rather unaffected. The major limitation of such biodiversity experiments with trees is the artificial assemblage of experimental communities and hence the deviation in several properties from natural stands, although they might well represent the conditions in plantation forests.

> *From a multifunctionality perspective, it is obvious that no single species is able to fulfil many functions simultaneously, and there might even be trade-offs between distinct services*

In three recent reviews, the available scientific evidence for tree diversity effects on ecosystem functioning has been compiled from the literature, covering the different study approaches mentioned above (Table 10). It has become clear that tree diversity has mostly positive effects on a large variety of ecological processes, but that neutral and negative effects are also common. Tree growth and biomass production as well as the abundance and diversity of associated flora and fauna are often positively associated with increasing tree diversity. Other ecological functions and services, especially those related to biogeochemical cycling, seem to be less sensitive to changes in tree diversity and are more strongly controlled by site conditions. Finally, the identity of dominant species also plays a major role in controlling ecological processes. However, from a multifunctionality perspective, it is obvious that no single species is able to fulfil many functions simultaneously, and that there might even be trade-offs between distinct services. Hence, moving towards a management of mixed species stands might help to sustain multiple benefits from forest ecosystems.

Table 10. Summary of three different literature reviews on the effects of tree diversity for ecosystem functions and services. Thompson et al. (2009) compiled the literature up to 2009, focusing on biomass production only. Nadrowski et al. (2010) analysed the literature published between 2007 and 2010 and considered only studies covering a diversity gradient extending beyond two species mixtures; several ecosystem functions were included. Scherer-Lorenzen (2013) reviewed studies published between 2005 and 2013, which also cover multiple functions and services. Examples for functions and services include above- and belowground biomass production, stemwood production, growth, mortality, litter production, pool sizes of nutrients in tree biomass and soil, rates of nutrient fluxes between ecosystem compartments, carbon sequestration in biomass and soil, water fluxes, diversity of associated flora and fauna, and herbivore and pathogen damage.

Diversity effect	**Thompson et al 2009**	**Nadrowski et al. 2010**	**Scherer-Lorenzen 2013**
Negative	-	5	13
Neutral or unimodal	5	25	9
Positive	15	40	45

Box 40. A new European project on the functional significance of forest biodiversity

Since October 2010, the new EU-funded project FunDivEUROPE (www.fundiveurope.eu) combines these abovementioned approaches to study the functional significance of forest biodiversity in Europe. It has established a network of more than 250 study plots in six different forest types, ranging from Mediterranean forests in Spain and Italy, to central and eastern forests in Germany, Poland, and Rumania, and to boreal forests in Finland. In each region, the plots have been established along a gradient of tree species richness, replicated with different species compositions. The project also includes the European sites of the TreeDiv-Net network, with experiments in France, Belgium, Germany, and Finland (see Figure 72). In both approaches, a multitude of ecological processes and functions are studied by partners from 24 scientific institutions from 15 countries. Finally, data from selected European National Forest Inventories are also being analysed for potential tree diversity effects on ecosystem functions.

Figure 72. Within the FunDivEUROPE project, mature forest stands (left) and experimental plantations (right) differing in tree species richness and composition are analysed for biodiversity effects on ecosystem functioning and the provision of ecosystem services. Photos by S. Müller (left), M. Scherer-Lorenzen (right).

> *Despite the fact that we are still far from a general theory about the functional role of biodiversity in forests, recent evidence suggest that the conservation of genetic, structural, and functional diversity in forest communities is a good basis for multifunctional and sustainable forest use*

Thus, biodiversity is not only a "good" to monitor, conserve, and manage, but could also be used as a tool to achieve certain management goals, such as the delivery of multiple ecosystem services. In addition, forest diversity and complexity will certainly play a crucial role for the stability of forests, becoming an important element of adaptation strategies facing the challenges of global climate and environmental change. Hence, an adaptive forest management that accounts for future climate and pressures may capitalize on biodiversity effects, which could help to sustain the delivery of various ecosystem services simultaneously. This should be done at the stand level by developing and adopting management options for age-structured multi-species mixtures and at the landscape scale by developing concepts for multifunctional ecosystem management. For example, trade-offs between ecosystem services imply that maximization of several services is difficult at the stand scale, but positive biodiversity-ecosystem function relationships suggest that monoculture patches of different species would not optimize multifunctionality at the landscape scale. Hence, a mosaic of mixed stands with different species composition may potentially maximise the delivery of ecosystem services societies depend on. And even for new developments in silviculture, such as short rotation forestry, the insights from functional biodiversity research could be taken into account to optimize both economic and ecological aspects: perhaps the next generation of such plantations will not rely on a single highly productive clone or species, but on a carefully selected mixture of different and complementing species, resulting in high and stable wood production, efficient resource use, and stability against pests and pathogens.

References

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I. and Gonzalez, A. 2011. *The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.*

de Groot, R.S., Alkemadeb, R., Braatc, L., Heina, L. and Willemen, L. 2010. *Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making Ecological Complexity 7:260–272.*

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J. and Bengtsson, J. 2013. *Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340.*

Hooper, D.U., Chapin, F.S.I., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. 2005. *Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. Ecological Monographs 75:3–36.*

Jacob, M., Leuschner, C. and Thomas, F.M. 2010. *Productivity of temperate broad-leaved forest stands differing in tree species diversity. Annals of Forest Science 67:503.*

Kelty, M.J. and Cameron, I.R. 1995. *Plot design for the analysis of species interactions in mixed stands. Commenwealth Forestry Review 74:322–332.*

Millennium Ecosystem Assessment (MA) 2005. *Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC. 137 p.*

Mölder, A., Bernhardt-Römermann, M. and Schmidt, W. 2008. *Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? Forest Ecology and Management 256:272–281.*

Nadrowski, K., Wirth, C. and Scherer-Lorenzen, M. 2010. *Is forest diversity driving ecosystem function and service? Current Opinion in Environmental Sustainability 2:75–79.*

Naeem, S. 2002. *Ecosystem consequences of biodiversity loss: the evolution of a paradigm. Ecology 83:1537–1552.*

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M. and Tjoelker, M.G. 2005. *Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecology Letters 8:811–818.*

Scherer-Lorenzen, M. 2013. *The functional role of biodiversity in the context of global change. In: Burslem, D., Coomes, D. and Simonson, W. (eds.). Forests and Global Change. Cambridge University Press, Cambridge. Pp. 195-238.*

Scherer-Lorenzen, M., Körner, C. and Schulze, E.-D. (eds.) 2005. *Forest Diversity and function: Temperate and boreal systems. Ecological Studies 176. Springer, Berlin, Heidelberg, New York.*

Sobek, S., Steffan-Dewenter, I., Scherber, C. and Tscharntke, T. 2009. *Spatiotemporal changes of beetle communities across a tree diversity gradient. Diversity and Distributions 15:660–670.*

Thompson, I., Mackey, B., McNulty, S. and Mosseler, A. 2009. *Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Technical Series no. 43. Secretariat of the Convention on Biological Diversity, Montreal.*

4.3 Invasive neobiota in forest ecosystems: opportunity or threat?

Nicola Schoenenberger and Marco Conedera

With the onset of Roman domination in the southern fringe of the Alps in roughly the first century B.C., the non-native chestnut (*Castanea sativa*), a tree of great economic importance, was widely introduced. Its man-made monospecific stands, generally managed as coppice woods or fruit orchards, replaced large areas of the native forest and deeply altered ecosystem functioning. Chestnut litter decomposes slowly, acidifies soils, and increases the fire regime, which in turn perpetuates chestnut forests and their species-poor acidophilic understory. If we were to apply today's criteria for describing invasive neobiota, we would probably call the chestnut tree an ecosystem transformer species with an adverse effect on biodiversity. Its cultural and economic importance and ancient introduction, however, do not allow for such considerations, and chestnut is still highly valued in most of its introduced area. In 2002 the invasive chestnut gall wasp *Dryocosmus kuriphilus*, which is considered the most dangerous pest of chestnut worldwide, was recorded for the first time in Europe in the Piedmont region of northern Italy. It had presumably been introduced a few years earlier through contaminated Asiatic nursery material, where the pest is native. To obviate the damage caused by the chestnut gall wasp to fruit production and to respond to public pressure because of strong cultural identification with the chestnut tree, the hymenopteran parasitoid *Torymus sinensis*, native to China, has been widely released as a biological control agent in Italy as well as more recently in France. The species establishes self-sustaining populations and has the ability to spread naturally. From Japan, where *Torymus sinensis* was previously introduced for the same purpose, it is known to spread quickly, interbreed with a native *Torymus species*, and displace it through genetic assimilation – an unexpected outcome and a unique case worldwide. Despite this, European introductions occurred without a formal assessment of the potential risks associated with *Torymus sinensis*, and in 2012 hybridisation between the non-native biocontrol agent and a native *Torymus* species (associated with oak galls) was discovered in Europe. The Japanese history is about to repeat itself on the European continent. This example of an invasive neozoan deliberately used to combat another invasive neozoan threatening a non-native forest tree illustrates the complexity of the field of biological invasions when it comes to defining their causes, mechanisms, impacts, management options, and terminology under socio-cultural, economic, and ecological perspectives.

> *Neobiota are organisms that are able to spread naturally in geographic areas where they previously were not native and include plants (neophytes), animals (neozoans), and fungi (neomycetes)*

Neobiota are organisms that are able to propagate and spread naturally (i.e. are naturalised) in geographic areas where they previously were not native and include plants (neophytes), animals (neozoans), and fungi (neomycetes). This terminology is often used in Europe, whereas in other parts of the world, terms such as “alien” or “exotic” species are more commonly used and have a similar meaning. Generally, species introduced through human activity to new geographic areas after the end of the Middle Ages are considered neobiota. Long distance dispersal occurs intentionally or unintentionally over biogeographic boundaries such as oceans, deserts, or mountain ranges. Neobiota spread to new areas as free riders attached to transported goods and living beings or as deliberately introduced, economically important species (pets, livestock, crops, ornamentals, or biological control organisms). Once introduced, their establishment in nature depends on a multitude of factors, such as land-use change, human and natural disturbance, eutrophication, or climate change. The on-going global increase of these processes favours the spread and establishment of an ever-increasing number of neobiota. This trend is still continuing as a consequence of the increase in intercontinental exchange of goods and people, and the outcome of this global biological homogenisation is far from complete.

Increasing numbers of neobiota continue to be introduced: the outcome of this global biological homogenisation is far from complete

Some neobiota may eventually become invasive, i.e. produce offspring in very large numbers and with high dispersal ability. Invasive neobiota can cause a variety of negative impacts; however, only a fraction of the overall neobiotic species is considered harmful. As an example, only about 20% of the neophyte species in the UK and the Baltic states are considered to have an adverse impact (DAISIE 2009:43–61). If related to overall plant richness (native and non-native species), this proportion is often less than 2% in European countries. Several of the claims that neobiota, particularly plants, represent an ominous threat to biodiversity are not supported by data. A different approach is thus required, possibly focussing more on the function of a species in an ecosystem rather than its origin.

Invasive neobiota may represent an important threat to society and nature and involve a multitude of negative impacts, including tremendous monetary costs

However, invasive neobiota may represent an important threat to society and nature and involve a multitude of negative impacts, such as increased human and animal health hazards; yield losses through pests, pathogens, and competitors in agriculture, forestry, and fishery; impacts on biodiversity and ecosystem functioning (including the recreational quality of nature); and damage to infrastructure. Although some invaders are responsible for the extinction of species, particularly in the case of predators and pests in freshwater bodies and on islands, they do not seem to pose a major extinction threat to species in most environments, at least at present (Davis 2009). In some cases even beneficial ecological impacts have been discovered. However, there is no definitive answer to many aspects of invasions by neobiota, particularly in relation to their long-term effect on biodiversity and in combination with other factors (e.g. pollution or habitat destruction).

Invasive neobiota may cause tremendous costs in terms of damages and expenditures for management measures. For instance, the yearly cost of control measures against invasive knotweeds (*Fallopia* spp.) in the United Kingdom has been estimated to amount to about 1.5 billion pounds, or the economic damage caused by 20 invasive neobiota in Germany to about 167 million euros per year, mainly related to yield loss, costs to public health, or for control measures. The European Union assumes accruing amounts of 10–12 billion euros per year for damages and control measures on its territory.

In forest ecosystems the most damaging invasive neobiota are likely to be insect pests and pathogens. The East Asiatic ascomycete *Cryphonectria parasitica*, for instance, which also attacks chestnut trees and causes bark cancer, was introduced in Europe about 60 years earlier than the chestnut gall wasp. Although it did not dramatically decimate chestnut stands, it remains a constant threat and a factor of loss in productive chestnut orchards and coppices. In North America, however, chestnut bark cancer is responsible for the near extinction of the American chestnut (*Castanea dentata*). Within 40 years the nearly four-billion-strong population in Northern America was devastated – only a few clumps of chestnut trees remained in its native range.

> *In forest ecosystems the most damaging invasive neobiota are likely to be insect pests and pathogens*

In comparison to man-made and frequently disturbed habitats such as urban or agricultural land, littoral, and riverine habitats, in European forest ecosystems, the present level of neophyte invasion, i.e. the actual proportion of neophytes among all plant species, is much lower and often less than 5% (Chytrý et al. 2009). However, this proportion does not mean that forest habitats are necessarily less susceptible to biological invasion. In the presence of high propagule pressure from neophytes, i.e. the absolute number and scattering ability of plant parts able to disperse and reproduce (such as seeds, buds, or rhizomes), forest ecosystems may become heavily invaded (see Box 41 on laurophyllisation). This is particularly true for forests located in warm lowlands and close to urbanised areas. At least 622 woody plant species (trees and shrubs) are known to be invasive somewhere in the world, and 21 woody plant species feature on the famous list of "100 of the World's Worst Invasive Alien Species", which covers animals, plants, and fungi. Over 60% of the invasive trees and shrubs of the world have been introduced as ornamentals in horticulture, whereas 13% were forestry, 10% food, and 7% agroforestry species (Richardson and Rejmánek 2011). A surprisingly high proportion of invasive trees and shrubs have their seeds dispersed by birds, which typically feed on berries of ornamental plants in gardens and parks and disperse the seeds in nearby forests (Figure 73).

Box 41. Laurophyllisation: vegetation change in broadleaved forests in southern Switzerland.

In the Insubric area of southern Switzerland, local deciduous forests have been successfully and increasingly colonised by evergreen broad-leaved woody species since the late 1970s. Both native (e.g. *Ilex aquifolium* and *Hedera helix*) and non-native species (e.g. *Cinnamomun glanduliferum*, *Elaeagnus pungens*, *Laurus nobilis*, *Prunus laurocerasus* and *Trachycarpus fortunei*, Figure 73) have invaded. All these species produce berries and are dispersed by birds. The process, which has been interpreted by some authors as a biome shift from deciduous vegetation to an evergreen broadleaved forest ("laurophyllisation") dominated by neophytes, has been tentatively explained as caused by factors such as propagule pressure, i.e. the cultivation of large amounts of evergreen ornamental species in gardens and the dispersal of their seeds by birds from the gardens to the forests; land use change, i.e. the explosion of the urbanised area and the change of forest use since the late 1960s; and climate change, i.e. a significant reduction of frost days since the 1970s, encouraging evergreen growth.

Figure 73. First generation laurophylls (particularly the palm tree *Trachycarpus fortunei*) after escaping cultivation. Birds disperse the seeds up to 200 m from the garden edge, where they successfully colonise and outcompete species-rich hop hornbeam (*Ostrya carpinifolia*) and manna ash (*Fraxinus ornus*) forests. Photo by N. Schoenenberger.

Many of the invasive neophytes in forests are economically important forestry tree species, and the perception of their usefulness or harmfulness greatly varies among different stakeholders according to their various fields of interest. The invasive nitrogen-fixing black locust *Robinia pseudoacacia*, for instance, is a valued tree both in forestry for its wood and in apiculture for its abundant nectar but is considered a nightmare for biodiversity protection goals and prevents utilization of the forest for leisure activities as it produces impenetrable thickets. In southern Germany, there are concrete indications that the economically very important Douglas fir (*Pseudotsuga menziensii*) also produces adverse ecological impacts and alters the character of the landscape through its ability to invade forest-free rocky hillsides (reviewed in Kowarik 2010:183–187).

> *Several invasive neophytes in forests are economically important forestry species; the perception of their usefulness or harmfulness greatly varies among different stakeholders*

Woody climbers or lianas represent another important category of invasive neophytes in forest edges and floodplain forests. Several among them are still rather unknown in Europe but may increasingly become threatening in the future. A good example is the Kudzu vine *Pueraria lobata*, native to Eastern Asia and a well-known invader in North America and elsewhere, which has been recommended for regulation as a quarantine pest by the European and Mediterranean Plant Protection Organisation (EPPO). The neophyte is known in Europe

Figure 74. The Kudzu vine (*Pueraria lobata*) invading a forest edge, covering and completely smothering the native vegetation. Photo by N. Schoenenberger.

in more than 30 populations, located in northern Italy, southern Switzerland (Figure 74), and Bosnia-Herzegovina. Once considered to be able to spread only through vegetative reproduction and man-mediated dispersal, it has recently been discovered to produce viable seeds in late autumn, probably favoured by particularly mild seasons.

Avoiding the introduction and establishment of invasive neobiota, limiting their spread, and mitigating their impacts represent a challenge. The biology may profoundly differ among species. So do the introduction pathways and impacts, which may be multiple and depend on local conditions. Moreover, because impacts tend to increase over time with growing populations, prevention, early detection, and rapid response are often the cheapest options available to avoid damage. However, this means recognizing the problem and taking action before adverse impacts are visible. It is therefore necessary to develope properly designed risk assessment protocols and basic data on single species, particularly when introduction pathways exist and therefore establishment is a likely event. Assessing the risks and deciding on management measures needs a case-by-case approach for each species, each biogeographic area, and each protection goal. Controlling invasive neobiota requires both international cooperation and local networking as they do not respect political boundaries and typically affect several sectors of society transversally.

Preventive measures such as avoiding introduction, early detection, and rapid response are the cheapest options available to avoid ecological and economic damage

Four strategies can be applied to avoid or to oppose biological invasions: implement preventive measures, detect and quickly eradicate early stages of an invasion, contain further expansion when eradication becomes difficult to achieve, and control widespread invaders in order to mitigate their negative impact, ideally keeping them below a bearable threshold (Davis 2009). Containment and control strategies do not have a temporal endpoint. Besides some rare cases of possible biological control, in the case of forestry-relevant insect pests and pathogenic fungi or bacteria, preventing their introductions is often the sole possible management option. Once established, due to the non-confineable character of forest systems and the mobility of pests and pathogens, eradication is mostly not attainable; it may only be possible to slow down further expansion, leaving some time for forest managers to adapt strategies to the arriving nuisance. In the case of forestry-relevant invasive neophytes, all four management options may be applied.

Preventive actions are generally considered the most cost-effective and are achieved through risk analyses, quarantine regulations, and other biosafety measures. By applying the principle of extended producer responsibility, costs arising from management of invasive neobiota may be shifted to those business sectors that profit from the movement of organisms. Regulations may be set in place to require transporters to make sure they are not transporting invasive neobiota as contaminants of traded commodities or as commercialised organisms as they bear a significant degree of responsibility for the environmental impacts that may arise from such introductions.

> *By applying the principle of extended producer responsibility, costs arising from management of invasive neobiota may be shifted to those business sectors that profit from the movement of organisms*

Control measures after successful introduction and establishment of an invasive neobiota always depend on the specific organism, the invaded habitat and its exploitation, the range of the invasion, and the damage. Generally, three possible control measures are recognized: mechanical, chemical, or biological control. In the case of neophytes, cultural methods may be applied (i.e. increasing competition from native crops). Often only a combination of the different control methods leads to success. Prioritisation within management goals is essential; action needs to be taken in view of the protection goals at stake and where the probability of success is highest (i.e. first manage small populations of invasive neobiota in habitats where the potential for damage is highest).

Box 42. Countering biological invasions to avoid adverse economic and ecological impacts needs coordinated approaches integrating scientific, technical, political, and legal actions.

Preventive measures may include following activities:

- Interrupting introduction pathways
- Avoiding disturbance
- Planning of follow-up inspections and action plans for biological invasions after forestry works or re-naturalisations
- Surveillance of areas where control measures have taken place to avoid secondary invasions
- Contractually agreeing to keep building sites free of invasive neobiota after the building works
- Commercialising alternative species to invasive neobiota
- Avoiding the dumping of garden waste in forests and other ecosystems
- Informing stakeholders
- Containing land abandonment

Monitoring of priority sites and their surroundings in terms of probability of first introduction, including:

- Nurseries and botanical gardens
- Parks and private gardens
- Building sites and places where soil movement takes place
- Ports and Airports
- Composting plants

- Landfill sites and deposits of building materials and machinery
- Transport axes (including forest roads)
- Storm- or fire-damaged areas, landslides, and flooded areas
- Places where wild animals are fed
- River systems and floodplains
- Areas where touristic and recreational activities take place

Early detection and rapid response programs imply the availability of the following elements:

- Access to technical assistance and scientific information on single species, species diagnostics, fact sheets, risk analyses, and distribution models
- Functioning international, national, and regional stakeholder networks
- Databases with known distributions and where it is possible to notify findings
- Alert system when new species first appear
- Organized structures for rapid response in order to start eradication programs when control measures are still feasible
- Inclusion of civil society, citizen science

References

Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C., and Vilà, M. 2009. *European map of alien plant invasions based on the quantitative assessment across habitats. Diversity and Distributions 15:98–107.*

Clout, M.N. and Williams, P.A. (eds.). 2009. *Invasive species management. A handbook of principles and techniques. Oxford University Press, Oxford, UK. 308 p.*

DAISIE (ed). 2009. *Handbook of alien species in Europe. Springer, New York, USA. 399 p.*

Davis, M.A. 2009. *Invasion Biology. Oxford University Press, Oxford, UK. 244 p.*

Kowarik, I. 2010. *Biologische Invasionen. Neophyten und Neozoen in Mitteleuropa. 2. Auflage, Ulmer, Stuttgart. 380 p.*

Richardson, D.M. and Rejmánek, M. 2011. *Trees and shrubs as invasive alien species – a global review. Diversity and Distribution 17:788–809.*

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F. 2002. *Ecological responses to recent climate change. Nature 416:389–395.*

Weber, E. 2013. *Invasive Pflanzen der Schweiz. Erkennen und Bekämpfen. Haupt, Bern Switzerland. French edition at Rossolis, Lausanne Switzerland. 224 p.*

4.4 Genetic diversity of forest trees

Jarkko Koskela and François Lefèvre

The genetic diversity of forest trees ensures the occurrence and functioning of forest ecosystems in a broad range of environmental conditions

Genetic diversity is the fundamental basis of all biological diversity. Trees are the keystone species of forest ecosystems, and recent studies have revealed that heritable traits in a single tree species can also influence community structure and ecosystem-level processes in forests (Whitham et al. 2006). Forest trees differ from other plant species in their capacity to maintain high levels of genetic diversity within populations rather than among populations (Hamrick 2004). Many tree species have a large distribution range, and local adaptation has led to significant differentiation in adaptive traits among populations of tree species (Savolainen et al. 2007). However, this adaptive selection does not greatly affect the genetic diversity of tree populations as most adaptive traits are controlled by a large group of genes rather than a single gene (Le Corre and Kremer 2012). Genetic diversity in a given tree population is largely determined by evolutionary history and population dynamics.

Genetic diversity can be measured in different ways. Phenotypic variation within tree species and their populations has a genetic and an environmental component. Phenotypic variation can be easily observed, but it is more difficult to quantify these two components. In forestry, provenance trials have long been used for distinguishing the genetic from the environmental components and for analysing genetic variation in quantitative traits related to growth (e.g. diameter increment), physiology (e.g. nutrient or water use efficiency), and phenology (e.g. bud flush). Variation in these traits reflects the result of adaptive processes, while laboratory analyses with different molecular markers mostly reveal historical and demographic processes. However, recent developments in forest tree genomics offer tools to link genetic diversity at the molecular level, or even individual genes, to adaptive traits (Neale and Kremer 2011).

Provenance tests (e.g. common garden experiments) have also shown that most forest trees have a high degree of phenotypic plasticity, i.e. large variation in the phenotype of a provenance across different environments. As trees are long-lived organisms, they often experience variable environmental conditions during their lifetime and subsequently have to acclimate to the prevailing conditions in the given period of time. Phenotypic plasticity drives the acclimatization process, which can alter both physiological and morphological characteristics of trees (e.g. Juurola 2003; Wagner et al. 1996). While genetic variation allows a tree species to occur under a broad range of environmental conditions, phenotypic plasticity determines the range of environments where selected provenances or genotypes (in case of clones) can be grown. Phenotypic plasticity, which also varies among tree populations, is part of the response to climate change and may interfere with evolutionary processes (Nicotra et al. 2010).

The level and distribution of genetic diversity in tree species and their populations are continuously changing over time as a result of evolutionary processes (natural selection, genetic

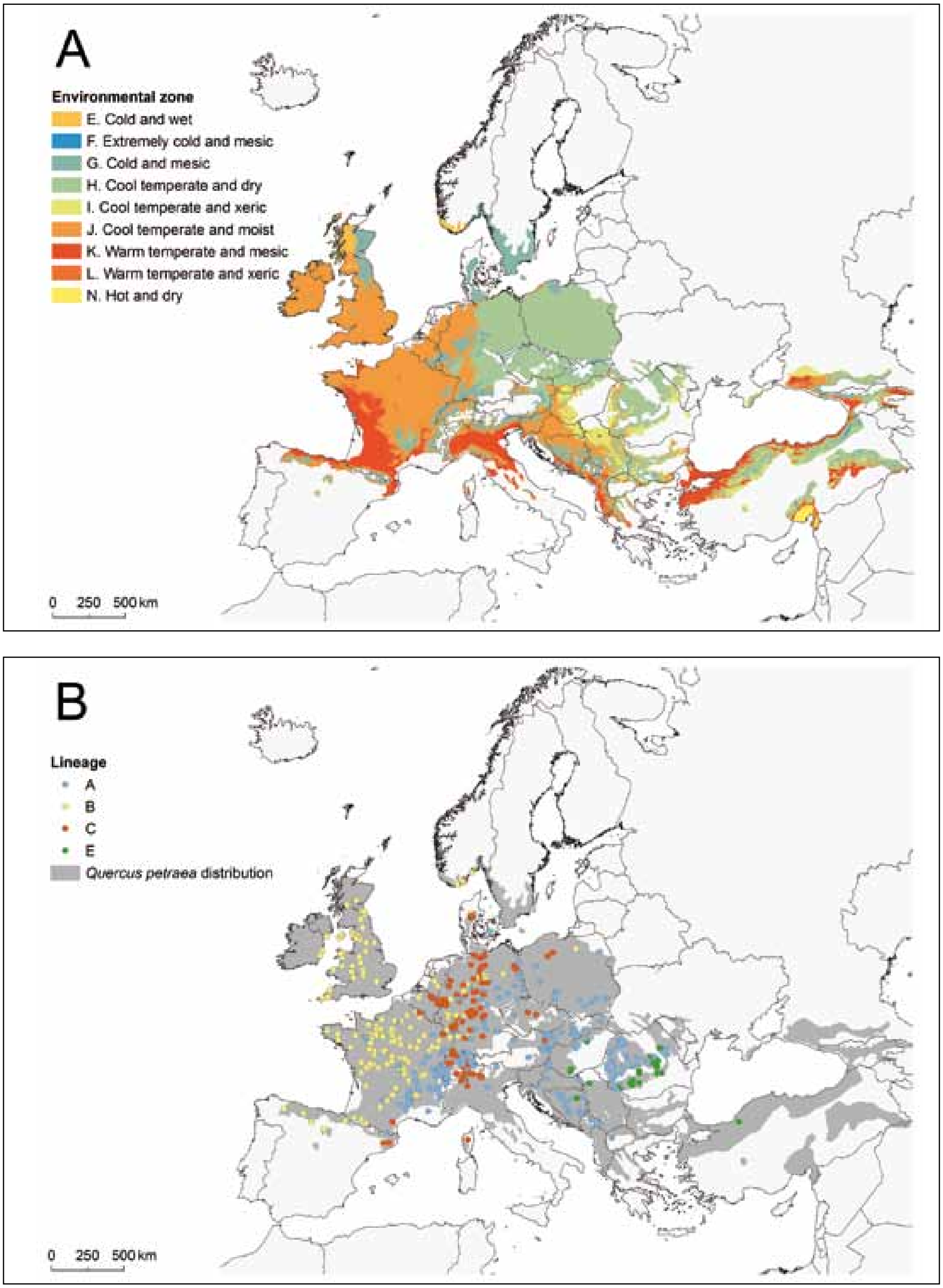


Figure 75. Diversity of selection pressure and phylogeographic history of sessile oak (*Quercus petraea*) illustrated by a) environmental zones (Metzger et al. 2013) within the species' distribution range and b) chloroplast DNA lineages based on Petit et al. (2002) and Slade et al. (2008). Source: a) EUFORGEN, www.euforgen.org; b) GD2 database, http://gd2.pierroton.inra.fr/gd2/home.

drift, gene flow, and mutation). The main goal of genetic conservation is the maintenance of these evolutionary processes within tree populations rather than preservation of present-day genetic diversity. This dynamic conservation approach (e.g. Lande and Barrowclough 1987; Eriksson et al. 1993) is typically implemented through *in situ* conservation of tree populations and can be complemented by static conservation efforts, such as *ex situ* collections and seed banks, especially in the case of rare and endangered tree species or populations. *Ex situ* conservation can also be dynamic if man-made tree populations are exposed to natural selection and competition and are allowed to evolve across generations.

Genetic diversity of forest trees is crucial for adaptation of forests to climate change

Tree populations can respond to climate change in three different ways (Aitken et al. 2008). They can persist through phenotypic plasticity, migrate to new areas with more suitable climate, or adapt (genetically) to new climatic conditions. Results of provenance trials have been used for developing transfer functions for individual tree populations based on climatic variables (e.g. Rehfeldt et al. 2002). These studies have shown that tree populations can grow well under a range of climatic conditions around their climatic optimum. However, they have also shown that the ability of tree populations to withstand climatic changes has its limits.

The migration potential of trees is also limited. Climate and species distribution models indicate that migration rates should be more than 1,000 meters per year to allow plants to follow the predicted shifts in their current climatic niches (Malcom et al. 2002). However, it has been estimated that the postglacial migration rates of forest trees were less than 100 meters per year (McLachlan et al. 2005). Therefore, it is unlikely that forest trees would be able to cope with the current climate change through natural migration. Considering the intensively managed forests in most parts of Europe, it is also unrealistic to assume that natural migration could take place spontaneously.

During the past 2.6 million years (Quaternary period), the distribution ranges of tree species have not been stable but have contracted, expanded, or shifted as a response to climate changes (Hewitt 2000). Tree populations, mostly in the southern part of their distribution range, have been able to adapt to the changing climatic conditions and then migrate northwards when climatic conditions again became more favourable. Northern tree populations often but not always experienced local extinction. Recent studies have provided evidence that small tree populations also survived at intermediate or even high latitudes during the last glacial episode, which reached its maximum about 20,000 years ago (Hu et al. 2009; Parducci et al. 2012). No tree species went extinct during the last glacial episode, but fossil records show that several tree species belonging to *Magnolia*, *Taxodium*, and *Sequoia*, for example, disappeared from Europe between 2.4 and 1.6 millions years ago (Kremer 2007).

New adaptations can emerge from the existing genetic variation or new variation generated by mutation. Past climatic changes often occurred over relatively short periods of time (one or a few tree generations) and this suggests that tree populations were able to adapt rapidly and frequently. More recent evidence from provenance trials and transfer of tree populations also

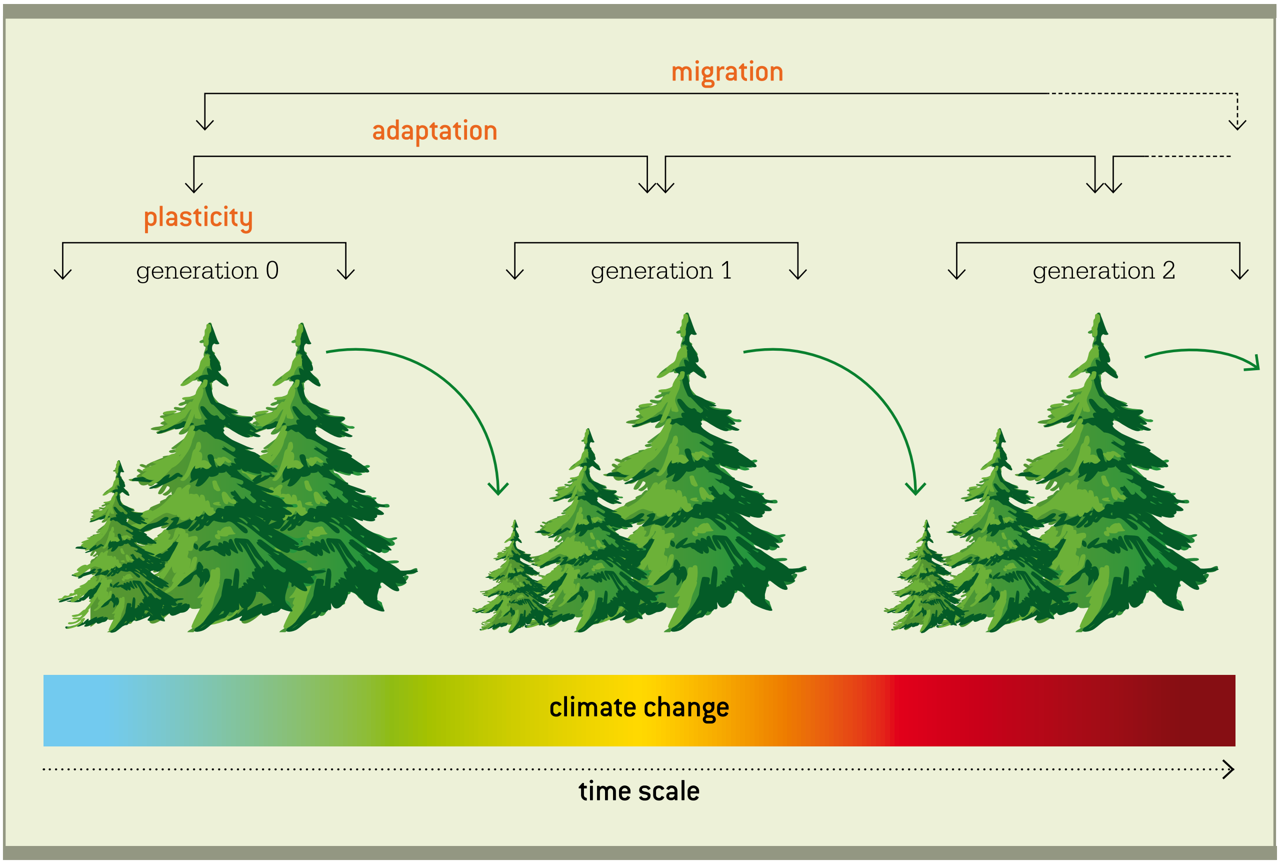


Figure 76. Time scale of phenotypic plasticity, adaptation, and migration of tree populations as a function of climate change.

demonstrates that trees can develop local adaptations rapidly, even within one generation (Kremer 2007). When tree populations adapt to local conditions, they generally maintain high genetic variation in adaptive traits (Savolainen et al. 2007). As tree populations accumulate fewer mutations per unit of time than populations of short-lived plants (Petit and Hampe 2006), most new adaptations in forest trees are likely to have emerged from the existing genetic variation instead of being generated by mutation (Alberto et al. 2013). This means that genetic diversity is a prerequisite for the adaptation of tree populations to climate change. Therefore, it is crucial to conserve the evolutionary processes within tree populations that maintain this diversity. Furthermore, part of the genetic diversity that is currently considered as "neutral" might become adaptive in the future (e.g. genes controlling resistance to emerging pathogens may emerge from the previously "neutral" diversity).

Dynamic conservation of genetic diversity can be integrated with biodiversity conservation and forest management

Integration of genetic aspects into biodiversity conservation and forest management is often perceived as a complex and difficult task. In reality, genetic conservation is rather straightforward and can be implemented as part of biodiversity conservation and forest management. However, the suitability of protected forest areas and managed forests for genetic conservation of forest trees should be analysed carefully before taking any action.

Protected forest areas are typically established for conserving endangered animal and plant species or maintaining specific habitats. It is assumed that habitat conservation also maintains the genetic diversity of tree populations occurring within protected forest areas. However, protected areas have often reached a late succession stage, and many tree species cannot regenerate in such stands without disturbances or human intervention. This problem may be difficult to solve when silvicultural treatments are not allowed in these areas. The conservation value of tree populations in protected forest areas should also be evaluated from both national and European perspectives and based on the results of genetic studies or provenance trials, when possible. In conservation planning, species richness is often taken as a surrogate of genetic diversity, but it is not suitable for this purpose (Taberlet et al. 2012).

In the case of production forests, their suitability for genetic conservation should be analysed more carefully. Dynamic conservation of genetic diversity is only possible in naturally regenerated forests or in those stands which have been established using local seed sources over several generations. It is generally difficult to know and verify what genetic material managed forests have been established with. Historical documents show that forest reproductive material has been traded and distributed across Europe for hundreds of years (König 2005), but there is usually no information available about where this material was finally planted. Today, the use of reproductive material is still poorly documented in most European countries. Even if managed forest is not used for genetic conservation, it is in the interest of a forest owner or manager to know the origin of the genetic material used. The impacts of climate change on growth can then be better estimated and, if problems occur, the same material can be avoided in the future. In artificially established forests, the physiological and genetic quality of reproductive material largely determines the survival and growth of trees as well as the level of genetic diversity and phenotypic plasticity within the stand. If the genetic base of the material used is large, subsequent silvicultural interventions, such as thinnings, do not drastically reduce genetic diversity during one tree generation (Savolainen and Kärkkäinen 1992; Lefèvre 2004), and many silvicultural systems applied in Europe maintain genetic diversity in tree populations rather well (Geburek and Müller 2005). However, as forest management changes evolutionary processes within tree populations, it can have a more profound impact on genetic diversity over generations (Lefèvre et al. 2013b).

Box 43. Recommendations for management.

The pan-European minimum requirements for genetic conservation units of forest trees (Koskela et al. 2013) provide an example on how genetic aspects can be integrated into biodiversity conservation and forest management. These units consist of natural or man-made tree populations that are typically located in forests managed for multiple uses, protected areas, and seed stands. The minimum requirements are based on a dynamic conservation approach (e.g. Lande and Barrowclough 1987;

Eriksson et al. 1993) that aims at maintaining evolutionary processes and adaptive potential across generations instead of preserving a static sample of genetic diversity.

Basic requirements: Each unit has a designated status as a genetic conservation area of forest trees. This status can be based on a law or an administrative degree, depending on the country. The units also have a management plan in which genetic conservation of forest trees is recognized as one of the management goals. One or more tree species are identified as target species for genetic conservation in the management plan. Furthermore, a conservation objective is clearly stated for each target tree species (the objective options are 1) to maintain genetic diversity in large tree populations; 2) to conserve specific adaptive or other traits in marginal or scattered tree populations; or 3) to conserve rare or endangered tree species with populations consisting of a small number of remaining individuals.

Population size: The required population size is linked to the stated conservation objective. If the unit aims at conserving genetic diversity of widely occurring and stand-forming conifers or broadleaved species, the unit must consist of 500 or more reproducing trees. If the unit was established to conserve specific adaptive or other traits in marginal or scattered tree populations, the unit must harbour a minimum of 50 reproducing trees. As an exceptional case, the unit can have only 15 reproducing trees if the purpose is to conserve genetic diversity in remaining populations of rare or endangered tree species.

Management: The units are actively managed for genetic conservation and silvicultural interventions are allowed, as needed, to ensure the continued existence of target tree populations and to create favourable conditions for growth and vitality of the target tree species and their natural regeneration.

Monitoring: Field inventories are carried out in the units every five or ten years to assess regeneration success and the population size of the target species and to update the management plan. Between the inventories, the units are visited regularly to check that they have not been damaged or destroyed.

Conservation of forest genetic diversity still needs to be improved in Europe

During the past 20 years, European countries have made good progress in conserving the genetic diversity of forest trees. Following the first Ministerial Conference on the Protection of Forests in Europe (now called FOREST EUROPE) in 1990 and the adoption of the Convention on Biological Diversity in 1992, many European countries developed or strengthened their national programmes or strategies on forest genetic resources. The countries also established the European Forest Genetic Resources Programme (EUFORGEN) in 1994 to facilitate and coordinate international collaboration in this area. However, the implementation of these national programmes and strategies has suffered from various difficulties in many countries, such as poor or non-existing linkages with national forest programmes and complexities of national administrative structures related to forests.

One indicator of the pan-European indicator set for sustainable forest management tracks the area managed for conservation of genetic resources. This indicator shows that, in addition to about 8,000 hectares of *ex situ* conservation areas, nearly a half million hectares were reportedly managed for *in situ* conservation in 2010 (FOREST EUROPE 2011). A group of five economically important tree species (*Abies alba, Fagus sylvatica, Picea abies, Pinus sylvestris,* and *Quercus petraea*) alone accounted 74 per cent and 66 per cent of the total areas managed for in situ and ex situ conservation, respectively (FOREST EUROPE 2011). This indicator is useful for monitoring a trend in the conservation efforts, but it cannot be used for assessing how well forest genetic resources are conserved in Europe.

To better assess the conservation status of forest genetic resources at the continental scale, European countries carried out a concerted action between 2007 and 2011 to collect geo-referenced and harmonized data on dynamic conservation units of forest trees. Based on this new data, a more comprehensive assessment with gap analyses was recently carried out for 33 European countries (Lefèvre et al. 2013a). The results of the study show that the pan-European network of the dynamic conservation units covers all environmental zones and also confirmed that the genetic conservation efforts are highly variable among tree species. Furthermore, the gap analyses carried out for 11 tree species revealed that there are significant gaps in the genetic conservation efforts at different geographical scales (Table 11). Firstly, many countries within the distribution range of these tree species do not even have a single genetic conservation unit for them (country index, Table 11). Secondly, different environmental zones (used as a proxy for adaptive genetic diversity) within the distribution range of the tree species are not covered by the conservation efforts (environmental zone index, Table 11). Thirdly, the genetic conservation efforts poorly cover different environmental zones within the countries (country x zone index, Table 11).

Data on all dynamic conservation units of forest trees across Europe can be viewed through the EUFGIS Portal (http://portal.eufgis.org), which currently contains information on 3,005 units and 98 tree species. During recent years, European countries have established additional conservation units and documented them to the EUFGIS database. Subsequently, the situation has improved slightly from what is presented in Table 11, but significant gaps still remain in the genetic conservation efforts. Some countries do not have any genetic conservation units that would meet the pan-European minimum requirements, while a few other countries have not yet evaluated their units and provided their data to the EUFGIS database. In 2012, a EUFORGEN working group prepared a pan-European genetic conservation strategy that guides the countries in implementing their genetic conservation efforts so that these gaps can be filled. It is expected that the implementation of this strategy will considerably improve the genetic conservation status of European forest trees in the near future.

Table 11. Number of European countries within the distribution range of 11 tree species and results of gap analyses based on different indices (Lefèvre et al. 2013a). The values of the indices range from 0 (no genetic conservation units for a given species) to 1 (no gaps in the conservation efforts).

		Index		
Species	**Number of countries within the distribution range[1]**	**Country[2]**	**Enviromental zone[3]**	**Country x zone[4]**
Abies alba	17	0.65	0.70	0.38
Fagus sylvatica	27	0.59	0.92	0.33
Fraxinus excelsior	31	0.48	0.75	0.20
Pinus brutia	2	1.00	0.75	0.75
Pinus halepensis	7	0.57	0.40	0.21
Pinus sylvestris	27	0.52	0.77	0.28
Populus nigra	26	0.31	0.31	0.07
Prunus avium	29	0.52	0.54	0.16
Quercus petraea	28	0.64	0.69	0.26
Sorbus torminalis	24	0.38	0.36	0.08
Ulmus laevis	26	0.23	0.36	0.07

[1] of the 33 countries which were included in the study; [2] number of countries with conservation units (at least one) divided by the number of countries within the distribution range; [3] number of environmental zones with conservation units divided by the number of environmental zones within the distribution range; [4] number of combined country x zones with conservation units divided by the number of country x zones within the distribution range

References

Aitken, S. N., Yeaman, S., Holliday, J. A, Wang, T. and Curtis-McLane, *S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1: 95–111.*

Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A. et al. 2013. *Potential for evolutionary responses to climate change – evidence from tree populations. Global Change Biology 19: 1645–1661.*

Eriksson, G., Namkoong, G. and Roberds, J. H. 1993. *Dynamic gene conservation for uncertain futures. Forest Ecology and Management 62: 15–37.*

FOREST EUROPE, UNECE and FAO 2011. *State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. FOREST EUROPE Liaison Unit Oslo.*

Geburek, T. and Müller, F. 2005. *How can silvicultural management contribute to genetic conservation? In: Geburek, T. and Turok, J. (eds.). Conservation and Management of Forest Genetic Resources in Europe. Arbora Publishers, Zvolen. Pp. 651–669.*

Hamrick, J.L. 2004. *Response of forest trees to global environmental changes. Forest Ecology and Management 197: 323–335.*

Hewitt, G. 2000. *The genetic legacy of the Quaternary ice ages. Nature 405:907–913.*

Hu, F. S., Hampe, A. and Petit, R. J. 2009. *Paleoecology meets genetics: deciphering past vegetational dynamics. Frontiers in Ecology and the Environment 7:371–379.*

Juurola, E. 2003. *Biochemical acclimation patterns of* Betula pendula *and* Pinus sylvestris *seedlings to elevated carbon dioxide concentrations. Tree Physiology 23:85–95.*

Koskela, J., Lefèvre, F., Schueler, S., Kraigher, H., Olrik, D.C., Hubert, J. et al. 2013. *Translating conservation genetics into management: Pan-European minimum requirements for dynamic conservation units of forest tree genetic diversity. Biological Conservation 157:39–49.*

Kremer, A. 2007. *How well can existing forests withstand climate change? In: Koskela, J., Buck, A. and Teissier du Cros, E. (eds.). Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome. Pp. 3–17.*

König, A.O. 2005. *Provenance research: evaluating the spatial pattern of genetic variation. In: Geburek, T. and Turok, J. (eds.). Conservation and Management of Forest Genetic Resources in Europe. Arbora Publishers, Zvolen. Pp. 275–333.*

Lande, R. and Barrowclough, G. 1987. *Effective population size, genetic variation, and their use in population management. In: Soulé, M.E. (ed.). Viable Populations for Conservation. Cambridge University Press, Cambridge. Pp. 87–123.*

Le Corre, V. and Kremer, A. 2012. *The genetic differentiation at quantitative trait loci under local adaptation. Molecular Ecology 21:1548–1566.*

Lefèvre, F. 2004. *Human impacts on forest genetic resources in the temperate zone: an updated review. Forest Ecology and Management 197:257–271.*

Lefèvre, F., Koskela, J., Hubert, J., Kraigher, H., Longauer, R., Olrik, D.C. et al. 2013a. *Dynamic conservation of forest genetic resources in 33 European countries. Conservation Biology 27(2):373–384.*

Lefèvre, F., Boivin, T., Bontemps, A., Courbet, F., Davi, H., Durand-Gillmann, M., Fady, B., Gauzere, J., Gidoin, C., Karam, M.J., Lalagüe, H., Oddou-Muratorio, S., Pichot, C. 2013b. *Considering evolutionary processes in adaptive forestry. Annals of Forest Science DOI 10.1007/s13595-013-0272-1*

Malcolm, J.R., Markham, A., Neilson, R.P. and Garaci, M. 2002. *Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29: 835–49.*

McLachlan, J.S., Clark, J.S. and Manos, P.S. 2005. *Molecular indicators of tree migration capacity under rapid climate change. Ecology 86:2088–2098.*

Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Sayre, R., Trabucco, A. and Zomer, R. 2013. *A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. Global Ecology and Biogeography 22:630–638.*

Neale, D. B. and Kremer, A. 2011. *Forest tree genomics: growing resources and applications. Nature Reviews Genetics 12:111–122.*

Nicotra, A.B., Atkin, O., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U. et al. 2010. *Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15:684-692.*

Parducci, L., Jørgensen, T., Tollefsrud, M. M., Elverland, E., Alm, T., Fontana, S. L. et al. 2012. *Glacial survival of boreal trees in northern Scandinavia. Science 335:1083–1086.*

Petit, R.J., Csaikl, U.M., Bordacs, S., Burg, K., Coart, E., Cottrell, J., et al. 2002. *Chloroplast DNA variation in European white oaks: Phylogeography and patterns of diversity based on data from over 2600 populations. Forest Ecology and Management 156: 5–26.*

Petit, R. J. and Hampe, A. 2006. *Some evolutionary consequences of being a tree. Annual Review of Ecology, Evolution and Systematics 37:187–214.*

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina,N.A. and Milyutin, L.I. 2002. *Intraspecific responses to climate in* Pinus sylvestris. *Global Change Biology 8:912–29.*

Savolainen, O. and Kärkkäinen, K. 1992. *Effect of forest management on gene pools. New Forests 6: 329–345.*

Savolainen, O., Pyhäjä, T. and Knurr, T. 2007. *Gene flow and local adaptation in trees. Annual Review of Ecology, Evolution and Systematics 38: 595–619.*

Slade, D., Skvorc, Z., Ballian, D., Gracan, J. and Papes, D. 2008. *The chloroplast DNA polymorphisms of white oaks of section* Quercus *in the Central Balkans. Silvae Genetica 57: 227–234.*

Taberlet, P., Zimmermann, N.E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., et al. 2012. *Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. Ecology Letters 15:1439–1448.*

Wagner, F., Below, R., De Klerk, P., Dilcher, D.I., Joosten, H., Kürschner, W.M. and Visscher, H. 1996. *A natural experiment on plant acclimation: Lifetime stomatal frequency response of an individual tree to annual atmospheric CO2 increase. Proceedings of the National Academy of Sciences 93:11705–11708.*

Whitham, T. G., Bailey, J. K., Schweitzer, J. A, Shuster, S. M., Bangert, R. K., LeRoy, C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., Fischer, D. G., Gehring, C. A, Lindroth, R. L., Marks, J. C., Hart, S. C., Wimp, G.M., Wooley, S.C. 2006. *A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics 7: 510–523.*

4.5

Monitoring forest biodiversity in Europe: state of the art, challenges, and opportunities

Yoan Paillet, Jari Parvainen, Marion Gosselin, Frédéric Gosselin and Markus Lier

The direct and indirect benefits of conserving and enhancing forest biodiversity, in addition to economic and social objectives, have been widely recognized as an essential element of sustainably managed forests and have been addressed since the 1990s by several policy processes worldwide. In Europe, forest biodiversity conservation has been addressed since the second FOREST EUROPE[1] Conference in Helsinki, Finland in 1993, and most recently in the European Union (EU) 2020 Biodiversity Strategy, as a response to the objectives set out in the Convention on Biological Diversity (CBD) adopted in Nairobi, Kenya in 1992. Two complementary approaches to maintain biodiversity in forests were proposed in the 1993 Helsinki resolution:

(i) the creation of a protection area network within each country, and

(ii) the integration of silvicultural practices that secure the maintenance of biodiversity on a large scale in forest areas outside of protected areas.

> *At the European level, the assessment and monitoring of forest biodiversity has become a challenge for many countries. Monitoring data on the state and dynamics of biodiversity should be reliable and comprehensive enough for assessment of the effectiveness of environmental policies*

The assessment and monitoring of forest biodiversity has become a challenge for many countries in Europe. Data on the state and dynamics of biodiversity should be reliable and comprehensive enough to assess the effectiveness of environmental policies, such as the EU biodiversity policy and the Habitats Directive. However, in spite of European initiatives for improving reporting on biodiversity such as the Streamlining European Biodiversity Indicators (SEBI) or the Criteria and Indicators for Sustainable Forest Management of FOREST EUROPE (see Lier et al. this issue), coordinated international biodiversity monitoring systems remain rare. For example, the BioSoil demonstration was launched with a standardised approach

---

[1] pan-European policy process for sustainable forest management (former The Ministerial Conference on the Protection of Forests in Europe).

to forest biodiversity monitoring in 14 countries (Bastrup-Birk et al. 2007). A few taxa are monitored using similar protocols at a national scale in several countries. A harmonised protocol is applied for the monitoring of birds and butterflies, or tree species in National Forest Inventories (NFIs). NFIs are conducted in the majority of European countries (Tomppo et al. 2010) and comprise the collection of data on forest biodiversity (generally tree diversity and vascular ground flora), which are used for reporting indicators (FOREST EUROPE et al. 2011).

Forest policy decisions and the development of integrated forest management methods as well as their practical application require timely and updated information on forest biodiversity:

- Forest biodiversity data are helpful for creating and strengthening protected forest area networks, for restoration activities in protected and managed areas, and for the planning of voluntary protection areas in private forests;
- The effects of biodiversity-friendly measures can be monitored through the number of threatened species, which can be seen as indicators of change in forest ecosystems;
- A multi-ecosystem biodiversity monitoring scheme based on large ecological amplitude taxa would enable comparison of the effects of global changes on biodiversity across various ecosystems (for example, threats to forest biodiversity vs. farmland biodiversity).

In France the Breeding Birds Survey shows how forest data can be integrated in biodiversity monitoring programs

In France the Breeding Birds Survey (BBS) was launched in 1989 to detect changes in common bird abundance on a national scale (Figure 77). The aim of the BBS, which is carried out by volunteers, was essentially to detect changes in bird communities without aiming at analysing the drivers. Hence, few habitat characteristics (basically habitat type) are sampled in the field during the point counts. Data are analysed using large-scale datasets such as climate prediction models or conservation area maps (e.g. Jiguet et al. 2012; Pellissier et al. 2013).

The species are classified according to their habitat preferences, and the major trends in different guilds revealed that the occurrence of generalist birds increased by 20% between 1989 and 2009, whereas woodland and farmland specialists decreased by 12% and 21%, respectively, over the same period (Figure 78, Jiguet et al. 2012).

Although these results are of crucial importance for detecting changes in bird communities, the possible explanatory factors of the changes remain unclear. In the absence of local environmental data (especially forest structure) linked with count points, the consequences of forest management or conservation policies on bird communities are difficult to assess using the BBS data (see Pellissier et al. 2013 for an example involving Natura 2000 areas). The monitoring of spotted owl demography in the Pacific Northwest (USA) demonstrates similar limitations (Gosselin 2009).

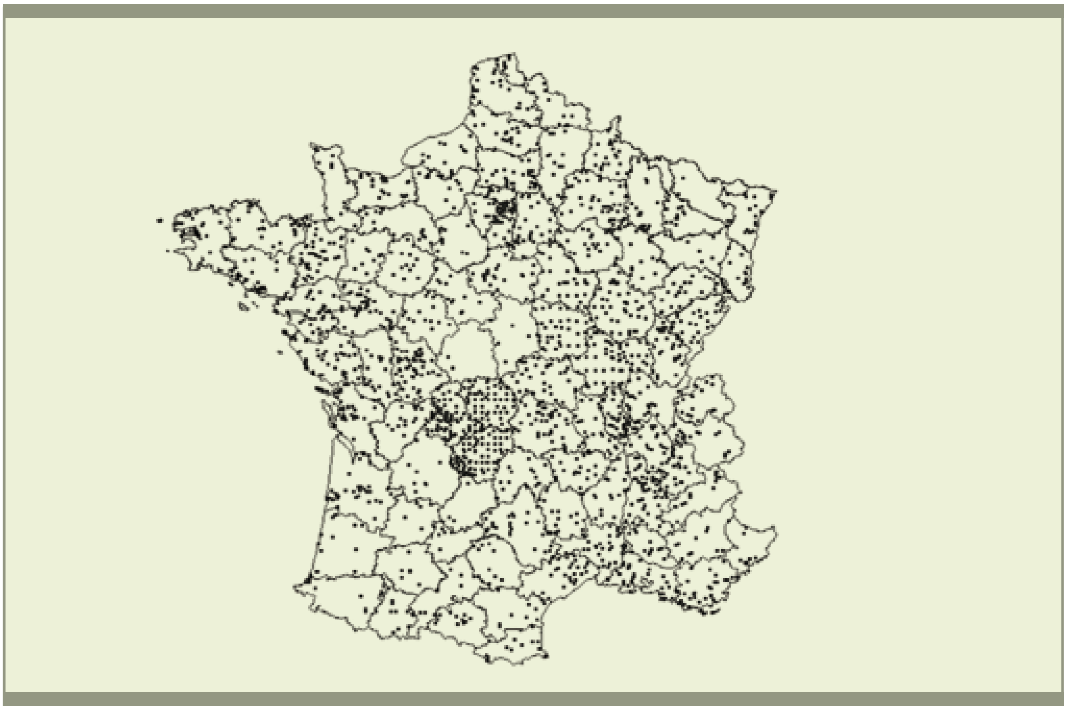


Figure 77. Distribution of the 2000 squares monitored by the French Breeding Birds Survey between 2001 and 2009. Despite its national coverage, the sampling design of the BBS was biased at first since the observers had the freedom to choose the location of the sampling points. The sampling design was modified in 2001 to introduce partial randomization in the choice of sampling plots: they were drawn at random within a radius around an observer's residence. The sampling design is thus distorted by the place of residence of the observers, and some regions are poorly covered. Great Britain, in contrast, introduced a fully randomized sampling scheme after 2001. Source: Jiguet et al. 2012. Copyright © 2013 Elsevier Masson SAS. All rights reserved.

In Finland the use of the red-listed species system has proved its effectiveness in monitoring biodiversity response to forest policy

The International Union for Conservation of Nature (IUCN) Council adopted a new Red List system in 1994. The Red List is used not only in IUCN publications and listings, but also in national and even local evaluations in various ecosystems, including forests. Finland and Sweden were among the first countries to publish (in 2000) their Red Lists using this system, with an emphasis on forests being the main ecosystems in these countries (Gärdenfors 2010; Rassi et al. 2010). Biodiversity-oriented forest management that mimics the natural forest development cycle has been a statutory requirement in Finland for 15 years. The main methods for safeguarding biological diversity in commercial forests are the protection of valuable habitats and biotopes, favouring mixed tree stands, and increasing the amount of decayed wood. Safeguarding biological diversity has been enshrined as a parallel goal with wood production since the Forest Act of 1997. At the same time, the production of information about biodiversity along with related research, discussion, and consultation, has been a key

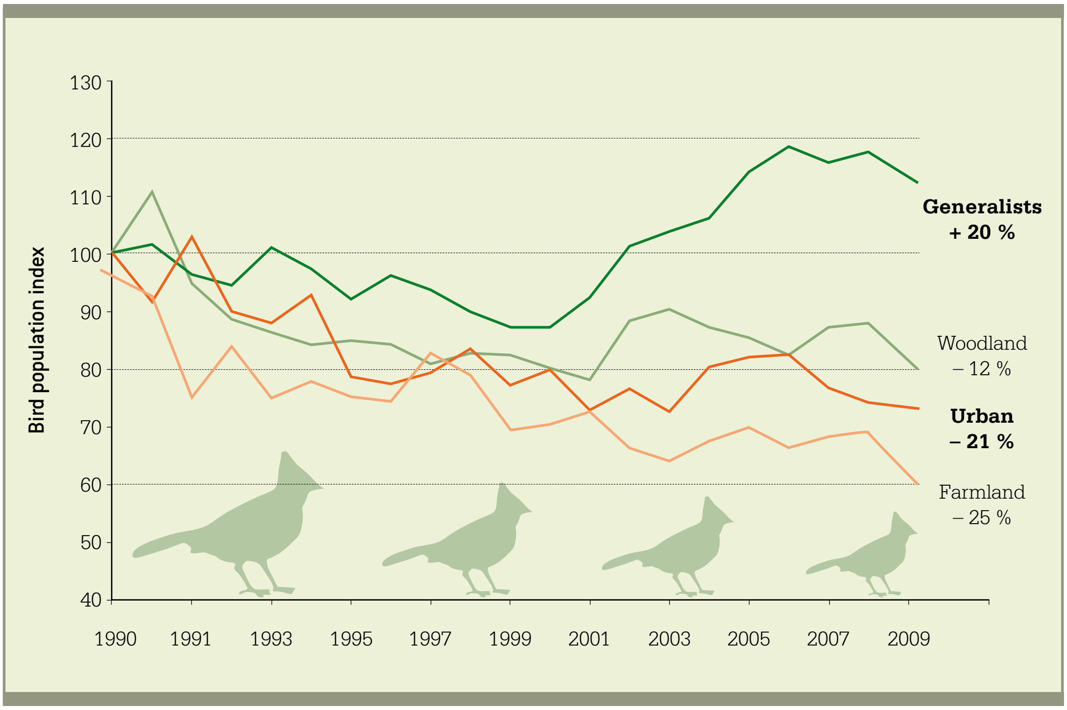


Figure 78. Trends of breeding bird populations in France according to habitat specialisation from 1989 to 2009. Source: Jiguet et al. 2012. Copyright © 2013 Elsevier Masson SAS. All rights reserved.

area, with broad participation by forest owners and other actors and interest groups in forest management.

The selected new forest management policy has brought measurable positive changes to commercial forests. Since the 1990s, the rate of decline of certain forest species has slowed considerably in Finland, and has even stopped in some cases, although it has not been possible to halt the decline in forest species overall. An evaluation of threatened species conducted in 2000 and 2010 showed that the decline had slowed or stopped for 81 forest species but continued for 108 species. Retention trees at felling sites (i.e. trees set aside during clearcuts) have been particularly important in curbing the decline (Parviainen and Västilä 2011).

Most forest biodiversity monitoring and indicators reporting are based on biodiversity data issued from National Forest Inventories

Despite the fact that some countries plan biodiversity monitoring at large scales, Lee et al. (2005) note that most biodiversity monitoring and subsequent international reporting are based on national forest inventories, cynegetic monitoring (hunting plans), or air and water quality resource assessments. As a consequence, the level of observation and the techniques used for monitoring are largely derived from forest inventory techniques.

Tomppo et al. (2010) have synthesized the use of national forest inventories to report on forest biodiversity at the international level. Among the 37 countries analysed, 27 used forest data to report on biodiversity to FOREST EUROPE (Criterion 4), the Food and Agriculture Organisation (Forest Resources Assessment), or the European Environment Agency (Streamlining European Biodiversity Indicators, SEBI). Most of the time, the data, such as deadwood volume or vertical forest structure, are indirect indicators of forest biodiversity. Direct taxonomic data are rare outside of tree species and vascular plants. Due to the huge number of species, forest inventories tend to concentrate on key species (most typical or vulnerable species), which are considered to be surrogates (keystone or umbrella species) for other species in similar habitats. Indeed, only 18 countries have species-specific samplings, some of which are limited to:

- Vascular plants only (including trees) for half of the countries;
- Targeted species list: Germany (8 frequent vascular plants), Spain (selection of epiphytic lichens), Norway (1 vascular plant), and Switzerland (11 saproxylic fungi);
- Groups at stake: epiphytic lichens (6 countries), bryophytes (2), and fungi (2). For bryophytes and fungi, the samplings are sometimes limited to ecological groups: ground bryophytes (France) and saproxylic fungi (Switzerland).

In addition, in several cases biodiversity data have been sampled at supra-species levels: the vegetation layer covers all species confounded, morphologic group for lichens (e.g. foliose lichens), or genus only (e.g. *Usnea*, *Bryoria* or *Alectoria*).

> *The current forest biodiversity monitoring system is mainly based on indirect structural indicators (proxies) rather than on taxonomic and intraspecific data*

Within FOREST EUROPE's Criterion 4 for biodiversity, three indicators are based directly on species: 4.1 Tree species composition, 4.6 Genetic resources, and 4.8 Threatened forest species. Collecting information on various species groups is very demanding and time-consuming and therefore also expensive (see Box 44). Hence, for some countries the indicator on threatened species does not always target the species at stake: the taxa most extensively covered by Red Lists are threatened tree species, vascular plants, and mammals and birds, whereas invertebrates, cryptogams, and fungi remain the least extensively covered. Information is particularly lacking in countries of East-Central, Southeast, and Southwest Europe.

Based on the previous considerations, there are two possibilities for implementing an effective forest biodiversity monitoring framework: biodiversity inventories could be complemented with environmental (including forest) data, or national forest inventories could be complemented through biodiversity sampling.

Box 44. What is the cost of monitoring?

The cost of biodiversity monitoring is non-negligible. It totals 2.5 million euro a year in Switzerland (tax excluded), which corresponds to approximately 60 euro/km^2 considering the country's total surface area. Monitoring in Alberta (Canada) costs around 9 million euro a year. The intensity of sampling as well as the nature and the quantity of structural and taxonomic data are of course taken into account in the assessment of the monitoring cost. Another important point to mention is the degree of professionalism of the people involved in field sampling: for example, the French BBS is a volunteer-based monitoring programme that costs around 0.3 million euro a year but would cost around 1 million euro if performed by professionals (Levrel et al. 2010). Complementing the current monitoring system would have to take into account such constraints, especially if saproxylic taxa, for which professional assistance would be needed, are targeted.

The Biodiversity Monitoring (BDM) of Switzerland complemented the National Forest Inventory with taxonomic data

The BDM (www.biodiversitymonitoring.ch) was created in 2001 under the auspices of the Federal Office of Environment. This monitoring program is not exclusively focused on forests and produces indicators within a balanced Pressure (15 indicators), State (12 indicators), and Response (7 indicators) framework. Most of the indicators are calculated using external data, but at least three state indicators are based on biodiversity data sampled directly in the field. Hence, every five years, the BDM samples vascular plants, bryophytes, butterflies, birds, and molluscs on a systematic grid of permanent plots. This country-wide network comprises two sub-networks:

- The first consists of 520 1 km^2 zones regularly distributed across Switzerland with more intensive sampling in the Jura Mountains and the Alps. This network is used for breeding birds, butterflies, and vascular plants;
- The second consists of 1600 10 m^2 plots and is used to assess the diversity of vascular plants, bryophytes, and molluscs. A part of this sub-network is congruent with the plots of the Swiss National Forest Inventory (Fig. 79). This allowed the first correlative approach between species richness of different groups and forest structure data (Bühler et al. 2007). This study shows that there were no reliable and unequivocal relationships between the diversity of the analysed taxa and forest stand features. The authors conclude that stand features may be used as a proxy for biodiversity on a large scale but that the state and dynamics of biodiversity may only be assessed through direct species sampling.

The MBD is coordinated by an external management board, which organises data collection, analyses, reporting, and quality assurance. Field sampling is done by specialists after a call for proposals, including dedicated Swiss institutions for rare species (e.g. Swiss Biological Records Centre). See Box 44 for information on costs.

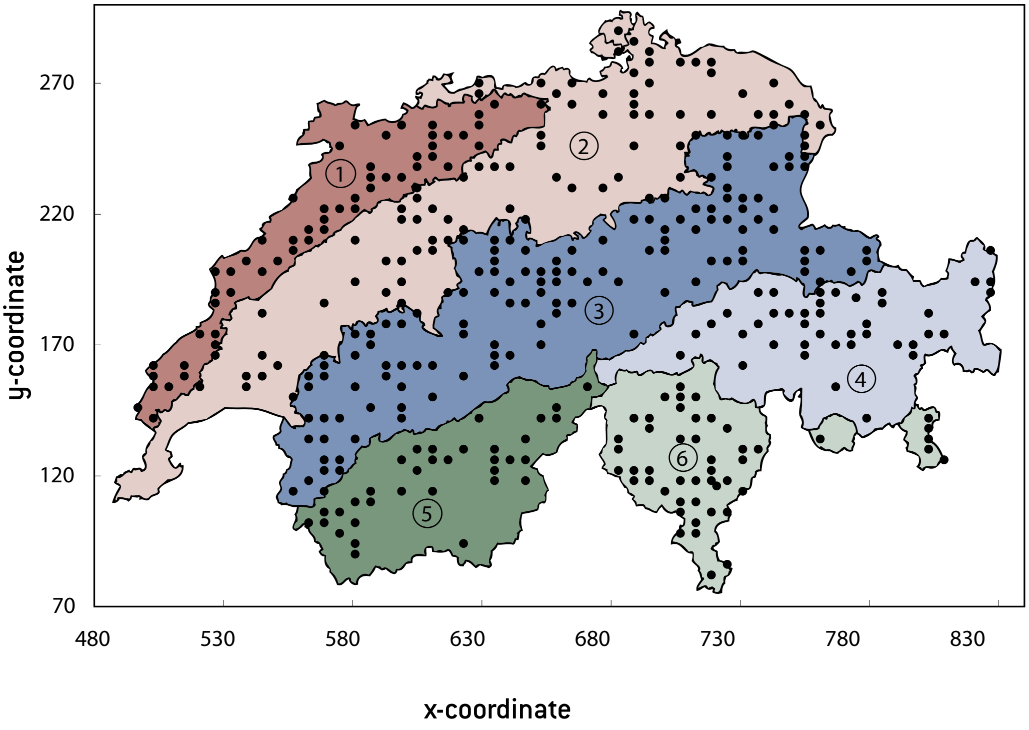


Figure 79. Congruence between the forest plots of the Biodiversity Monitoring (BDM) and the National Forest Inventory (NFI) sampling designs in Switzerland. Source: Bühler et al. 2007.

Another similar example that will not be developed further here is the Alberta Biodiversity Monitoring Institute, created by the Canadian state of Alberta in 2003, in charge of monitoring biodiversity across ecosystems of the entire state. More information on this process can be found at www.abmi.ca.

To date, there has been some discrepancy between taxa currently monitored (butterflies, birds, vascular plants) and forest taxa at stake (e.g. saproxylic taxa)

Monitoring biodiversity in forests at large scales needs a broader taxonomic approach, as the current main indicators in many Central European countries concern mainly tree species, vascular plants, birds, and butterflies. There is a lack of information on the most specialised forest species and on the taxa potentially most threatened by global changes (notably saproxylic taxa). This results in a discrepancy between the taxa monitored and the taxa at stake. Several options (or a combination of them) are available to improve the current system (see Box 44 for an overview of the potential costs and Gosselin et al. 2012 for a short analysis):

- The current Forest Europe indicator 4.8 "Threatened forest species" is the forest component of an indicator used for other ecosystems that allows comparisons of the degree of pressure experienced by different ecosystems. However, in France, this indicator concerns only amphibians, reptiles, mammals, and birds, whereas no list is available yet for saproxylic beetles, fungi, bryophytes, or lichens. In addition, this indicator could be improved by focusing on taxa or species benefiting from restoration plans in order to assess the effectiveness of conservation policies. This kind of monitoring could easily include a demographic and/or intraspecific component;
- In order to compare biodiversity dynamics in forest and in other ecosystems, it would be interesting to monitor taxa with a large ecological amplitude, as is the case for Red List species. Such data could be analysed by ecosystems for all species, but also by guilds, notably using strict habitat specialists (e.g. woodland birds);
- It is important to note that the taxa currently monitored are probably not the most impacted by sustainable forest management; this would include dispersal-limited or compaction-sensitive species. In this sense, the monitoring of species depending on deadwood for at least a part of their life cycle (i.e. saproxylic species) could be a fruitful alternative. Indeed, saproxylic species represent more than a quarter of forest species (around 10,000 species, mostly fungi and beetles) and have seen a dramatic decrease in their habitat over the past centuries due to over-exploitation of forest resources and deforestation in Western Europe. Even if the forest ecosystem is likely recovering, with higher deadwood levels than several decades ago, the status of saproxylic species is still poorly known. Given the potential extinction debt due to the bottleneck effect they experienced between the Middle Ages and the 19th century, such species may still be vulnerable, and some may even be on the verge of extinction. Only large scale monitoring could answer these questions;
- Finally, it would be useful to have multi-taxa monitoring for common species to assess more broadly the effects of environmental pressure on forest biodiversity and policy responses for its maintenance. Regarding the current FOREST EUROPE Criteria and Indicators for Sustainable Forest Management, it would be interesting to include in Criterion 4 "Maintenance, Conservation, and Appropriate Enhancement of Biological Diversity in Forest Ecosystems, indicator 4.8 "Threatened forest species":
  - saproxylic taxa to complement data on birds, e.g. beetles, lichens, and bryophytes;
  - dispersal-limited taxa such as the molluscs that are monitored in the BDM.

> *Monitored taxa should include groups that are specific to forests and/or potentially threatened by (global) changes in silvicultural practices*

Regarding existing forest biodiversity monitoring approaches in Europe, we emphasize the need to enrich the system with a higher proportion of taxonomic data to describe the state and dynamics of biodiversity (Gosselin et al. 2012). Indeed, most of the indicators used in international reporting systems on forest biodiversity are indirect structural features used as proxies for biodiversity (e.g. deadwood volume). These proxies have several weaknesses that may make their interpretation difficult: the relationship between the proxy and biodiversity is not always clearly demonstrated and is sometimes ambiguous, depending on the context and the scale of the study used as a reference. For example, it has been shown that deadwood volume is more correlated to the species richness of saproxylic organisms in the boreal biome than in the temperate biome (Lassauce et al. 2011). The relationship may also vary in time, for example due to changes in abiotic conditions, and the response of biodiversity to a given pressure (increasing or decreasing) may be delayed (namely, an extinction debt may remain unpaid). Monitoring biodiversity per se in parallel to forest variables would enable the detection of these kinds of effects.

The IUCN red list system uses both direct and indirect information on species from various sources, including monitoring results, other surveys, research observations, old data, and validated voluntary observations. Emphasis is on habitats as the basis for the classification of the living conditions for the majority of species. Observations of habitat changes are used to predict changes in the number of species. The reliability and accuracy of the information vary depending on the quality and coverage of data as well as on the method used to assess the risk of a species becoming threatened. There have occasionally been many difficulties in distinguishing between forest and non-forest species. Such data must, however, be interpreted cautiously, especially at the European scale, for several reasons:

- species richness is generally higher in Southern Europe than in Northern Europe. However, forest-occurring species are proportionally more abundant in the north and in countries with high forest cover (Puumalainen et al. 2003). Comparisons of absolute numbers between countries are therefore difficult;
- when the total number of forest-occurring species is related to the unit area, i.e. divided by the area of forests and other wooded land in a country, small countries tend to be the most species-rich;
- the situation of threatened forest species may differ across the whole European area. For instance, species that have a limited distribution in one country may be classified as threatened in the national report, while at the European level the species can be more widely spread.

Monitoring species, forest structures, and habitats is necessary and should be combined in optimal monitoring systems

Current forest monitoring systems are mostly based on indirect (structural) indicators of biodiversity or on habitats rather than on taxonomic data. To date, there has been some discrepancy between the taxa currently monitored (butterflies, birds, vascular plants) and the taxa at stake (e.g. saproxylic taxa). The monitoring of species, such as red-listed species, as well as forest structures and habitats, is necessary and should be combined in optimal monitoring systems. In addition, monitored taxa should include groups that are specific to forests and/or potentially threatened by (global) changes in silvicultural practices. Comparing biodiversity dynamics between managed and unmanaged forests in equivalent conditions would allow an improved assessment of the effects of forest management on biodiversity.

Box 45. How to monitor forest biodiversity? A few things to take into account

Among the monitoring schemes detailed in this chapter, some have been built in an opportunistic manner such that their sampling design might be biased (for example, due to the location of the volunteers in the French BBS – Fig. 1). To avoid such discrepancies, some important points are worth considering when building a monitoring system:

- Sampling design: it should be explicit and designed at the beginning of the monitoring to avoid costly compensations. The sampling design could be systematic (BDM, Alberta) or randomized (most of the National Forest Inventories), and stratified or not, including the strict forest reserve network.
- Permanent vs. temporary plots? Both strategies have their pros and cons. Alberta and Switzerland have chosen permanent plots to be periodically revisited, but their position remains confidential to avoid bias linked to modified management nearby. In any case, the compromise between a small number of plots frequently visited vs. a large number of plots less frequently visited should be evaluated regarding the respective levels of spatial and temporal autocorrelation.
- A link with environmental variables: in order to assess the sustainability of forest management and to be able to analyse correlations in a robust way, it is important to link biodiversity data with environmental (structure) data. For example, the BDM has decided to link the sampling design with plots of the National Forest Inventory for plots located in forests (Fig. 3). Hence, analyses of correlations between proxies and taxonomic data are possible, thus improving both knowledge on factors influencing biodiversity and international reporting using structural data.

References

Bastrup-Birk, A., Neville, P., Chirici, G. and Houston, T. 2007. *The BioSoil Forest Biodiversity Field Manual. ICP Forests, Hamburg.*

Bühler, C., Brändli, U. and Zangger, A. 2007. *Does forest structure indicate biodiveristy? In; WSL (ed.) Monitoring the Effectiveness of Nature Conservation. Birmensdorf, Switzerland.*

FOREST EUROPE, UNECE, and FAO. 2011. *State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. Ministerial Conference on the Protection of Forests in Europe.*

Gärdenfors, U. 2010. *Rödlistade arter i Sverige 2010 – The 2010 Red List of Swedish Species. ArtDatabanken, SLU, Uppsala.*

Gosselin, F. 2009. *Management on the basis of the best scientific data or integration of ecological research within management? Lessons learned from the Northern spotted owl saga on the connection between research and management in conservation biology. Biodiversity and Conservation 18:777–793.*

Gosselin, F., Gosselin, M. and Paillet, Y. 2012. *Suivre l'état de la biodiversité forestière : pourquoi ? comment ? Revue Forestière Française LXIV:683–700.*

Jiguet, F., Devictor, V., Julliard, R. and Couvet, D. 2012. *French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecologica 44:58–66.*

Lassauce, A., Paillet, Y., Jactel, H. and 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.*

Lee, W., McGlone, M. and Wright, E. 2005. *A review of national and international systems and a proposed framework for future biodiversity monitoring by the Department of Conservation. Landcare Research, Wellington, New Zealand.*

Levrel, H., Fontaine, B., Henry, P. Y., Jiguet, F., Julliard, R., Kerbiriou, C. and Couvet, D. 2010. *Balancing state and volunteer investment in biodiversity monitoring for the implementation of CBD indicators: A French example. Ecological Economics 69:1580–1586.*

Parviainen, J. and Västilä, S. 2011. *State of Finland´s Forests 2011 Based on the Criteria and Indicators of Sustainable Forest Management. Ministry of Agriculture and Forestry, Finnish Forest Research Institute.*

Pellissier, V., Touroult, J., Julliard, R., Siblet, J. P. and Jiguet, F. 2013. *Assessing the Natura 2000 network with a common breeding birds survey. Animal Conservation.*

Puumalainen, J., Kennedy, P. and Folving, S. 2003. *Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. Journal of Environmental Management 67:5–14.*

Rassi, P., Hyvärinen, E., Juslén, A. and Mannerkoski. I. 2010. *The 2010 Red List of Finnish Species. Ministry of the Environment and Finnish Environment Institute.*

Tomppo, E., Gschwantner, T., Lawrence, M. and McRoberts, R. E. 2010. *National Forest Inventories : pathways for common reporting. Springer.*

5 Integrative management approaches: a synthesis

Frank Krumm, Andreas Schuck and Daniel Kraus

Forest management in Europe has traditionally been geared towards timber production, and this has remained the governing principle in most European forests. Biodiversity conservation is to some extent increasingly in conflict with traditional forest management

One of the approaches to reconcile these goals (biodiversity conservation and timber production) is the concept of integrative multifunctional forest management, where several ecosystem services can be obtained from the same area (see **Chapter 1, Section 1.1**). Although more than 70 % of European forests are primarily managed for timber production, the remaining proportion is assigned to other forest functions such as protection against natural hazards or conservation of habitat for rare species. The increasing importance of ecological values and other forest functions relative to timber production has promoted multifunctionality in different parts of the world. However, multifunctionality in forests has its limitations since it can be easily watered down, particularly on a larger scale, and therefore often creates conflicts (see **Section 1.5**). The European trend in sustainable silviculture aims at integrating habitats and key structural elements over the entire forest estate (see **Section 1.6**). This originates from a long land use tradition in Central and Southern Europe due to high population and settlement density and has led to strong pressure on forest areas. The subsequent disappearance of pristine habitats in Europe has made integration the principal strategy for forest biodiversity conservation. However, setting conservation targets in managed forests is crucial to promote the return and maintenance of certain species and structures; in this sense assessing the degree of naturalness of a given ecosystem may constitute an adequate reference (see **Section 1.4**). Research in the past 20 years has shown that old-growth forests can serve as valuable references for the assessment of habitat quality and integrity of forest communities. Strict forest reserves in particular are an integral part of Europe-wide research in forest ecology. Without these reference areas, the successful development of conservation strategies for commercially managed forests does not seem viable (see Section 1.3).

Integration of key structural characteristics and old-growth attributes at the tree and stand level provides a general basis for biodiversity conservation in European forests

Forest management in Europe has caused drastic changes to forest ecosystems and resulted in the loss of structural elements such as deadwood and large trees. Tree age and heterogeneity of forest sites have also changed markedly (see **Chapter 2**). The approach of retaining key structural elements such as deadwood during the production cycle and thus increasing naturalness is strongly limited by the small extent of such habitat islands and the subsequent edge effects (see **Sections 2.1**, **2.2**, and **2.3**).

Increasing fragmentation of the landscape and exclusion of natural disturbances as a driver of forest development have also triggered drastic changes to forest structures and functions (see **Section 2.4**). The crucial question is whether more set-aside areas without human interference are necessary to reach conservation goals in the cultural landscapes of Europe and whether such forest reserves should have to more or less carry the total load of biodiversity conservation. Strict forest reserves often serve as surrogates for primary forests and special forest reserves as substitutes for historical forest types with special conservation value (see **Sections 2.5** and **2.6**).

Management goals such as biodiversity conservation and ecosystem functions can be met in both set-aside forest reserves and off-reserve forests

The major argument for protected forest reserves is the increase of alpha-diversity due to extended succession periods and turnover cycles. Also, habitat tradition is linked to the preservation of forest areas and is a prerequisite for the survival of relict or ancient forest species. Therefore, it is crucial to know the habitat requirements and respective habitat thresholds for a range of species or species groups to provide a basis for setting the relevant conservation targets and consistent conservation planning (see **Chapter 3**).

However, the establishment of new protected areas is limited due to space and competing management goals, and trade-offs have to be made where such conflicts of interest occur. Accordingly, emphasis is shifted towards integrating special protected areas, such as rare forest biotopes and habitats, wildlife refuges, and corridors, as well as structural attributes, such as old-growth elements, habitat trees, and forest ecotones, into production or protection forests. Integrative forest management systems discriminate strictly protected areas and forest reserves with habitat management directed towards a specific conservation target (active management), whereas in segregative forest management systems, strictly protected areas (passive management) are embedded in a matrix of intensively managed forests or plantations. Although vast areas in Central Europe are still characterised by the legacies of past forest management, one of the main silvicultural management principles in Central Europe is close-to-nature forestry. Such forest management concepts encompass a range of management intensities, longitudinal and latitudinal gradients, and topographies and therefore produce a variety of forest structures within the close-to-nature approach. Generally, habitat quality is better and the habitat resistance for dispersal patterns is lower among reserves in such a matrix with high forest management standards and high structural diversity. The more diverse the demand for structural elements in a forest is, the more diverse and complex the applied silvicultural system has to be in this respect. This aspect is especially important when considering adaptive management options for the key challenges that will become more evident in the near future; opportunities and threats associated with a changing climate and the resilience of forest ecosystem functioning are best served in diversely structured forests (see **Chapter 4**). Additionally, invasive species and the maintenance of genetic diversity will be challenges for integrative management approaches on a large scale (**Section 4.3** and **4.4**).

> *Integrative forest management systems aim to maximise the cross-section between the different main functions of modern forestry: production, protection, and conservation*

However, recent studies have shown that the area of synergy is limited, and a certain amount of exclusive area is needed to meet the targets of different ecosystem functions. Segregative instruments seem to be more effective in providing the essential habitat types and characteristics, particularly when it comes to large-scale elements of biodiversity conservation and to the conservation of certain species with specific demands (e.g. large predators or some lichens depending on high amounts of deadwood; see **Sections 1.1**, **2.2**, and **2.3**). Also, the production cycles in commercially managed forests are much shorter than natural development cycles. In contrast to the disturbance regime in unmanaged forests, production forests are regularly disturbed at short intervals, and economically important trees are either favoured or planted. Consequently, the rotation periods are shortened, and old-growth stands with large aboveground biomass and natural regeneration are underrepresented over large areas. This contributes to the generally detrimental effect that production forests have on habitat continuity and heterogeneity. Silviculture based on patterns and processes found in old-growth forests will help maintain a variety of non-timber forest functions and ecosystem services, especially the provision of habitat for biodiversity (**Section 1.5**).

> *Effective conservation and restoration of habitats heavily relies on well-developed segregative instruments that complement sustainable, integrative forest management practices. Thus, there is a need for a comprehensive hierarchical dual strategy with both integrative and segregative instruments for the conservation of representative forest biota*

Integrative, segregative, or combined concepts and their respective instruments have different spatial impacts, thus scale has to be considered. Instruments used as surrogates of primary forests (e.g. National Parks, large strict reserves) need to be planned at the macro-scale, whereas close-to-nature forest management concepts can provide minimum habitat quality over an entire area when minimum standards are implemented (**Section 1.1**). The overall impact of conservation can be improved when these habitats are complemented by segregative elements such as strict forest reserves under natural dynamics, special biotopes, and key structural attributes through retention measures (see Fig. 80). A representative network of actively and passively managed forest reserves offers unique and rare niches for habitat specialists, but it is crucial to specify that the distribution of structural elements within the landscape should be adapted to the dispersal capacities of certain species. Many aspects of such an idealized forest landscape can be found in various regional conservation concepts to a certain degree, depending on the conservation goals and requirements. In **Box 46**, we present an example of a model forest landscape where such an integrative approach has already been implemented and is approaching the idealized concept.

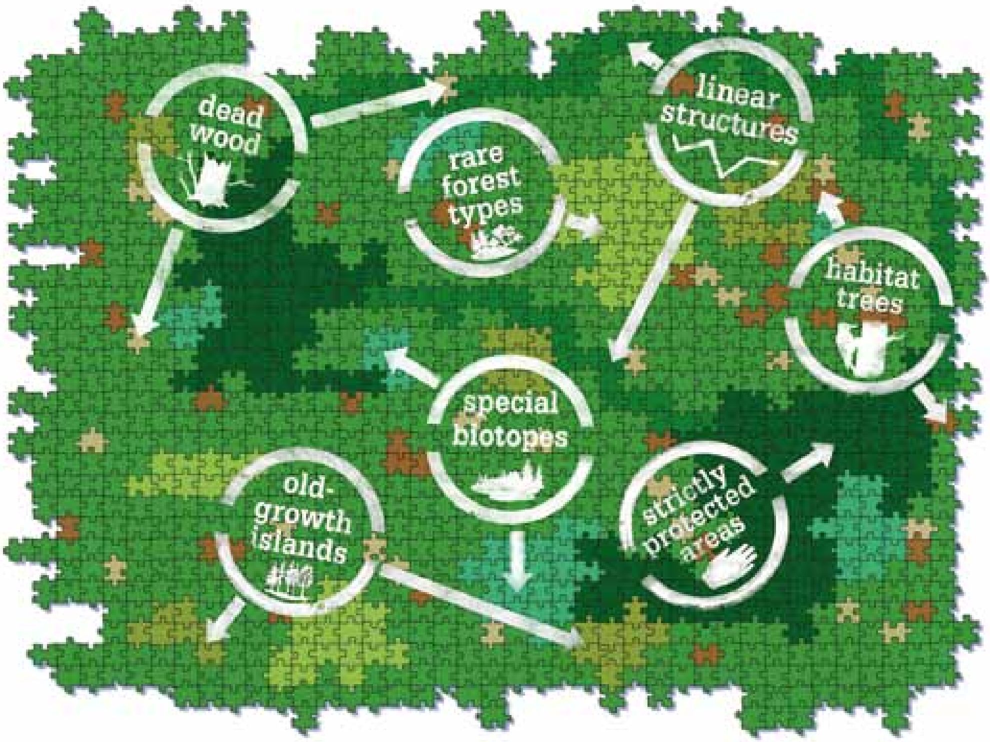


Figure 80. Model forest landscape with elements of a dual management strategy on different scales: several segregative elements, such as special biotopes, old-growth islands, linear structures, strict reserves, habitat trees, and deadwood, are embedded within a matrix of forest managed by close-to-nature principles.

From a conservation perspective, it is thus far more important to focus on strategic planning of conservation instruments for managed forests than to concentrate on the total protected area. Therefore, habitat requirements and thresholds of target species as representatives of the typical forest community have to be considered for the development and cross-linking of conservation instruments. In this context the current status, i.e. the actual applied silvicultural system, should be taken into account since a diversity of silvicultural systems and strategies across the landscape is needed to increase diversity in structures, functions, and biota and consequently support a broad range of other ecosystem services. The crucial question is which general objectives need to be addressed by conservation planning in forest management, and what are the respective thresholds for habitat requirements? In addition, in the case of competing conservation goals, what are effective means to deal with trade-offs? These questions are directly linked to biogeographic regions, historical land use, and potential sources for re-colonisation as well as to the aims of national biodiversity strategies, their respective road maps, and social acceptability.

Box 46. Protection despite utilization – the biodiversity concept of the Ebrach State Forest Enterprise in the Steigerwald region of Franconia (Bavaria, Germany)

Ulrich Mergner and Daniel Kraus

The Ebrach State Forest Enterprise is responsible for one of the most important beech forests in Germany in terms of the conservation of forest dwelling species. Biodiversity conservation of these species is central to its conservation concept. Special emphasis is given to saproxylic beetles, of which approximately 480 species occur in the Steigerwald region. The conservation of this key indicator species group ensures the existence of all other species groups in these beech forests.

The management approach implemented in Ebrach is often coined “protection despite utilization” and can be described as an integrative approach that strives to ensure biodiversity conservation and timber production over the whole productive forest area of the state enterprise. To ensure diversity of forest dwelling species, structural diversity and the supply of living and deadwood is crucial. The deadwood concept applied in Ebrach goes beyond its importance for the conservation of forest dwelling species: the latest evidence suggests that deadwood remaining in forest stands is crucial to ensure sustainable nutrient cycling in a forest – cations such as potassium, calcium, phosphorous, and magnesium are stored in wood and may serve as long-term fertilizer since they are released continuously over a long period of time by large decaying wood pieces and are thus available for tree growth. Additionally, deadwood stores large amounts of water while decaying and in the form of humus later on. In light of a changing climate and forecasted prolonged drought periods, this important attribute of deadwood may be also seen as a measure to secure the future of our forests.

The centerpiece of the Ebrach biodiversity concept is a carefully selected and cross-linked system of (1) set-aside and (2) extensively managed forest areas.

(1) Stands with a high ecological value fall under set-aside forest, which comprises the following categories:

- strictly protected nature reserves (429 ha)
- stepping stone habitats (403 ha)
- wet forest biotopes (96 ha)
- thermophilous dry forest biotopes (6 ha)
- forest edges: strips 5–20 m in width (63 ha)

These areas are taken out of forest management over the long term. They represent in total 997 ha or about 6% of the total productive forest (i.e. 15,500 ha, without set-aside and non-wooded areas) of the Ebrach State Forest Enterprise. All timber use and silvicultural activities are waived – only measures to ensure public safety and to prevent forest damage are allowed. They can serve as the basic safeguarding of biodiversity and as donor areas for temporal colonisation of habitat structures such as habitat trees and deadwood that automatically also occur in productive forests. Additionally, stepping stone habitats as punctual elements and forest edges as linear elements complement the cross-linking of dispersed habitats.

(2) Another important element of the Ebrach biodiversity concept is extensively managed forest. Extensification is mainly realized in old stands or in younger stands with a high number of old trees. Currently, extensification of forest management activities affects 3,824 ha and is assigned to the following categories:

- class 1 forests: near-natural stands over 180 years (37 ha)
- class 2 forests: near-natural stands between 140 and 180 years (3,062 ha)
- class 3+ forests: near-natural stands under 140 years with high number of old trees (725 ha)

Extensification in old stands is carried out with extensive retention of old trees in class 1 forests and maintenance of a constant amount of 40m3/ha of deadwood in class 2 forests. In class 3+ forests, all old trees that are remnants of the previous stands remain on the area; in all other class 3 forests, a systematic build-up of deadwood is planned with the aim of having a constant 20m^3/ha from the age class 100 onward. In the frame of the extensification of forest management, 10 habitat trees per hectare of the total productive area are allowed to grow old and carry out a completely natural life cycle, including decay after natural death. Even if only 50 m^2 (a value at the low end of the range) of canopy cover per habitat tree crown is assumed, this would amount to an additional 750 ha of set-aside area, and 10 % of the whole forest area would be left to natural processes and forest development.

All other stands are managed according to legal requirements regarding nature protection and species conservation, so the persistence of sufficient future habitat trees is ensured during pre-commercial thinnings.

The annual increment was measured at 8.5 m^3/ha or 140,000 m^3 over the total forest area including set-asides (132,000 m^3 over the productive forest area only). The loss occurring through measures in the frame of biodiversity conservation amounts to nearly 12,000 m^3 per year, including losses from legally protected forest areas (nature reserves and strict forest reserves) and through the above described set-aside areas representing stepping stone habitats. In these set-aside areas, the loss amounts to 7,000 m^3 per year, whereas in extensification areas it is 4,700 m^3 because of the build-up of deadwood.

The Ebrach biodiversity concept also comprises nature conservation in open habitats as well as riverine habitats and buildings. Targeted conservation programmes for bats, crayfish, and stag beetles have additionally been developed.

Figure 81. Timber use and conservation of forest dwelling species is not necessarily a contradiction: standing and fallen deadwood in a forest enterprise that harvests more than 100,000 m^3 of timber per annum. Photo by D. Kraus.

Hence, the current challenge is to identify thresholds at which productive functions can be maintained while, at the same time, protecting biodiversity (see respective Boxes with recommendations for management in the sections of **Chapter 3**). In particular, species groups that are linked to old-growth structures, deadwood, and natural disturbances, such as saproxylic beetles, birds breeding in cavities, molluscs, lichens, wood decaying fungi, and bryophytes, can serve as excellent indicators of the conservation success of integrative management approaches. However, finding the correct thresholds is strongly dependent on the conservation and management goals and the respective reference systems, i.e. either legacies of natural forest development or cultural forest landscapes. To be efficiently assessed, biodiversity-compatible forest management should be surveyed within a large-scale and multi-taxa monitoring programme (**Section 4.5**). Considering scenarios of increasing pressure on wood resources in Europe due to growing wood demand, it is crucial to ensure that the quality and efficiency of biodiversity conservation in forest management is not downgraded by new management goals.

Figure 82. Forest landscapes of the early 17th century were very different from today´s forests shaped by modern forest management: many large and crooked trees ensured the survival of old-growth species over the centuries even under intense human influence. Source: "Busy Forest Road" by Jan Brueghel the Elder, Bayerische Staatsgemäldesammlungen – Alte Pinakothek, München.

Compilation of Key Messages

Chapter 1. Concepts

1.1 To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests

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.

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

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

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

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. 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.

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

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.

1.2 The use of European criteria and indicator systems for measuring changes in forest biodiversity

The challenge is to reconcile established instruments for assessing and measuring the development of forest biodiversity in order to produce balanced, politically relevant, scientifically sound, and practically feasible information.

The pan-European FOREST EUROPE criteria and indicators, based on the concept of sustainable forest management, encompass a broader concept of sustainability, including ecological, economic, and social aspects.

The Streamlining European Biodiversity Indicators (SEBI) informs progress towards the EU 2020 targets of halting biodiversity loss for major European habitat types, including forests. Feedback can be provided to policy makers through the use of the DPSIR conceptual framework for assessing the effectiveness of biodiversity conservation policies.

The Finnish example shows how a change in forest management policy has influenced the state of biodiversity, as assessed through repeated monitoring of red-listed species (FOREST EUROPE indicator on threatened forest species).

The France case study illustrates the remaining difficulties of criteria and indicators in reaching their goals, and provides solutions to improve biodiversity monitoring and forest policy assessment.

As a monitoring tool, the set of national biodiversity indicators could be used to assess the efficacy of forest biodiversity conservation policies.

Current forest biodiversity indicator sets have allowed the sharing of common figures for a given criterion, but the linkage of common policy goals with biodiversity indicators is still lacking in several countries.

The next step should include a more structured approach in order to use indicators to monitor the effects of policies and forest management on biodiversity and assess the efficacy of biodiversity-orientated measures.

1.3 Research in old-growth forests and forest reserves: implications for integrated forest management

Restoring some old–growth features in managed forests provides habitat for old-growth dependent species.

Old-growth forests are living laboratories for ecological studies.

Research in forest reserves helps to understand the effects of management on forest structure and biodiversity.

Old-growth forests provide inspiration for foresters and the public.

If a goal of forest management is preservation of biodiversity, both integrative and segregative approaches are needed.

1.4 Forest Naturalness as a key to forest biodiversity preservation

Concepts of naturalness and its assessments emerged as a consequence of unbalanced forest management.

A scientifically sound and diagnostically conclusive naturalness assessment reports biodiversity conservation as reliably as a financial statement reports economic output.

Without a commonly accepted naturalness definition and a naturalness assessment approach, there can be no effective means of monitoring forest biodiversity trends.

After one decade of practice, naturalness-promoting forest management effects are already detectable and measurable by naturalness assessment.

High forest naturalness in common forests under use is the only possibility to preserve biodiversity at a high level.

Under the current dominance of economically-based forest management, the integrated management process is successful when naturalness assessment scores increase.

1.5 Silvicultural systems and multiple service forestry

Identifying structural elements within forest ecosystems is fundamental to understanding the link between management of forests and their ability to provide ecosystem goods and services (ESS).

The natural diversity of an ecosystem builds the ecological foundation of an integrative management approach in forestry through the diversity of structural elements.

Indicators and criteria allow assessment of the appropriateness of a chosen stand structure and silvicultural strategy to meet preset objectives.

Some ESS are linked to the structural richness of forest ecosystems. However, the diversity in structural attributes in selection systems is accompanied by some weaknesses as well.

A diversity of silvicultural systems and strategies across the landscape/region is needed to increase diversity in structures, functions, and biota and consequently support a broad range of ESS.

Structural elements become tools in a modular system that can mirror societal demands.

Options for integrative multiple service forestry are bound by the question of available space. A successful methodological approach to integration of multiple services thus has to take into account and manage space conflicts.

Once the links between structure and ESS have been identified and the underlying processes have been understood, the next step for silviculture is to design a dynamic system to promote and maintain the desired structure.

1.6 Retention forestry: an integrated approach in practical use

Scientific information about natural disturbance legacies may guide retention approaches.

In retention forestry the emphasis is just as much on what is left behind at harvest as on what is taken out.

Retention forestry is one component of multi-scale conservation.

Retention strategies can be integrated into all silvicultural systems.

Retention is also required in selection forests.

Retained structures help to maintain a higher level or facilitate a more rapid recovery of biodiversity and ecosystem functioning on site.

Since retention forestry is such a young forestry model, there is large potential for its future development and improvement.

Chapter 2. Key elements of biodiversity conservation in forests

2.1 Habitat trees: key elements for forest biodiversity

Habitat trees are very large, very old, and dead or living microhabitat-bearing trees. They are of prime importance for specialised forest flora and fauna.

Habitat trees are common in unmanaged forests but require specific attention in managed forests.

Cavity-bearing trees are among the most important habitat trees for forest wildlife. Old cavities with decayed residue host several of the most threatened forest beetles.

Managing for natural features, including habitat trees, strengthens the ecological services that are becoming increasingly valued by society. Efficient management strategies include the retention of "old-growth islands" at the management unit level combined with the retention of habitat trees at the stand level when harvesting.

Setting up a network of trees and stands that will never be logged is essential to guarantee the minimum habitat requirements of logging-sensitive species, though this appears incompatible with economic interests.

Habitat tradition – defined as the continuity in supply of old-growth, deadwood, and various forest structures – also seems to play an important role for preserving forest biodiversity.

Microhabitats could also be adopted for use as biodiversity indicators in European forests. A clear list of habitat tree features should be drawn up to help monitor microhabitats and correlate them to biodiversity levels.

2.2 Dead wood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity

Besides its major role for the conservation of saproxylic species, deadwood also contributes to carbon sequestration, nutrient supply, natural regeneration, and protection against falling rocks.

The survival of saproxylic species is not only dependent on the quantity, but also on the quality of deadwood, such as the tree species, diameter, or decay stage. However, the presence of a species is not a guarantee for good habitat conditions. It might be a legacy of the time when its habitat was still available.

Depending on the forest type, deadwood quantities ranging from 20 to 50 m^3/ha have been identified as a threshold to maintain the majority of saproxylic species. Very demanding species require more than 100 m^3/ha.

Management practices that promote deadwood should be organized on large scales as the influence of deadwood on saproxylic species increases with increasing spatial scales. The temporal dimension should also be considered because the continuity of forest cover and deadwood availability might play a major role in the protection of saproxylic biodiversity.

The diversity of deadwood in terms of tree species, diameter, decay class, and type (lying/standing) has a positive effect on the conservation of saproxylic species assemblages.

Most saproxylic species are either specialised on coniferous or broadleaved trees, and few generalists are known. Species with a narrower host-range are also known. However, the effect of tree species declines with the decomposition of deadwood.

Few large diameter logs cannot be substituted by many small ones for a given volume of deadwood because both have their own species assemblages. Large decay logs have been identified as essential for the conservation of saproxylic species as they are missing in most managed forests.

During the decay process from fresh deadwood to mould wood, species assemblages and richness evolve in deadwood. Furthermore, how a tree dies has an important effect on the composition of the saproxylic community.

Abiotic factors such as temperature and humidity and biotic drivers such as predation and competition also strongly influence species assemblages occurring on deadwood.

Deadwood has been increasing over the last decade throughout Europe. However, the conservation goals for saproxylic species have not yet been achieved as the quantitative thresholds determined for the conservation of most saproxylic species have generally not been reached in commercial forests.

The ecological threshold for deadwood quantities of between 20–50 m3/ha should be reached within a network of forest stands at the landscape scale rather than aiming for a lower mean amount in all stands.

2.3 Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements

Conservation of biodiversity in commercial forest stands is mainly a question of retention of specific elements to overcome the “harvest shortcut”.

In order to be effective for the conservation of saproxylic biodiversity, these old-growth elements should be arranged in a functional network.

Saproxylic organisms can be considered as populations that live on melting icebergs and that need to be able to reach the next suitable iceberg before the original one is gone.

A functional network of old-growth elements enables target species to develop and sustain viable metapopulations. Continuity and connectivity in time and space are essential elements. Like other organisms (e.g. vascular plants), saproxylic species can be subdivided into different life-strategies, from fast-colonising ruderals to stress-tolerant sedentary survivors.

The required configuration of a functional network of habitat is strongly dependent on these life strategies: fast colonisers require a continuous supply of (often very short-lived) habitat over larger areas; slow colonisers are often dependent on the conservation and enlargement of relict habitat islands.

A functional network of old-growth elements should be tailored to these different life strategies and therefore requires the combination of larger and smaller set-asides, intertwined with a dense enough network of habitat trees, both dead and alive.

2.4 Natural disturbances and forest dynamics in temperate forests of Europe

The defining structural and compositional patterns of a given forest are largely the result of a particular natural disturbance regime, characterized by the different types of disturbances in a forested ecosystem and the frequency, severity, and size distribution of these disturbances.

A sound understanding of how natural disturbance processes influence forest structure and composition at different spatial and temporal scales is key for successful conservation of biodiversity in integrative forestry.

In contrast to traditional conceptual models of natural forest dynamics that emphasized stability, ecologists and foresters now accept a non-equilibrium view that highlights the role of natural disturbance as an important driver of forest dynamics.

Direct observations of intermediate severity damage following storms in temperate old-growth forests show complex patterns of mortality, ranging from scattered individual gaps to small blowdown patches.

Implementing practical forestry measures that emulate natural disturbance processes is challenging and often fraught with difficulties.

Forest management at the landscape scale should not only mimic or restore late successional forest structural and compositional patterns, but also successional stages and structural complexity that arise from higher severity disturbances. The latter goal, for example, could be partly achieved by simply refraining from salvage logging after high severity disturbances on some sites.

Understanding the historic range of natural disturbance variability is necessary for gauging the influence of climate change on disturbance regimes and forest dynamics.

2.5 Conservation and management of specialised species: sustaining legacies of natural forests and cultural landscapes

There is a need to sustain legacies of both natural forests and cultural landscapes for the conservation of specialised species that are not provided with habitat in landscapes managed to maximise the production of wood, fibre, food, and energy.

Understanding landscape history is critical for the conservation of natural and cultural biodiversity, i.e. species, habitats, and processes in natural forests and cultural landscapes.

The maintenance of species landscapes with forests, woodlands, and trees requires consideration of legacies of both naturally dynamic forests and pre-industrial cultural landscapes.

Intensified use of forests and abandonment of cultural woodlands are two processes that are currently taking place simultaneously in European landscapes. This involves both challenges and opportunities for the conservation of both natural forest species and culture followers.

Knowledge about reference landscapes for natural and cultural biodiversity can be gained by studying remnants of natural and cultural landscapes as well as landscape history.

Maintaining natural and cultural biodiversity requires management of species, habitats, and processes across entire landscapes.

How much is enough? Performance targets as norms for assessment of sustainability.

Informed dialogue that aims at enhancing stakeholder collaboration in landscapes and regions is a prerequisite for successful conservation of natural capital. Biosphere Reserves, Model Forests, and LTSER are examples of concepts that promote this.

To maintain viable populations of all naturally occurring forest species in Europe, legacies of habitat structures and ecosystem functions in both natural forests and cultural landscapes need to be considered.

2.6 Managing for target species

By focusing only on structural features we risk overlooking species with particular demands. Careful selection of target species is a critical stage for complementing the coarse filter approach and evaluating management outcomes.

Ideally, target species affected by different limiting factors should be selected since this will improve the general relevance of conservation management measures.

Analysis of thresholds can provide managers with quantitative target values, but there are limitations.

Chapter 3. Indicator species groups and their thresholds of habitat requirements

3.1 Birds and their habitat requirements

Bird populations act on large scales and, on such large scales, are good indicators for forest biodiversity and management.

For securing future forest bird species diversity, it will be crucial to develop management strategies that maintain a diversity of structures across the whole forested surface, providing key resources for birds.

Forest birds reflect the diversity of their habitats. Some species are good indicators for openness of forests; some, for stands with closed canopies; others, for large trees with many holes; and still others, for short-term successional stages after forest fires. Different forest management strategies help to maintain forest bird diversity.

For maintaining avian forest biodiversity, European forests should provide all the above-mentioned habitat elements on the whole forested surface.

3.2 Insects and their habitat requirements

Among insects, some well-known groups such as beetles, ants, butterflies, and moths are very suitable as indicators of biodiversity, ecological integrity, and management of forests.

Deadwood is a vital resource for thousands of saproxylic (wood-inhabiting) organisms. Beetles alone comprise more than 1,400 saproxylic species in Central Europe and are good indicators of biodiversity. Depending on the forest type, deadwood volumes from 20 to 80 m^3/ha are recommended to support a rich assemblage of saproxylic species.

Bees, wasps, hover flies, butterflies, and moths are similar in that they are potential pollinators but otherwise have a very broad range of ecologies. These indicators not only reflect the differing food demands for their larval development, but also the supply of flowers providing nectar and pollen to the adult insects and thus represent the openness of a stand.

Insect predators and parasitoids consume mostly herbivorous insects. They represent the different ecologies of their prey. Therefore, a high species richness of these natural enemies indicates rich prey diversity.

3.3 Forest-specific diversity of vascular plants, bryophytes, and lichens

In temperate forests, a great diversity of vascular plants, bryophytes, and lichens exists. Epiphytic and epixylic bryophytes and lichens represent another highly significant component of overall forest diversity, whose richness outnumbers that of vascular plants in many forest types.

Many vascular plants, bryophytes, and lichens in forests occupy highly specific realized ecological niches along certain environmental gradients. These species therefore lend themselves as indicator plants for resource availability or old-growth forest sites.

Vascular plants have the lowest and lichens the highest proportion of extinct and threatened species in Central Europe.

Lichens, which comprise a large number of old-growth and deadwood specialists, are particularly sensitive to human intervention.

While continuous cover forestry is obviously detrimental to stress-tolerant plants, it is doubtful whether intensification of modern timber harvesting alone can benefit this species group without simultaneously favouring ubiquitous ruderals and even invasive plants.

Draining of wetlands and damming of floodplains have exerted broad-scale effects on forest sites, often leading to improved production, but severe habitat loss for specialised plants.

Epiphytic and epixylic diversity of forest plants in Central Europe has declined in the past 100–150 years due to removal of old trees and deadwood from managed forests.

A considerable proportion of threatened forest vascular plants, bryophytes, and lichens are bound to special habitats in forests.

Land-use history and habitat continuity has substantial impacts on ecological processes and plant species composition in forest ecosystems.

High proportions of forest species in the total floras of the three plant groups underpin the great responsibility that forestry holds for preserving biodiversity in Central Europe.

3.4 Biodiversity of mycorrhizal fungi as a crucial player in forest ecosystem functioning

More than 6,000 mycorrhizal fungi live in forest ecosystems worldwide, fulfilling important functions in nutrient and water mobilisation. A high diversity of these fungi in forests is important for the functioning and resilience of forest ecosystems, allowing them to adapt to changing environmental conditions.

Mycorrhizal fungi secrete extracellular enzymes involved in the decomposition of organic matter. The activity of these enzymes can be measured and help describe the functional role of mycorrhizal fungi.

Mycorrhizal fungi form underground hyphal networks that link trees to each other and allow nutrients, water, and carbon to be transferred. They facilitate the regeneration of seedlings, particularly in harsh environments such as those that prevail after

windthrow or during drought. The importance of these networks will become more critical to the stability of forest ecosystems under the predicted climate change scenarios.

Mycorrhizal diversity usually increases with forest diversity and successional stage. After disturbances such as clear-cut, wild fire, or windthrow, mycorrhizal diversity is higher in the initial stand stages when vital remnants of trees and tree seedlings are left over.

Mycorrhizal diversity can be assessed by fruitbody monitoring or by molecular analysis of soil or root samples.

Nitrogen fertilization of forests through atmospheric deposition or direct fertilizer inputs reduces the fruitbody production of mycorrhizal fungi and decreases mycorrhizal diversity. A strong reduction of the mycorrhizal species pool increases the vulnerability of the forest ecosystem to additional stresses since appropriate adaptation of the mycorrhizal community and the maintenance of its functions may no longer be guaranteed.

3.5 Lichens: sensitive indicators of changes in the forest environment

Lichens are a species-rich component of the forest biota that contributes to forest functioning. Tree age, stand continuity, and tree species composition are among the main factors influencing the patterns of forest lichen diversity.

Past forest management and landscape context influence large-scale regional processes of epiphytic lichen metapopulations.

Selective cutting should be preferred over the shelterwood system or clear cutting.

Valuable woodland key habitats should be identified and preserved.

3.6 Spiders in forest ecosystems

Spiders are a key component of forest ecosystems, occupying a unique position in food webs as both predators and prey.

Spider diversity is strongly influenced by variation in habitat structure in litter and vegetation layers from the ground to the canopy.

Spider fauna changes markedly over the growth cycle of a forest and is influenced by canopy tree species.

Spiders are affected by processes acting at stand and landscape scales as well as at very small scales (e.g. among microhabitats).

3.7 Snails and slugs as indicators of sustainable forest management

True forest gastropods are a substitute indicator group for a vast number of forest floor biota. Closed canopies create a forest microclimate and foster forest species.

Microhabitat requirements for specialist conservation are an estimated minimum amount of 20-50 m^3 of coarse woody debris per ha in managed forests and rigorous restrictions for deadwood removal from still pristine systems.

Tree composition influences gastropod assemblages though leaf litter quality. Trees such as maple and lime provide high quality resources, whereas conifers provide those of low quality. Fragmentation induces edge effects that significantly reduce the core habitat area in warm climatic conditions.

The remnant size and the species extinction debt: (inappropriate) management increases the forest fragment size needed for survival.

Forest turnover is accompanied by a loss of specialist species and cryptic effects in recolonizing populations. Reforestation is thus not an alternative to forest protection and sustainable management.

Chapter 4. Key challenges

4.1 Biodiversity conservation and forest management in European forest ecosystems under changing climate

Climate is changing, but many uncertainties remain about the likely impacts of climatic changes on forest ecosystems, species distributions, and the implications for biodiversity conservation.

Future conservation efforts should be fully aware that the distribution of biodiversity, and species of concern, will be dramatically altered by climate change and that increased extinction risk is one of the possible outcomes. Conserving biodiversity will require approaches above and beyond those that are currently implemented in Europe.

Forests and forest related species will not only have to adapt to long-term changes in climate but also to increased variability with more extreme weather events, such as prolonged drought, devastating storms and floods. Additionally, combinations of direct climate stresses (e.g. heat waves) and indirect climate-induced pressures (e.g. pest outbreaks) will exacerbate the situation.

Under climatic change not all of a species' historic range remains suitable habitat. Plans and assumptions about protected areas will have to be reconsidered.

Conservation management should be adapted to better respond to the challenges of climate change.

It is important to quantify how much extra area, patches, or connecting elements are needed for habitat cohesion considering the regional circumstances.

Traditional conservation policies are not suitable under changing environmental condition, thus there is a need for a paradigm shift in conservation management.

4.2 The functional role of biodiversity in forests

European forests cover a large gradient of compositional, structural, and functional diversity. Changing biodiversity has several consequences for ecosystems.

Functional traits of species determine the underlying biological mechanisms for mixture effects.

Species richness is among the major determinants of ecological processes in ecosystems.

Recent inventory-based diversity-functioning studies reported positive relationships between tree species diversity and productivity.

From a multifunctionality perspective, it is obvious that no single species is able to fulfil many functions simultaneously, and there might even be trade-offs between distinct services.

Despite the fact that we are still far from a general theory about the functional role of biodiversity in forests, recent evidence suggest that the conservation of genetic, structural, and functional diversity in forest communities is a good basis for multifunctional and sustainable forest use.

4.3 Invasive neobiota in forest ecosystems: opportunity or threat?

Neobiota are organisms that are able to spread naturally in geographic areas where they previously were not native and include plants (neophytes), animals (neozoans), and fungi (neomycetes).

Increasing numbers of neobiota continue to be introduced: the outcome of this global biological homogenisation is far from complete.

Invasive neobiota may represent an important threat to society and nature and involve a multitude of negative impacts, including tremendous monetary costs.

In forest ecosystems the most damaging invasive neobiota are likely to be insect pests and pathogens.

Several invasive neophytes in forests are economically important forestry species; the perception of their usefulness or harmfulness greatly varies among different stakeholders.

Preventive measures such as avoiding introduction, early detection, and rapid response are the cheapest options available to avoid ecological and economic damage.

By applying the principle of extended producer responsibility, costs arising from management of invasive neobiota may be shifted to those business sectors that profit from the movement of organisms.

4.4 Genetic diversity of forest trees

The genetic diversity of forest trees ensures the occurrence and functioning of forest ecosystems in a broad range of environmental conditions.

Genetic diversity of forest trees is crucial for adaptation of forests to climate change.
Dynamic conservation of genetic diversity can be integrated with biodiversity conservation and forest management.

Conservation of forest genetic diversity still needs to be improved in Europe.

4.5 Monitoring forest biodiversity in Europe: state of the art, challenges, and opportunities

At the European level, the assessment and monitoring of forest biodiversity has become a challenge for many countries. Monitoring data on the state and dynamics of biodiversity should be reliable and comprehensive enough for assessment of the effectiveness of environmental policies.

In France the Breeding Birds Survey shows how forest data can be integrated in biodiversity monitoring programs.

In Finland the use of the red-listed species system has proved its effectiveness in monitoring biodiversity response to forest policy.

Most forest biodiversity monitoring and indicators reporting are based on biodiversity data issued from National Forest Inventories.

The current forest biodiversity monitoring system is mainly based on indirect structural indicators (proxies) rather than on taxonomic and intraspecific data.

The Biodiversity Monitoring (BDM) of Switzerland complemented the National Forest Inventory with taxonomic data.

To date, there has been some discrepancy between taxa currently monitored (butterflies, birds, vascular plants) and forest taxa at stake (e.g. saproxylic taxa).

Monitored taxa should include groups that are specific to forests and/or potentially threatened by (global) changes in silvicultural practices.

Monitoring species, forest structures, and habitats is necessary and should be combined in optimal monitoring systems.

Chapter 5. Integrative management approaches: a synthesis

Forest management in Europe has traditionally been geared towards timber production, and this has remained the governing principle in most European forests. Biodiversity conservation is to some extent increasingly in conflict with traditional forest management.

Integration of key structural characteristics and old-growth attributes at the tree and stand level provides a general basis for biodiversity conservation in European forests.

Management goals such as biodiversity conservation and ecosystem functions can be met in both set-aside forest reserves and off-reserve forests.

Integrative forest management systems aim to maximise the cross-section between the different main functions of modern forestry: production, protection, and conservation.

Effective conservation and restoration of habitats heavily relies on well-developed segregative instruments that complement sustainable, integrative forest management practices. Thus, there is a need for a comprehensive hierarchical dual strategy with both integrative and segregative instruments for the conservation of representative forest biota.


Rosalia alpina

Glossary

This glossary was compiled with the help of the contributing authors to ensure consistency among their working definitions. Therefore, the definitions given below may differ from other sources.

Abiotic
That which is not derived from living beings.

Allochtonous
Describes an organism not originally from the region where it is found (opposite of native or autochtonous).

Alpha diversity
A discrete number of species within habitats.

Anthropogenic
Describes phenomena (for example, anthropogenic disturbances) that are caused or maintained by the conscious or unconscious actions of humans.

Asynchronous
Not occurring at the same time.

Autotroph
An organism capable of converting inorganic compounds to more complex organic compounds as a source of nourishment. Green plants are autotrophs for carbon.

Basal area
Area of the section of a tree trunk, measured at breast height (1.30 m).

Beta diversity
Dimensionless comparative number of species in different units of vegetation or between habitats.

Biodiversity
Encompasses the variability of biological entities across all levels of biological hierarchies, i.e. from the level of genes to ecosystems.

Biotic
Pertaining to living beings.

Climax stage
State of a plant community that has attained a stage of sustainable equilibrium with the climatic and edaphic factors of the environment in the absence of human intervention.

Delta diversity
Dimensionless comparative number of species applied to changes over large scales; the functional equivalent of beta diversity at the higher organizational level of the landscape.

Ecological optimum
Range of environmental factors that are the most favourable to the development of an organism or a population.

Ecosystem processes
The physical, chemical, and biological actions or events that link organisms and their environment, e.g. biomass production, litter decomposition, nutrient cycling.

Ecosystem properties
The size of compartments, e.g. pools of material such as carbon or soil organic matter.

Ecosystem functions
The capacity of ecosystems to provide services – directly and indirectly – underpinned by biophysical structures and processes. They can be seen as intermediates between processes and services.

Ecosystem functioning
Activities, processes, or properties of ecosystems that are influenced by its biota

Ecosystem services
Benefits people obtain from ecosystems, including provisioning services (e.g. food, fibre, genetic resources), regulating services (e.g. erosion control, climate regulation, pollination), cultural services (e.g. spiritual and religious, recreational, educational), and supporting services (e.g. soil formation, primary production, nutrient cycling).

Edaphic
Concerns physical and chemical properties of the soil that affect vegetation.

Epigeic
Living in/on the soil.

Epiphytic
Living on another living plant.

Epixylic
Living on deadwood.

Epilithic
Living on rock surfaces.

Even-aged
A stand or a forest comprised of trees of the same age.

Gamma diversity
A discrete number of species in a limited space.

Geophyte
A perennial plant whose survival from one year to the next relies on buds located in the soil (e.g. bulb plants).

Guild
Group of related species that belong to the same trophic level and utilize the same kinds of resources.

Heliophyte
A plant that seeks sunlight.

Hemicryptophyte
A perennial plant whose persistent parts are close to the ground in winter (rosettes of leaves, buds).

Heterotroph
An organism that has to ingest a substance in an organic form to be able to use it for the synthesis of its own substance. All animals are heterotrophic for carbon and nitrogen, unlike green plants (autotrophs).

Island biogeography
A field within biogeography that examines the factors that affect the species richness of isolated natural communities. The theory was developed to explain species richness of actual islands. It has since been extended to mountains surrounded by deserts, lakes surrounded by dry land, fragmented forest, and even natural habitats surrounded by human-altered landscapes.

Invasive species
Species producing offspring in very large numbers and with high dispersal ability with an adverse/disruptive effect on the ecosystem.

Liverwort
Marchantiophyta.

Metapopulation
A metapopulation consists of a group of spatially separated populations of the same species that interact at some level. It is generally considered to consist of several distinct populations together with areas of suitable habitat that are currently unoccupied.

Microhabitats
Ecological niches on standing live or dead trees.

Naturalness
The similarity of a current ecosystem state to its natural state. A natural state includes the impact of humans having no permanent influence on the ecosystem.

Necromass
Biomass of dead organisms.

Neobiota
Species introduced through human activity to new geographic areas after the end of the Middle Ages.

Niche
Position occupied by a species in an ecosystem, defined by its living requirements and its relationships with other species.

Nitrophytic
Organisms that require or tolerate high amounts of nitrogen.

Old-growth forests
Forests minimally affected by man, mainly left to spontaneous development, containing old trees, deadwood, etc.

Oligotrophic
Organisms that require or tolerate nutrient-poor site conditions.

Parasitoid
Parasitic insect whose larva feeds on a host and eventually kills it.

Photophytic
Plants demanding high levels of light.

Polypores
Basidiomycetes (fungi) generally living on trees. Polypores are characterised by a hymenium (superficial layer covered with spores) made of parallel tubes that form a perforated surface.

Propagule
A part of a plant that serves as means of generative (seeds and spores) or vegetative reproduction (corms, tubers, offsets, or runners).

Retention forestry
An approach to forest management based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest, at the time of harvest. The aim is to achieve a level of continuity in forest structure, composition, and complexity that promotes biodiversity and sustains ecological functions.

Resilience
The property of an ecosystem to remain in a state of equilibrium despite the various ecological disturbances it faces.

r/K strategy
r-selection predominates in unstable environments and is characterised by species or populations with high reproductive rates, little parental investment, small body sizes, and rapid development. K-selected species favour quality over quantity of offspring, invest more into parental care, and are better adapted to stable environments. The so-called K-traits represent the “carrying capacity” of a specific habitat.

Saproxylic
Any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened, or dead trees.

Snag
Part of a log (uprooted or broken tree) that remains standing.

Taxon
Any group organized in a classification of living beings, of whatever rank.

Thallus
Simple vegetative body undifferentiated into stem, leaves, or roots of a plant form devoid of wood.

Trophic level
Within the food chain or a trophic network (several chains), stage in the course of matter and energy cycles, starting with producers and ending with tertiary consumers.

Vascular plants
Plants that possesses vessels or tracheids (gymnosperms, angiosperms, and pteridophytes (including ferns, lycophytes, and horsetails).

Project partners:

WSL

inbo
Instituut voor
Natuur- en Bosonderzoek

METLA

ALTERRA
WAGENINGEN UR

ARCTIC CENTRE

BAYERISCHE STAATSFORSTEN
Nachhaltig Wirtschaften.

Bioversity International

CZU
CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

ECOFOR
ECOSYSTEMES FORESTIERS

Edge Hill University

EUFORGEN

Forêt Privée Française
CNPPF
IDF

FORST Brandenburg
Landesbetrieb

FVA
Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg

HOCHSCHULE
WEIHENSTEPHAN-TRIESDORF
UNIVERSITY OF APPLIED SCIENCES

INRA
SCIENCE & IMPACT

irstea

LAND BRANDENBURG
Ministerium für Umwelt, Gesundheit und Verbraucherschutz

LEUPHANA
UNIVERSITÄT LÜNEBURG

Mittuniversitetet
MID SWEDEN UNIVERSITY

Museo
cantonale
di storia
naturale

Nationalpark
Bayerischer Wald

Naturalis
Biodiversity
Center

NW-FVA
Nordwestdeutsche
Forstliche Versuchsanstalt

PENNSTATE
1855

SLU

TECHNISCHE
UNIVERSITÄT
DRESDEN

THÜNEN

UNIVERSITÀ
DEGLI STUDI DI TRIESTE

UNIVERSITY OF
EASTERN FINLAND

UNI
FREIBURG

University of Ljubljana

TARTU ÜLIKOOL · UNIVERSITAS TARTUENSIS
1632

vogelwarte.ch

WAGENINGEN UNIVERSITY
WAGENINGEN UR

In Focus – Managing Forest in Europe


Oxychilus cellarius


Antrodiella citrinella


Cladonia digitata

Management goals and ecosystem functions such as biodiversity conservation can be met in both set-aside forest reserves and off-reserve forests. The major argument for well developed and protected forest reserves is the increase of alpha-diversity with extended succession periods and turn-over cycles. However, the establishment of new protected areas is limited due to space and competing management goals. Trade-offs have to be made where such conflicts of interest occur. Accordingly, emphasis is shifted towards integrating rare forest biotopes and structural attributes into production forests. Forests in Central Europe are often managed on the basis of silvicultural principles with high forest management standards. Integrative forest management aims to maximize the cross-section between the different main functions of modern forestry: production, protection and conservation. The area of synergy, however, is limited and a certain amount of exclusive area is needed to guarantee different ecosystem functions.

The present volume contains a compilation of the results of the research project **Integrate**. Based on the contributions from more than seventy renowned scientists in this field, **Integrate** has attempted to make available the most recent knowledge and the best international scientific expertise on the complex relationships, trade-offs and emerging challenges regarding the integration of forest biodiversity conservation into forest management.