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Biodiversity in European beech forests – a review with recommendations for sustainable forest management

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In this review we compare stand-scale patterns of biodiversity in managed and unmanaged European beech *Fagus sylvatica* forests and discuss the implications for sustainable forest management. Beech forests managed with single stem or group harvest systems retain the multi-layered and multi-aged stand structure of old-growth beech forest, but old and senescent trees are removed and the amount of dead wood is significantly reduced. Shelterwood or clearcut management involves an additional change to large single-layered, even-aged stands. Beech forests managed with traditional shelterwood systems possess a relatively low value for the conservation of most species groups reviewed. The general sensitivity of different species groups to shelterwood forestry roughly increased in the following order: herbaceous plants < soil macrofungi < ground dwelling arthropods < land snails < saproxylic fungi < hole nesting birds and saproxylic insects < epiphytic lichens and bryophytes < epixylic bryophytes. The retention of substantial numbers of trees in shelterwood systems will improve the situation considerably for saproxylic species and for species which use dead wood for shelter and foraging, e.g. ground arthropods and snails. Measures to promote biodiversity in managed stands should also include the maintenance of a natural hydrology. Selectively harvested beech forests provide generally more suitable habitat than shelterwood managed forests for epiphytic and epixylic species by maintaining a stable micro-climate. The most demanding epiphytes need a substantial number of slow-growing trees which are retained. A continuous availability of habitat trees older than 180 yr and >20 m^3 ha^{-1} dead wood are probably required to maintain a rich biodiversity in managed beech forests. The results suggest that only selectively harvested stands retaining many trees may approach the overall biodiversity of old-growth beech forests. Due to the patchy distribution of such forests, more knowledge on how rare beech forest species disperse between suitable habitats is necessary to design reliable concepts for biodiversity management at a landscape scale.

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Beech *Fagus sylvatica* is one of the major forest trees in Europe. The total area of beech dominated forest in Europe is estimated to cover ca 14–15 Mha (excluding the Caucasian mountains) with the largest areas in France, central and southern Germany, and the southeast European mountains (Carpathians, Dinaric and Balkan mountains) (Hermansen 1962, Hahn and Fanta 2001, Standovár and Kenderes 2003).

Beech occurs on a wide range of soils including acid podzols and calcareous rendzic leptosols. It grows however, best on well-drained cambisols and luvisols and does not tolerate waterlogging or severe drought (Peters 1997). Beech prefers a temperate, mild and humid climate. Low winter temperatures, a short growing period and late spring frosts have been assumed to limit its distribution in northern and eastern Europe (Jahn 1991, Peters 1997, Bolte et al. 2007). Water deficiency during the growing period limits the distribution in the southern European lowlands (Peters 1997).

Beech trees usually reach a height of 30–40 m, in exceptional cases >50 m. In closed stands, maximum stem diameter ranges from 100 to 150 cm and maximum age from ca 200–300 yr, in exceptional cases up to 400 yr (Korpel 1995, Peters 1997). Beech casts heavy shade, but advanced regeneration can persist under a relatively closed canopy and is able to fill canopy gaps after small-scale disturbance (Korpel 1995). Under favourable climatic and edaphic conditions, beech is therefore able to dominate in old-growth stands (Ellenberg 1988, Jahn 1991, Meyer et al. 2003). Important accompanying species in old-growth beech forests include silver fir *Abies alba*, maples *Acer platanoides*, *A. pseudoplatanus*, hornbeam *Carpinus betulus*, ash *Fraxinus excelsior*, oaks *Quercus petraea*, *Q. robur*, Norway spruce *Picea abies* and lime *Tilia cordata* (Korpel 1995, Peters 1997, Standovár and Kenderes 2003).

Temperate broadleaved forests, including European beech forests, have been transformed by human activities to a larger extent than any other forest biome (Hannah et al. 1995). Most beech forest areas that escaped clearance and cultivation are managed for timber production with far-reaching effects on forest structure and biodiversity (Lonsdale et al. 2008). By reducing the amount of senescent trees and coarse woody debris (CWD), the effect of forest management for timber is particularly pronounced for saproxylic and epiphytic species (Harmon et al. 1986, Grove 2002, Ódor et al. 2006, Winter and Möller 2008). Recent focus on biodiversity loss in managed beech forests has resulted in considerable research efforts (e.g. the EU 5th framework programme Nat-Man, Ódor et al. 2006). The aim of this review is to provide a general overview of this recent progress with a focus on the effects of forest management on biodiversity patterns at the stand scale.

Specifically, we focus on the following questions: 1) how are stand structure and habitat availability changed by shelterwood and selective harvest systems compared to old-growth forests? 2) Are there general differences in the sensitivity of different species groups to timber harvesting? 3) Are there thresholds in habitat availability affecting species diversity? 4) How valuable are retained old-growth structures in managed beech forests for biodiversity?

Methods

The outstanding role of beech as a broadleaved forest tree in central Europe has resulted in an immense body of literature concerning the biodiversity in beech forests. Studies in this review concern mainly more or less pure beech forests but also mixed forests with beech as a co-dominant species, e.g. *Fagus–Quercus* forests and *Fagus–Abies alba–Picea abies* forests. Increasing tree species diversity usually implies higher overall biodiversity, but effects of conversion of more or less pure beech forest to mixed stands are outside the scope of this review.

A special focus was laid on comparative studies of unmanaged and managed beech stands (Table 1). The term forest management refers exclusively to management for timber and wood production in this review. The term old-growth refers to beech forest with a long-term absence of both human disturbance and large-scale natural disturbance (Bauhus et al. 2009).

The review also includes studies on biodiversity of environmental gradients that are influenced by forest management, e.g. tree age and size of decaying wood. The focus is on the effects at stand scale, more or less directly related to management measures. Disturbance regimes compared included natural gap dynamics in unmanaged reserves, close-to-nature forestry (single tree and group harvest), shelterwood systems and clear-felling systems, including varying levels of tree retention (Table 1). Most stands studied were not grazed by domestic animals, except for a few studies in wood pastures with widely spaced trees.

Relevant studies were identified through searches in the databases Agricola, Biosis previews, CAB abstracts, Web of Science and Scopus covering studies published before July 2009. The searches contained the terms beech or *Fagus sylvatica* together with several terms related to the organism groups surveyed, or with the terms biodiversity and conservation. In a second step, the reference lists of the studies obtained from the databases were checked for additional relevant papers. Studies considered in this review mainly comprise articles published in international peer reviewed journals (Table 1). A large number of studies have been published in local and national journals in many countries and languages. Within the scope of the review, it was however, not possible to include this literature. Furthermore, it was not possible to cover the entire range of taxonomical groups present in European beech forests.

The species groups reviewed include herbaceous vascular plants, epiphytic lichens, epiphytic and epixylic bryophytes, soil macrofungi, saproxylic fungi, saproxylic beetles and flies, ground-dwelling arthropods, terrestrial molluscs and hole nesting birds.

These taxa represent relatively species-rich and/or well-studied groups which depend on the three major habitat structures in forests, i.e. soil and litter, living trees and dead wood. They are also often used in surveys to indicate the conservation value of forests. By representing a wide range of life forms and habitat requirements, we assume that these groups will respond to silvicultural measures at stand-scale in different ways.

The studies available cover a relatively large part of the distribution range of *Fagus sylvatica* in Europe, but a majority is from central and northwestern Europe (Table 1). Conclusions from a particular study will probably be valid in other beech forests under comparable edaphic and climatic conditions, but not necessarily in all types of European beech forests.

The results are presented separately for the major species groups. The first section deals with general patterns of species diversity, usually emerging from studies of environmental gradients. The second section reviews comparisons of managed and unmanaged forests for the species group in question.

We mainly review effects of management on patterns of species richness (no. of species) and composition. Among the species reviewed, special emphasis is laid on species of conservation concern, i.e. red-listed and regionally rare species. Based on both quantitative and qualitative relationships between habitat structures and species richness, we estimate the general habitat value of different management systems for the species groups reviewed.

Natural dynamics in European beech forests

The dynamics of natural beech forests have been described by a forest development cycle which is characterized by small-scale gap dynamics and comprises 200–300 yr (Korpel 1995, Pontailler et al. 1997, Mountford 2001, Standovár and Kenderes 2003, Christensen et al. 2007). Old-growth beech forests are usually multi-aged and multi-layered as a consequence of small-scale gap dynamics, with an inverse J-shaped or rotated sigmoid diameter distribution (Korpel 1995, Meyer et al. 2003, Westphal et al. 2006).

Canopy gaps can be defined as openings in the upper crown layer of a forest produced by uprooting or the breakage of part of a tree, or several trees (Mountford 2001). Stand break-up is usually gradual and linked to moderate storm damage and/or senescence of single or small groups of old trees. Most gaps remain therefore, small to medium in size (100–500 m^2) and the gap size-distribution forms a negative exponential curve (Pontailler et al. 1997, Mountford 2001, Meyer et al. 2003, Christensen et al. 2007). The most commonly recorded gap is oval in shape and 2–3 times longer than wide, but further expansion may occur.

Gaps are mainly created by stem breakage of senescent trees, resulting in logs and snags (Pontailler et al. 1997, Brunet and Isacsson 2009b). Strong storms however, often result in a large proportion of uprooted trees (Pontailler et al. 1997), and the total area and size distribution of gaps can increase greatly with even large glades >1000 m^2 being created (Mountford 2001). Exceptionally, a severe windstorm may level an entire stand, leaving only a scatter of trees as in a shelterwood system (Pontailler et al. 1997, Mountford 2001).

Gaps are characterized by higher light availability, higher daytime soil and air temperatures, but also higher soil moisture (Rozenbergar and Diaci 2003, Gálhidy et al. 2006, Hahn et al. 2007). Coarse dead wood is usually created together with canopy gaps and is therefore exposed to these micro-climatic changes. This implies that gap creation has a direct influence on the species at the forest floor and on the species depending on dead wood. The increased light to the forest floor in gaps facilitates the establishment of new seedlings and releases suppressed understorey trees (Christensen et al. 2007). Stand regeneration may develop through several episodes of suppression and release of trees as multiple gaps consecutively form and close at the same location (Mountford 2001, Emborg 2007).

Compared to other broadleaved trees, beech has a strong ability to close small gaps by crown extension and by release of existing advanced regeneration (Christensen et al. 2007). Small gaps are therefore often filled by shade-tolerant beech, while light-demanding species (e.g. *Betula pendula*, *Fraxinus excelsior*, *Prunus avium*, *Quercus petraea*, *Q. robur*) may only establish in large, more persistant gaps (Pontailler et al. 1997, Rozenbergar and Diaci 2003).

The other main factors influencing the diversity of the woody species regeneration include soil and humus conditions, browsing pressure, occurrence of mast years and distance to seed sources (Peters 1997). High soil pH favours the regeneration of ash, elm, lime and maple, but these species are usually more heavily browsed than beech (Diaci and Rozenbergar 2001, Christensen et al. 2007). It is outside the scope of this study however, to review the extensive literature on factors influencing the regeneration of beech in relation to other woody species.

History of beech forest management in Europe

Until the introduction of regular forestry in the 18th and 19th centuries, beech forests had been kept for pasture and pannage (feeding pigs with beech nuts) for many centuries and they were usually selectively cut for wood (Peters 1997, Hahn and Fanta 2001). Relatively large areas were also managed as coppice for the production of firewood, charcoal and potash, especially in the lower mountain ranges. Beech has however, a lower ability to produce coppice shoots than oak and hornbeam and may be replaced by the latter species in the long-term (Peters 1997). When fossil fuels started to replace wood as the primary source of energy and the demand for timber for construction increased during the 19th century, large areas of beech forest were replaced by coniferous plantations, especially with Norway spruce (Hahn and Fanta 2001). There was however, also an increase in beech in many places where abandonment of coppice and coppice with standards systems led to a development towards high forest which favoured the regeneration of beech compared to oak and hornbeam (Hahn and Fanta 2001).

Shelterwood systems have dominated beech forest management in most European countries from the 19th century through most of the 20th century (Hahn and Fanta 2001). Shelterwood management involves the thinning of the canopy after a mast year to establish a dense natural regeneration (Fig. 1). After successful regeneration, the remaining seed trees are cut. Shelterwood management usually results in large, single-layered and even-aged beech stands. The rotation period of these systems is 90–140 yr, depending on soil fertility. Clear-cutting and replanting with bare root saplings was uncommon but occurred regionally, e.g. in southern England (Hahn and Fanta 2001). Planting, often with nurse trees such as *Betula* or *Larix*, is also used when new beech stands are established on open land or replace other forest types. In the beech and mixed

Table 1. Overview of the studies analysing the effects of forest management in beech forests included in the review. The species group studied, the country in which the field work was conducted, and the general study design or the main factor studied are given. The studies are listed by species group and author name.

Source	Species group	Country	Study design
Aubert et al. 2003	Herbaceous plants	France	Chronosequence
Aude and Lawesson 1998	Herbaceous plants	Denmark	Chronosequence
Brunet et al. 1996	Herbaceous plants	Sweden	Management gradient
Falkengren-Grerup and Tyler 1991	Herbaceous plants	Sweden	Management gradient
Gálhidy et al. 2006	Herbaceous plants	Hungary	Gradient of gap size
Godefroid and Koedam 2004	Herbaceous plants	Belgium	Gradient of soil compaction
Godefroid et al. 2005a	Herbaceous plants	Belgium	Chronosequence
Godefroid et al. 2005b, 2006	Herbaceous plants	Belgium	Clearcut versus closed forest
Graae and Heskjaer 1997	Herbaceous plants	Denmark	Managed versus unmanaged forest
Graae and Sunde 2000	Herbaceous plants	Denmark	Management gradient
Hahn and Thomsen 2007	Herbaceous plants	Denmark	Gaps versus closed forest
Kenderes and Standovár 2003	Herbaceous plants	Hungary	Managed versus old-growth forest
Naaf and Wulf 2007	Herbaceous plants	Germany	Gradient of gap size
Schmidt 1997	Herbaceous plants	Germany	Gaps versus closed forest
Standovár et al. 2006	Herbaceous plants, bryophytes	Hungary	Managed versus old-growth forest
von Oheimb and Härdtle 2009	Herbaceous plants	Germany	Group and selection cut
Aude and Poulsen 2000	Bryophytes, lichens	Denmark	Managed versus unmanaged forest
Bardat and Aubert 2007	Bryophytes	France	Shelterwood, coppice, and selection cut
Friedel et al. 2006	Lichens	Germany	Unmanaged versus shelterwood forest
Fritz 2009, Fritz et al. 2009a, b	Bryophytes, lichens	Sweden	Chronosequence
Fritz and Heilmann-Clausen 2010	Bryophytes, lichens, fungi	Sweden	Healthy versus damaged trees
Fritz et al. 2008	Bryophytes, lichens	Sweden	Ancient versus recent forest
Gustafsson et al. 1992	Bryophytes	Sweden	Successional gradient
Nascimbene et al. 2007	Lichens	Italy	Selection cut versus shelterwood
Ódor and Standovár 2001	Bryophytes	Hungary	Managed versus unmanaged forest
Ódor and van Hees 2004	Bryophytes	Hungary	CWD gradient
Ódor et al. 2005, 2006	Bryophytes	DK, NL, B, SLO, HU	Large scale geographical gradient
Di Marino et al. 2009	Mycorrhiza fungi	Italy	Coppice cycle
Tyler 1985	Soil macrofungi	Sweden	Soil gradient
Heilmann-Clausen and Christensen 2003, 2004, 2005	Saproxylic fungi	Denmark	Size and decay stage of CWD
Müller et al. 2007a, b	Saproxylic fungi	Germany	Management gradient
Ódor et al. 2006	Saproxylic fungi	DK, NL, B, SLO, HU,	Large scale geographical gradient
Gärdenfors 1992	Snails	Sweden	Limed versus unlimed soil
Kappes 2005	Snails	Germany	Management gradient
Kappes 2006	Slugs	Germany	Management gradient
Kappes et al. 2006	Snails	Slovakia	CWD gradient
Kappes et al. 2009	Snails, ground arthropods	Germany, Slovakia	CWD gradient
Müller et al. 2005	Snails	Germany	Management gradient

Table 1. Continued.

Source	Species group	Country	Study design
Brunet and Isacsson 2009a, b	Saproxylic beetles	Sweden	Gradients of CWD decay and CWD density
Fayt et al. 2006	Saproxylic beetles and flies	Belgium	CWD gradient
Harz and Topp 1999	Saproxylic beetles	Germany	Gradient of dead wood diameter and exposure
Kappes and Topp 2004	Saproxylic beetles	Germany	Gradient of dead wood decay and diameter
Kleinevoss et al. 1996	Saproxylic beetles	Germany	Gradient of dead wood decay and diameter
Müller et al. 2007b, 2008	Saproxylic beetles	Germany	Management gradient
Nilsson and Baranowski 1997	Saproxylic beetles	Sweden	Continuity of CWD
Schiegg 2000a, b, 2001	Saproxylic beetles	Switzerland	Dead wood connectivity and diameter
Winter and Möller 2008	Saproxylic beetles	Germany	Management gradient
Hövemeyer and Schauermann 2003	Saproxylic flies	Germany	Log decay stage
Sroka and Finch 2006	Ground beetles	Germany	Managed versus unmanaged forest
Tyler 2008	Ground beetles	Sweden	Podzol versus cambisol
Jabin et al. 2004	Ground arthropods	Germany	Distance to CWD
Jabin et al. 2007	Ground arthropods	Slovakia	Distance to CWD
Theenhaus and Schaefer 1995	Ground arthropods	Germany	Gaps versus closed forest
Topp et al. 2006a, b	Ground arthropods	Slovakia	Distance to CWD
Boncina 2000	Birds	Slovenia	Managed versus unmanaged forest
Laiolo et al. 2004	Birds	Italy	Managed versus unmanaged forest
Müller et al. 2007b	Birds	Germany	Management gradient
Moning and Müller 2009	Birds, snails, lichens	Germany	Chronosequence

beech-fir forests of the Alps, the Carpathians and the Dinaric mountains, single stem and group harvest systems have been developed (Hahn and Fanta 2001).

Few European beech forests have escaped human impact during the past centuries. Small patches of old-growth exist in most countries with beech forest (Fig. 2), but the best preserved old-growth beech forests are found in the mountains of southeastern Europe (Korpel 1995, Kenderes and Standovár 2003, Meyer et al. 2003). Comparisons between old-growth and managed beech forests show many differences in structural attributes (Table 2). Old-growth stands contain many veteran trees older than 150 yr and high amounts of CWD, ranging from ca 50–250 m^3 ha^{-1} (Christensen et al. 2005, Vandekerkhove et al. 2009). Beech forests managed with single stem or group harvest retain a multi-layered and multi-aged stand structure but old and senescent trees are removed and the amount of CWD is significantly reduced (Table 2). Shelterwood or clearcut management involves an additional change to large single-layered, even-aged stands. We conclude that the spatial and temporal connectivity of shaded areas, dead wood and old trees is lost in beech forests managed with shelterwood and clearcut systems as long as substantial retention measures are absent (Table 2).

From the end of the 20th century, interest in biodiversity conservation has led to increased areas of unmanaged beech forests in reserves and national parks, with an accumulation of veteran trees and CWD (Christensen et al. 2005, Vandekerkhove et al. 2009). In a few forest reserves, supplementary dead wood is provided and decay is induced in vital trees (Davies et al. 2008).

Close-to-nature forest management (also called continuous cover forestry) with single stem or group harvest has been introduced in public and private forests of several countries, aiming at the restoration of structurally more complex beech stands (Hahn and Fanta 2001, Meyer et al. 2003). Furthermore, different measures have been taken in shelterwood management to increase the value of these stands as habitat for saproxylic and epiphytic species. Logs and snags (high stumps) created by natural disturbances such as windfall, are left to decay naturally in the stands (Davies et al. 2008). In addition, a number of mature trees

Figure 1. Managed shelterwood beech stand under regeneration in Torup forest, southern Sweden. Photo by Jörg Brunet.

Figure 2. Old-growth beech forest in Söderåsen National Park, southern Sweden. Photo by Jörg Brunet.

are usually retained after the regeneration fellings (Rosenvald and Lohmus 2008).

Intensively managed shelterwood beech forests only contain between 1 and 10 m^3 ha^{-1} dead wood, most of which consists of cut stumps and small diameter branches of relatively low value for saproxylic species (Erdmann and Wilke 1997). In stands managed with increased tree retention and without salvage cutting, the total amount of dead wood may increase to 10–30 m^3 ha^{-1}, including a much higher proportion of coarse logs and natural high stumps (Winter and Möller 2008, Brunet and Isacsson 2009b, Kappes et al. 2009).

Herbaceous plants

General patterns

The herbaceous layer of beech forests is characterized by a pronounced seasonal variation where the flower carpet of spring geophytes (e.g. *Anemone* spp., *Corydalis* spp., *Gagea* spp.) is followed by a summer vegetation of shade-tolerant ferns, herbs and grasses. In canopy gaps, light demanding herbs and grasses are periodically favoured (Gálhidy et al. 2006, Hahn and Thomsen 2007, Naaf and Wulf 2007).

The species composition of the herbaceous layer in beech forests is strongly affected by soil pH, nutrient status and light conditions (Falkengren-Grerup and Tyler 1991, Brunet et al. 1996, Graae and Heskjaer 1997, Aude and Lawesson 1998, Härdtle et al. 2003, 2005). Species number generally increases with soil pH, whereas the positive effect of increasing light flux on species number is stronger on acid soils than on basic soils (Härdtle et al. 2003, 2005, Gálhidy et al. 2006). An admixture of other tree species has a favourable influence on humus quality and herb species richness (Godefroid et al. 2005a).

Effects of forest management

Most spring geophytes and shade-tolerant summer species are relatively tolerant to both selection harvest and shelterwood management in the long term (Falkengren-Grerup and Tyler 1991, Brunet et al. 1996, Schmidt 1997, von Oheimb and Härdtle 2009). Heavy regeneration cutting or clear-cutting has however, a negative effect on many shade-tolerant beech forest species, e.g. *Anemone nemorosa*, *Galium odoratum*, *Lamiastrum galeobdolon* and *Oxalis acetosella* (Brunet et al. 1996, Godefroid et al. 2005b, 2006). In addition, mechanized timber harvest leads to long-term

Table 2. Structural attributes (modified from Bauhus et al. 2009) of old-growth beech forests in comparison with selectively harvested stands (single tree and group cut) and shelterwood stands (both without tree retention). ++: frequent, +: less frequent, –: absent. An overall estimate of the value for biodiversity of each structural attribute according to the studies reviewed is also given. ++: very important, +: important, 0: less important.

Structure	Old-growth	Selective harvest	Shelterwood	Biodiversity
Several canopy layers	++	++	–	+
High variation of tree sizes	++	++	–	+
High spatial heterogeneity	++	++	–	+
Presence of advanced regeneration	++	++	–	0
Wide decay class distribution of CWD	++	++	–	++
Large number of big trees	++	+	+	+
High stand volume	++	+	+	0
Large number of trees older than 150 yr	++	+	–	++
Large number of snags (high stumps)	++	–	–	++
Large amount of fallen CWD	++	–	–	++
Diverse stem, branch and crown structures in living trees	++	–	–	++

soil compaction, which affects a large proportion of the herb layer species (Godefroid and Koedam 2004).

Old-growth beech forests are characterized by a fine-grained structure in the herb layer with small species-rich patches. In shelterwood stands the herbaceous plants often occur in larger patches dominated by a single species. These differences are probably related to more heterogeneous light conditions as a result of a multi-layered canopy and the presence of natural gaps in the old-growth forest (Standovár et al. 2006). Due to higher light availability in summer, the relative abundance of late flowering summer species may be higher in single-layered spacious shelterwood stands when compared to multi-layered natural beech forests (Kenderes and Standovár 2003).

The effects of shelterwood management on the herb layer structure persist for a long time in stands even where management has ceased. Differences between managed stands and most beech forest reserves are therefore, still relatively small, especially in central and northwestern Europe (Graae and Heskjaer 1997, Graae and Sunde 2000).

Herb layer composition and abundance change with stand age in shelterwood forests (Aude and Lawesson 1998, Godefroid et al. 2005a). Old stands with a closed canopy provide a relatively stable habitat and host vascular plant communities characterised by shade-tolerant species. This is also the successional stage where niche partitioning and equilibrium mechanisms are most likely to be of importance. Young plantations and old stands with an open canopy prior to final regeneration are characterised by the temporary coexistence of early-successional and late-successional species (Aubert et al. 2003). Overall species number is highest in old stands with relatively open canopies and lowest where there is dense regeneration.

Epiphytic lichens and bryophytes

General patterns

Beech forests on acid soils are often poor in herbaceous vascular plants, but may contain species-rich communities of lichens and bryophytes. The physical and chemical characteristics of the beech bark changes with increasing age and size of the tree. Tree age and trunk diameter are therefore, strongly correlated with the epiphytic composition (Gustafsson et al. 1992, Aude and Poulsen 2000, Friedel et al. 2006, Fritz et al. 2009a, b). Most pioneer species that grow on the smooth bark of young trees persist with increasing tree age as such patches are also available on old beech stems. Total species number therefore, steadily increases with tree age. Many substrate specialists require beech trees older than 180 yr because the suitable substrates, such as rough bark and rot holes only develop at high tree age, often on slow-growing and suppressed stems (e.g. the lichens *Lobaria pulmonaria*, *Pachyphiale carneola*, *Thelopsis rubella*; Fritz et al. 2009a, b). The rough bark near rot holes often has a high pH and nutrient availability, probably due to leakage from base rich wood mould in the rot holes (Fritz and Heilmann-Clausen 2010). These microhabitats are of great importance for many epiphytes of conservation concern (e.g. the lichens *Bacidia incompta*, *Bacidina phacodes*, *Biatoridium monasteriense*), in particular in beech forests on acid soils.

Effects of forest management

Comparisons between beech forests managed with shelterwood systems and unmanaged stands show that there is a lower total number of species and/or fewer specialist species of epiphytes in the managed forests (Aude and Poulsen 2000, Friedel et al. 2006, Nascimbene et al. 2007). Recent studies show that it is mainly trees older than ca 180 yr that provide habitat for rich assemblages of epiphytes in European beech forests. Species adapted to old-growth habitats are therefore absent in even-aged shelterwood beech forests with rotation periods between 90 and 140 yr (Bardat and Aubert 2007, Fritz et al. 2008, 2009a, b, Fritz 2009, Moning and Müller 2009).

As they are poikilohydrous organisms, lichens and bryophytes are favoured by high humidity and may suffer from the abrupt exposure to sunlight (Bardat and Aubert 2007). Both old-growth stands and multi-layered stands managed by selective harvest have a more humid and stable micro-climate than shelterwood beech forests. Accordingly, selectively harvested beech forests contain sub-oceanic epiphytic lichen species which are absent from shelterwood stands. The latter may instead be characterized by common generalist lichen species (Nascimbene et al. 2007).

Epixylic bryophytes

General patterns

There is a pronounced effect of decay stage of dead wood on bryophyte species composition. During the early stages of decay, epiphytic bryophytes are still most abundant. Well-decayed logs are dominated by epixylic species or opportunistic bryophytes. True epixylic liverworts (e.g. *Cephalozia catenulata*, *Nowellia curvifolia*, *Riccardia latifrons*) occur almost exclusively in old-growth forest with high amounts of CWD (Ódor et al. 2005, 2006). Substrate requirements interact with micro-climate to some extent. At sites with a drier micro-climate, larger logs are needed to provide suitable moisture conditions (Ódor and van Hees 2004).

Effects of forest management

Lower species diversity of epixylic bryophytes in managed stands can be explained by differences in the amount and quality of dead wood, which is less abundant and heterogeneous in managed stands (Aude and Lawesson 1998, Ódor and Standovár 2001, Standovár et al. 2006). True epixylic species occur mainly on large and well-decayed logs and are particularly disfavoured by forest management (Ódor and Standovár 2001, Standovár et al. 2006).

Soil macrofungi

General patterns

Mycorrhiza fungi and litter decomposing fungi are ecologically important groups in temperate forests, but pattern of species composition and diversity are difficult to study. The composition of soil fungi in beech forests changes along gradients of soil acidity and organic matter properties (Tyler 1985). Among the soil variables studied, organic matter content and base saturation are most important in explaining distribution patterns of the more frequent species. Base rich mull soils are characterized by decomposer fungi, and the frequency of mycorrhiza species increases sharply towards the most acid mor (raw humus) soils (Tyler 1985).

Effects of forest management

The sensitivity of soil macrofungi to different management systems is largely unknown. Di Marino et al. (2009) studied the composition and the structure of the ectomycorrhizal community in coppice beech woods of northern Italy. Species composition changed with slope and soil moisture but was uncorrelated with the time since the last cut, which indicates a stable mycorrhiza community during the coppice cycle.

Saproxylic fungi

General patterns

Dead wood volume and variability (length, surface area, decay stage of logs, number of forks and fractures) are key variables for explaining species number of saproxylic fungi (Heilmann-Clausen and Christensen 2003, 2004). Species number peaks in logs of intermediate decay stages, which indicates a maximum in the number of available niches during this stage of wood decay. Soil humidity and microclimatic conditions also seem to influence species number of saproxylic fungi.

Red-listed species seem to prefer more decayed trees than non red-listed species (Heilmann-Clausen and Christensen 2005). While species of conservation concern are positively correlated to maximum tree age, species number in general may be negatively associated with old-growth characteristics such as high tree age or log size, possibly due to a higher competitiveness of certain species or niche specialists as the fungal communities mature (Heilmann-Clausen and Christensen 2005).

Some heart-rot agents seem to have a preference for large trees but in general few species show a preference for a specific tree size (Heilmann-Clausen and Christensen 2004). Most species that do are associated with logs broken at the stem base and several are known to cause butt rot, e.g. *Ischnoderma resinosum*. Species of conservation concern in general, also have a preference for this type of log compared to uprooted trees or snags (Heilmann-Clausen and Christensen 2003).

Effects of forest management

Saproxylic fungi are strongly affected by the reduction of dead wood in managed beech forests. Intensively managed stands show a tendency towards lower species number compared to slightly thinned stands without salvage logging and strict forest reserves (Müller et al. 2007a, b). There are also clear differences in species composition and relative frequency between these three silvicultural treatments. Different fungal indicator species can be identified for each silvicultural treatment. The occurrence of indicator species of naturalness increased significantly when the total amount of dead wood exceeded ca 60 m^3 ha^{-1}. Trees colonized by tinder bracket fungus *Fomes fomentarius*, a common and important precursor for other species groups in natural forests, are usually removed in intensively managed stands (Müller et al. 2007a).

In a comparative study with data from five European countries, tree size and decay stage were confirmed as important factors for explaining species number per tree (Ódor et al. 2006). A high abundance of species of conservation concern in Hungary and Slovenia may reflect a higher degree of naturalness of the forest landscape in combination with a continental climate, factors that are believed to grant stress tolerant species such as the rare heart rot former *Ischnoderma resinosum* a competitive advantage. The forest landscapes in Belgium or the Netherlands have been highly influenced by intensive shelterwood forestry, which increases the fraction of freshly cut, small diameter dead wood, available for colonization by fungi with fast growth and rapid propagation (Ódor et al. 2006).

The development of pasture landscapes rich in old open grown oaks and beech trees in parts of northwestern Europe may have generated favourable habitats for several rare heart rot formers. Nowadays remnants of these habitats are often found in forest edges or in park-like forests, which may explain the occurrence of these species in the forests studied in Denmark (Ódor et al. 2006).

Land snails

General patterns

Land snails need calcium to build up their shells. Beech forests on calcium-rich soils therefore have a richer snail fauna than beech forests on acid soils, both in terms of species and individuals. Liming of acidified beech forest soils increased the mean snail densities by 4–40 times five years after liming, depending on the species (Gärdenfors 1992). There were highly significant correlations between snail density, pH and Ca concentration. The results indicate that liming positively affects land snail population densities in relatively nutrient-poor beech forests.

Concerning the small-scale distribution patterns of gastropods, more snail individuals and species occur at sites close to CWD compared to sites distant from CWD (Kappes 2005, Kappes et al. 2006). This pattern is explained by higher soil pH, base saturation and amounts of leaf litter at sites with CWD (Müller et al. 2005, Kappes et al. 2007). CWD also helps to maintain a moist micro-climate and provides favourable foraging habitat and refuges from predators (Kappes 2005, Kappes et al. 2006).

Stand climate also affects snail assemblages and moist north-facing slopes contain more snails than dry south-facing exposed slopes. A comparison between the variables CWD and slope aspect reveals that the influences of these two factors on snail abundance are of similar importance (Kappes et al. 2006). Species number and species densities of slugs were also positively affected by the presence of CWD. Slug densities are especially favoured by CWD on otherwise dry and sun-exposed sites (Kappes 2006).

Effects of forest management

Comparative studies of intensively managed beech forest, slightly thinned stands without salvage logging and strict forest reserves revealed that the abundance of dead wood, especially in late stages of decay, was an important factor for species number and snail density, probably due to its positive influence on base cation availability and microclimate stability (Müller et al. 2005, Kappes et al. 2009).

Snail abundance and species number increased with stand age and the amount of dead wood. Threshold values of 20–50 m^3 ha^{-1} CWD have been suggested for maintaining the snail fauna living on the dead wood itself, e.g. species of the Clausiliidae such as *Balea biplicata* and *Macrogastra ventricosa* (Müller et al. 2005, Kappes et al. 2009).

Furthermore, species richness of molluscs increases with stand age. Moning and Müller (2009) calculated a threshold of ca 170–190 yr beyond which species richness increased significantly. The positive effect of high stand age might be related to increased amounts of CWD and a higher habitat quality of the tree bark (e.g. rough bark with cracks).

Saproxylic beetles

General patterns

The fauna of old-growth beech forests may contain > 300 species of saproxylic beetles (Nilsson et al. 2001). The composition of this fauna is closely related to the decay stage of the dead wood. Total species number is usually highest at an intermediate stage of wood decay (Brunet and Isacsson 2009a).

Studies with emergence traps demonstrate that both fallen and standing dead wood of varying dimensions are necessary to maintain the saproxylic beetle fauna in beech forests. Branches with 5–20 cm diameter contain many species not present in larger dimensions, and vice versa (Kleinevoss et al. 1996, Harz and Topp 1999, Schiegg 2001, Kappes and Topp 2004). Larger dimensions (>40 cm diameter) are preferred by a specialized fauna of species developing in snags (e.g. *Anoplodera scutellata*, *Dorcus parallelepipedus*), logs (e.g. *Denticollis rubens*) and rot holes (e.g. *Quedius truncicola*) (Nilsson and Baranowski 1997, Brunet and Isacsson 2009a).

The amount and connectivity of dead wood seems to influence the distribution of certain species within a radius of 150–300 m around insect traps (Schiegg 2000a, b, Brunet and Isacsson 2009b), but probably not at a smaller spatial scale (Winter and Möller 2008).

Total species number may not differ between areas with long continuity of dead wood and areas with recent accumulation of CWD. Hollow trees and snags however, often contain less red-listed species in the latter areas. The absence of red-listed species thus seems to be related to low dispersal ability (Nilsson and Baranowski 1997, Brunet and Isacsson 2009b).

Effects of forest management

Müller et al. (2007b, 2008) compared saproxylic beetle assemblages in intensively managed beech forests, slightly thinned stands without salvage logging and strict reserves in southern Germany. Community structure changed along the gradient from unmanaged to high-intensity management. Strict reserves (>100 m^3 ha^{-1} CWD) and slightly thinned stands (ca 40 m^3 ha^{-1} CWD) had more threatened species than more intensively managed stands (which however, also contained ca 20 m^3 ha^{-1} CWD as a result of recently introduced retention measures). Overall species richness as well as the number of click beetles (Elateridae) and of red-listed species increased with the amount of dead wood. The number of flowering plant species relevant for saproxylic species (e.g. *Rubus* spp., *Sambucus* spp., *Sorbus* spp., *Urtica dioica*) had a positive effect on the number of longhorn beetles (Cerambycidae). There was also a positive relationship between the number of saproxylic fungi species and species numbers of Staphylinidae and Melandryidae. The different significant variables, depending on the family under focus, indicated that a range of different substrate qualities were important. Focusing on overall species richness, the total amount of dead wood and rich saproxylic fungi assemblages were the most powerful predictors for species richness. The authors conclude that the amount of certain habitats in the sampling plots is a better predictor for species richness than management intensity in general.

Similarly, no general differences in species richness were found between comparable dead wood substrates in adjacent unmanaged and managed stands in a study from southern Sweden (Brunet and Isacsson 2009a). This indicates that most species disperse easily within contiguous forest areas and search for suitable habitat. The total amount of habitat in a non-fragmented forest area is therefore more important for species diversity than the spatial distribution of this habitat.

In severely fragmented beech forests however, red-listed species in particular are not able to colonize when target areas are isolated from each other by several kilometres of unsuitable habitat, e.g. coniferous plantations (Brunet and Isacsson 2009b). These results suggest that red-listed species generally have a lower dispersal capacity than other saproxylic species. Retention of dead wood close to existing populations is thus more beneficial for saproxylic beetle species of conservation concern than an even distribution across the forest landscape.

Saproxylic flies

General patterns

Hövemeyer and Schauermann (2003) used emergence traps to follow the succession of saproxylic flies on branch wood of beech for ten years. Species richness reached a maximum in well decayed logs, suggesting that dead wood becomes a more valuable food resource in a later phase of decomposition for flies than for beetles. Species richness also increased with water content and moss cover and was negatively correlated with bark cover and wood density.

Effects of forest management

Fayt et al. (2006) found a positive effect of the amount of dead wood on species number of saproxylic hoverflies (Syrphidae) in Belgian oak and beech forests. High hoverfly richness was also associated with open stands containing large beech trees and a rich flowering herb layer required for reproduction.

Ground dwelling arthropods

General patterns

Coarse woody debris on the forest floor such as logs and stumps offers sheltered micro-habitats, food sources and breeding sites for ground dwelling arthropods. Jabin et al. (2004) studied the arthropod fauna close to and far from logs in a beech-oak forest in western Germany. The presence of CWD generally enhanced the density of macro-arthropods, including zoophagous, saprophagous and mycetophagous species. This effect was especially pronounced in forest edge habitats.

Topp et al. (2006a) found a similar gradient in species number and abundance of litter-dwelling beetles in old-growth beech forests in Slovakia. Mycetophagous and zoophagous beetles were especially favoured close to CWD but not phytophagous species.

In the same forests, an increase of the total number of species and individuals of woodlice (Isopoda), centipedes (Chilopoda) and millipedes (Diplopoda) occurred adjacent to coarse woody debris (Topp et al. 2006b, Jabin et al. 2007). This correlation is more pronounced on southern slopes, characterized by high temperatures and low precipitation, than on the northern slopes, characterized by low temperatures and high precipitation (Jabin et al. 2007).

Soil chemical gradients influence the composition of the herb layer which in turn affects the faunal composition. Ground beetle (Carabidae) assemblages differ between beech forest on podzol and cambisol (Tyler 2008). Almost twice as many species are found on the cambisol sites, but the total number of individuals is similar in both forest types. Gradients in litter properties and ground vegetation between podzol and cambisol sites probably cause differences in microclimate and food sources which influence ground beetle composition (Tyler 2008).

Effects of forest management

Theenhaus and Schaefer (1995) compared the soil macrofauna of artificial gaps (30 m in diameter) and the adjacent closed canopy stand. There was no clear treatment effect on most mycetophagous, necrophagous and zoophagous Diptera. Some groups of humiphagous Diptera increased in the gaps, probably favoured by an increase in soil moisture. Total density of beetles (Coleoptera) decreased in the gaps, mainly due to a decrease in Staphylinidae, Curculionidae and larvae of *Athous subfuscus* (Elateridae).

Carabid beetle richness was negatively affected by the recent impact of logging in beech forests of northwestern Germany (Sroka and Finch 2006). High soil moisture had a positive effect on the diversity of ground beetles in that study.

Hole nesting birds

General patterns

Species richness of forest birds increases with stand age in southern German beech forests (Steigerwald, Bavarian forest, Moning and Müller 2009). Slight thresholds of stand age could be identified below which species richness dropped significantly. Species richness of hole nesting birds show somewhat higher thresholds of stand age than the richness of bird species in general (120 vs 90 yr in the Steigerwald; 205 vs 180 yr in the Bavarian forest). Between-site variation is large, indicating that several other factors than stand age influence bird diversity (Moning and Müller 2009).

Effects of forest management

Bird species richness in general is not affected by management intensity in the Steigerwald beech forests, but management has a negative effect on the richness of hole nesting species (Müller et al. 2007b). Similarly, a comparison of the bird fauna in an old-growth reserve in Slovenia with an adjacent slightly managed forest resulted in more hole nesting bird species, more species feeding on and under bark, more wood pigeons and more other rare and endangered species in the old-growth forest remnant (Boncina 2000). These differences are probably explained by much higher amounts of CWD and large trees in the old-growth forest. Positive effects of standing dead wood on species richness start to appear even in relatively young forests. A comparison of 30–50 yr old managed and unmanaged beech stands shows that in particular some tits and the short-toed treecreeper *Certhia brachydactyla* are favoured by the higher number of snags in the unmanaged stands (Laiolo et al. 2004).

Several other studies show the dependence of certain hole nesting birds and woodpeckers on old and dead trees in beech forests (collared flycatcher *Ficedula albicollis*: Sachslehner 1995, white-backed woodpecker *Dendrocopos leucotos*, black woodpecker *Dryocopus martius*: Fernandez and Azkona 1996, greater spotted woodpecker *Picoides major*, middle spotted woodpecker *Picoides medius*, nuthatch *Sitta europaea*: Hertel 2003, white-backed woodpecker: Melletti and Penteriani 2003, middle-spotted woodpecker: Südbeck and Flade 2004).

Implications for forest management

The results of this review demonstrate that beech forests managed with traditional shelterwood systems are of relatively low value for the conservation of most species groups (Table 3). Only forest herbs, and probably soil fungi, are generally rather tolerant to this management system. Significant tree retention resulting in more than 20 m^3 ha^{-1} CWD will improve the situation considerably for saproxylic species and species which use CWD for shelter and foraging (Table 3). Selectively harvested beech forests provide generally a more suitable habitat for epiphytic species by maintaining a stable micro-climate. The most demanding epiphytes however, need a substantial amount of slow-growing retention trees. It is probably only the selectively harvested stands with many retention trees that approach the overall biodiversity of old-growth beech forests (Table 3).

Restoration measures to promote structural features of old-growth beech forests in managed stands should not

Table 3. Habitat value of different management systems for species groups in European beech forests, based on the studies reviewed. ++: high, +: moderate, –: low.

Species group	Shelterwood	Shelterwood with tree retention	Selective harvest	Selective harvest with tree retention
Herbaceous plants	++	++	++	++
Ground arthropods	+	++	+	++
Land snails	–	+	+	++
Saproxylic fungi	–	+	+	++
Saproxylic beetles	–	++	+	++
Hole nesting birds	–	+	+	++
Saproxylic flies	–	+	+	++
Epiphytic bryophytes	–	–	+	++
Epiphytic lichens	–	–	+	++
Epixylic bryophytes	–	–	–	++

only include tree retention measures and accumulation of CWD, but also the maintenance of natural soil characteristics, in particular small-scale heterogeneity in soil moisture (Table 4).

Maintenance of suitable soil conditions

Soil chemical conditions have a direct influence on litter properties and on the species composition of the moss, herb and shrub layer as well as on the composition of soil macrofungi. These changes influence again the composition of the soil fauna, e.g. arthropods and molluscs. The composition of the woody vegetation exerts in turn a certain influence on soil chemistry, and in particular on litter properties. An admixture of other broadleaved trees with litter which decomposes easily decreases top soil acidity in beech forests, which has positive effects on the soil fauna and ground vegetation (Godefroid et al. 2005a).

It is also evident from the studies available that the presence of CWD has a similar effect and enhances soil microbial biomass and the density of detritivores. Consequently, coarse woody debris influences nutrient fluxes and decreases the acidification by its function as a long-term store of base cations (Kappes et al. 2007).

Beech forests usually grow on well-drained soils, but especially in lowland beech forests, moist depressions and hollows are rather common. This small-scale topographical variation has a positive effect on most species groups associated with the forest floor by increasing habitat diversity in general and soil pH in particular. Moist sites also contribute to maintaining a suitable micro-climate for epiphytic lichens and bryophytes. In conclusion, any addition of other broadleaved trees and of dead wood as well as the maintenance of a natural hydrology increases species diversity and improves the nutritional soil status in managed beech forests (Table 4, 5).

Retention of old trees

Epiphytic and epixylic species are probably the most sensitive out of the species groups reviewed to a change from natural gap dynamics to shelterwood forestry (Table 3). The studies reviewed show that the rotation periods in shelterwood systems (90–140 yr) are too short for many late successional epiphytes that require bark substrates on trees older than ca 180 yr (Fritz et al. 2009b). In addition, many epiphytes on beech are favoured by high humidity and will suffer from the much drier micro-climate after large-scale logging. Dispersed retention trees are therefore, of relatively low value for epiphytic species in logged stands (Bardat and Aubert 2007).

The results indicate that a combination of conventional shelterwood beech forestry and conservation of epiphytic lichens and bryophytes is not possible at stand level. A spatial separation of the beech stands in production units and set aside areas for sensitive and substrate demanding epiphytes is probably the only possible option in areas where shelterwood systems dominate. These set aside areas should contain trees of mixed ages, preferably in sheltered humid sites.

The structure and micro-climate of multilayered beech forests managed with single stem or group harvest is more similar to natural beech forests with gap dynamics. Retention trees for epiphytes in such forests are probably much more valuable in the long term than in shelterwood stands (Table 3). In addition to the bark, living trees can have many other different micro-habitats that are used by saproxylic

Table 4. Structural features of old-growth beech forests and restoration measures to promote these in selection harvest systems and in shelterwood stands (modified from Bauhus et al. 2009).

Desired feature	Measure in shelterwood stands	Measure in selectively harvested stands
Natural soil characteristics	Fill drainage ditches Compensate harvest loss of base cations Increase CWD	Fill drainage ditches Compensate harvest loss of base cations Increase CWD
Late successional herbaceous vegetation	Retention of uncut areas	Already present
Vertical canopy stratification	Tree retention Reduce stand size	Already present
Large trees	Crown thinning to release trees Tree retention, especially in stand margins	Crown thinning to release trees Tree retention, especially in stand margins
Snags and high stumps and fallen CWD (logs)	Tree retention Self thinning No salvage following stem breakage/uprooting	Tree retention Self thinning No salvage following stem breakage/uprooting
Fallen CWD	Lower utilization standards	Lower utilization standards
Microhabitats in living trees	Longer rotation Tree retention	Larger target diameter Retention of old subcanopy trees

species and by other species using stem cavities (mammals, in particular bats, birds). Old-growth beech forests contain a higher number and diversity of such habitat trees (Winter and Möller 2008). This is because the diverse stem, branch and crown structures from which micro-habitats may originate are common in old-growth forest but these trees are usually removed in managed stands.

Increased tree retention in shelterwood and selective harvest systems should focus on these economically less valuable but biologically richer trees. In particular, different kinds of stand margins are suitable for retaining habitat trees. In these margins, veteran beech trees with wide crowns may develop micro-habitats for, e.g. several specialist saproxylic fungi and beetles.

Management of dead wood

Retention trees in stand margins or in open stands after regeneration logging eventually result in sun-exposed CWD. In old stands, there is also sun-exposed dead wood in the tree canopy that may harbour many thermophilous saproxylic species (Bußler et al. 2004). It may be more challenging to obtain a continuous supply of dead wood in shaded and moist conditions. Set aside areas are usually required to keep a suitable moist microclimate. Sites along water bodies or on northern slopes are especially suitable and will also favour moisture demanding epiphytes and fungi.

Wind thrown trees contain a high volume and a large diversity of CWD, especially of sun-exposed wood (Bouget and Duelli 2004). They thus provide a valuable habitat for saproxylic beetle species. The risk of bark beetle outbreaks damaging the standing forest is much lower in beech forests than in spruce stands (Harz and Topp 1999). Some wind thrown trees should therefore be retained in managed stands (Table 4, 5).The review shows that any retention of dead wood is valuable for saproxylic species, but species assemblages differ between snags, logs, limbs and branches, and entire trees should be retained in the forests (Heilmann-Clausen and Christensen 2004). From the results of this review, it is clear that a more intensive use of branches and tree tops for biofuel will seriously reduce the diversity of species using fallen dead wood in managed beech forests (Kappes 2006, Kappes et al. 2009).

Reservation, retention or restoration?

The species groups reviewed show general differences in habitat requirements and are therefore in need of a variety of conservation and restoration measures (Table 5). The review indicates that the area of unmanaged reserves for biodiversity needs to be larger in regions where shelterwood systems dominate than in regions with predominantly selective harvest systems (cf. Table 2–5). Substantial tree retention will particularly favour saproxylic insects in shelterwoods and epiphytes in selectively harvested forests. The most demanding saproxylic and epixylic species however, need the amounts and qualities of CWD found in old-growth beech forests, and tree retention in managed stands cannot replace the function of strict reserves.

Table 5. Species groups reviewed in European beech forests, important environmental factors and focal habitats for species of conservation concern within these groups, and restoration measures that will favour biodiversity in managed stands.

Species group	Environmental factors	Focal habitat for species of conservation concern	Restoration measures
Herbaceous plants	Soil pH, soil moisture, litter properties	Base rich forest soil	Restore natural hydrology Increase tree species diversity
Soil macrofungi	Soil pH, soil moisture, litter properties	Base rich forest soil	Restore natural hydrology Increase tree species diversity
Ground arthropods	CWD and litter properties, soil moisture	Moist forest soil, fallen CWD	Increase amount and variability of CWD Restore natural hydrology
Land snails	Soil pH, soil moisture, CWD properties	Base rich moist forest soil, fallen CWD, old trees	Restore natural hydrology Increase tree species diversity and amount of CWD
Saproxylic fungi	Dead wood properties	Old senescent trees, snags, fallen CWD	Increase amount and variability of CWD
Saproxylic beetles and flies	CWD properties, micro-climate	Old senescent trees, snags, fallen CWD	Increase amount and variability of CWD and of old trees Increase amount of flowering shrubs and herbs
Hole nesting birds	Tree age, CWD properties	Old trees, hole trees, snags	Increase harvest age Increase amount and variability of hole trees, snags and CWD
Epiphytic bryophytes	Tree age, bark pH, humidity	Forest stands with old senescent trees	Increase harvest age and apply selective harvest Retain slow-growing and damaged subcanopy trees
Epiphytic lichens	Tree age, bark pH, humidity	Forest stands with old senescent trees	Increase harvest age and apply selective harvest Retain slow-growing and damaged subcanopy trees
Epixylic bryophytes	CWD properties, humidity	Fallen CWD	Increase amount of CWD Restore natural hydrology

Protected stands older than 150 yr can relatively quickly accumulate high amounts of CWD (Vandekerkhove et al. 2005, von Oheimb et al. 2007), but restoration of multi-aged and multi-layered forests from even-aged shelterwood stands is a very long process and may require active management in reserves by means of gap creation and reduction of browsing pressure. Active management may also be necessary in reserves to secure the persistence of admixed tree species with high qualities for biodiversity, in particular *Quercus* spp. (e.g. crown thinning, enlargement of canopy gaps for oak regeneration).

Future research

Our review shows that we now have relatively firm knowledge regarding the most important habitat qualities on which major species groups depend on in European beech forests. More studies are however needed to understand the effects of forest management on several important species groups, in particular soil fungi and the large insect groups of Hymenoptera and Diptera which contain many saproxylic and cavity living species (Sobek et al. 2009).

The next step is to predict how biodiversity is affected by changes in the quantity and spatial distribution of the focal habitats (Bailey 2007). There has been some progress in the determination of critical thresholds of habitat availability. These extinction thresholds are species specific, with strong spatial and temporal components (Ranius and Fahrig 2006). Species number therefore increases more or less continuously with the amount of habitat, and does not show distinct threshold levels (Ranius and Fahrig 2006). Defining targets of dead wood or tree age may still however, be of ecological significance and of importance in practical conservation (Müller et al. 2005, 2007b, Fritz et al. 2009b, Kappes et al. 2009, Moning and Müller 2009).

So far, the studies available on thresholds indicate that only beech forests with trees that are at least 180 yr old and that have accumulated volumes of 20 m^3 ha^{-1} CWD or more contain rich assemblages of specialized epiphytic and saproxylic species. There is no doubt that such forests will have a patchy distribution even in a long-term perspective, due to the fact that the majority of the European beech forests will be used for wood production. More knowledge on how beech forest species disperse between patches of suitable habitat (often across a hostile matrix) is therefore necessary (Ranius 2006). Finally, new insights on critical thresholds for biodiversity need to be applied in the context of multiple-use forestry to optimize the effects of conservation measures in relation to other forest values (Boman et al. 2010).

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