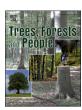
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Management and biodiversity conservation in Central European forests[☆]

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ABSTRACT

Active forest management and maintenance or restoration of biodiversity are intertwined. We describe several Central European forest types through typical management cycles and identify synergies and trade-offs with biodiversity conservation. Synergies emerge when the maintenance of forest structures supporting recognized human needs for biomass production create diverse habitats. On the stand level, relevant are tending interventions during stand development, the length of the production cycle, and the choice of tree species. Thinning promotes forest productivity, enhances structural heterogeneity, and the habitat diversity for many species groups. The vertical and horizontal diversity on the stand level is high in uneven-aged multi-species forests. The choice of the rotation period is controversial, because no balance between forest productivity, stand stability, and habitat quality is yet negotiated. On the landscape level heterogeneity arises when many actors implement a range of silvicultural concepts and management intensities. Deadwood of different dimensions provides multiple habitats and enhances biodiversity, but causes challenges for forest protection in some forest types. A possible compromise is setting aside unmanaged interconnected units with veteran trees (stepping-stone habitats). Damage caused by wildlife is an un-resolved issue in Central European forests. High ungulate populations are reducing the potentially emerging diversity of tree species by selective browsing. A controversial topic is the introduction of non-native tree species, potentially filling in where native tree species cannot cope with expected future site conditions. Their introduction may lead into uncharted territory with respect to biotic threats. In conclusion, the knowledge-based discourse between nature conservation and forest management needs to be continued to further develop the successful concept of multiple-use forestry.

1. Introduction

Central European forests host a wide diversity of flora and fauna that support vital ecological processes underlying the delivery of ecosystem functions and services (FOREST EUROPE, 2020). Biodiversity is fostered by habitat features such as dead wood and nutrients and the interactions among living elements of the forest ecosystem. Forests connect fragmented ecosystems, and support genetic diversity and migration of species (Brockerhoff et al., 2017; Liang et al., 2016; Stokland et al., 2012).

Amid the current biodiversity crisis and the adverse effects of climate change, all forms of land management are under scrutiny. Forestry, in particular, must critically assess its impact on biodiversity. In response,

multipurpose forest management aims to enhance biodiversity considerations in an economically beneficial way. However, the classical view of multipurpose forest management is no longer universally embraced (Tiebel et al., 2021). A strongly opinionated and dichotomous discourse on forest management versus nature conservation has developed, insufficiently reflecting win-win situations (Betts et al., 2021).

Deforestation, overexploitation of lannd, large wildlife populations, and climate change are drivers of global biodiversity loss and are threatening many species. Protection areas and restoration activities are needed where forests are unsustainably managed (Bastin et al., 2019; Harrison et al., 2022; Hochkirch et al., 2023; Stanturf et al., 2014). We focus explicitly on Central Europe, where forests are predominantly semi-natural and tree species diversity and the amount of deadwood are

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increasing since at least 2005. Forest harvest rates are since several decades below forest growth rates and are rated 'sustainable' (FOREST EUROPE, 2020).

For centuries European forests were removed to provide space for agriculture, and timber was often in short supply. Sustainability principles were introduced to cope with imminent forest degradation (von Carlowitz, 1713). During the 18th and 19th century, Central Europe witnessed a substantial reduction in forest coverage attributed to extensive logging and grazing, to satisfy the food and energy demand of a growing population. Only few unmanaged stands have outlasted history (Dieler et al., 2017; Frank and Müller, 2003). Forest degradation diminished protection against natural hazards. In response, many countries implemented Forest Acts and anchored forestry in Higher Education. A skilled multipurpose forestry provided ecosystem services including protection against natural hazards (Daily et al., 1997; FOREST EUROPE, 2020; Teich et al., 2022). Since decades the area and the biomass stocks of Central European forests are growing (UNECE and FAO, 2019).

The appropriation of land for human needs such as biomass production exerts a considerable pressure on flora and fauna. Forest management practices across Central Europe significantly shape forest biodiversity. Forests harbor a large share of terrestrial biodiversity, and sustainably managed forests often are habitats of high ecological value or endangered species (Muys et al., 2022). In Austria approximately 50% of the protected areas are sustainably managed forests. Additionally, the Natura 2000 network includes sustainably managed forest sites to protect species of European conservation interest (Alberdi et al., 2019).

The impact of forest management on biodiversity was analysed with models, meta-analyses, and field research (e.g. Ammer et al., 2017; Asbeck et al., 2021; Biber et al., 2020; Burrascano et al., 2023; Dieler et al., 2017; Hilmers et al., 2018; Schall et al., 2020). Adverse effects of management practices have been found for several taxonomic groups, and managing forests as even-aged single-species stands threatens biodiversity (Aszalós et al., 2022; Tomao et al., 2020). There is a need for a better understanding of the site-specific impacts of forestry practices on species richness, communities, and species migration under climate change and other threats to biodiversity. Improving this knowledge could enhance future planning of conservation and forest management measures, supporting their synergies (Soto-Navarro et al., 2020). A Europe-wide harmonized forest biodiversity assessment with thresholds and target ranges for different European forest types and a focus on functional indicator groups is required (Oettel and Lapin, 2021; Paillet et al., 2010).

In this study, we aim to highlight the critical elements that need to be resolved. We exemplarily describe several Central European forest types and evaluate the impact of silvicultural practices at the stand level on biodiversity. A case-study driven assessment facilitates the dialogue on improving biodiversity conservation in managed forests. We recognize the high ecological value of unmanaged pristine forests patches, but we focus on managed forests to address relevant conservation challenges. We aim to identify the weaknesses and strengths of multipurpose forestry practices to strengthen synergies and pinpoint knowledge gaps that need to be addressed in the future.

2. Case studies for the impact of forest management on biodiversity

We describe forest management at the stand level, and the findings can be aggregated on a larger spatial scale. We describe both synergies and tradeoffs between forest management and biodiversity conservation, accepting that not in all cases diverging interests can be reconciled. We include the response to hypothetical disturbances, for situations that are commonly encountered in forestry. Bark beetle attacks are discussed in the context of Norway spruce (*Picea abies* (L.) H.Karst.) forests. European beech (*Fagus sylvatica* L.) and Norway spruce forests represent

the dominant deciduous and conifer forests, Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands for the use of non-native trees, and floodplain forests represent highly dynamic and diverse forests that are managed in short rotation (Fig. 1).

Disturbances are an integral part of forest dynamics with a strong impact on economy and biodiversity. Disturbances due to wildlife (Fig. 2 a); are technically easier to control than the consequences of extreme events, that are increasingly linked to climate change (Fig. 2 b, c, d). Active management can increase the resilience of forests against disturbances and can to some extent control the economical impact (Seidl et al., 2017; Vanomsen, 2006).

2.1. European beech forests in the submontane zone

At low elevation, beech forests are embedded in the agricultural landscape that historically have satisfied the regional timber and energy demand. Nowadays, beech forests are often extensively managed. Beech timber is a mass product and high qualities are not awarded by market prices. The timber industry is increasingly developing technologies for beech in constructive elements and furniture (Pramreiter and Grabner, 2023).

On spatial scales of few hundred square meters to several hectares, managed beech forests tend to be structurally homogeneous; the characteristic is owed to its high competitivity against other tree species. Deadwood of different dimensions during all phases of stand development increases the diversity and provides habitats for many organisms, e.g. fungi and beetles (Meyer and Schmidt, 2008). Best practice silviculture focusses on tending small groups to develop target trees for timber production, and unmanaged space between them (Wilhelm and Rieger, 2018).

The early development comprises a dense stand with habitats for wildlife in the underbrush. Herbaceous plants are sparse. Interventions for the spatial organization with hindsight to later stand management create additional habitats. With advancing age and gaps in the canopy appear, offering opportunities for subdominant trees, shrubs, the herbal layer, and natural regeneration of beech.

2.2. Mountain Norway spruce forests and secondary spruce forests in lowlands

Mountain areas of Central Europe are optimal for Norway spruce (Ellenberg and Leuschner, 2010), and are an economic backbone of forestry. Commonly, Norway spruce dominates, and larch (*Larix decidua* Mill.), rowan (*Sorbus aucuparia* L.), white beam (*Sorbus aria* L.), Silver fir (*Abies alba* Mill.), maple (*Acer sp.* L.), European beech and aspen (*Populus tremula* L.) are present; not all of them are economically relevant.

During the establishment of a new stand the diversity of herbaceous plants and habitats is high. Harvesting along narrow, long cuts instead of clear cutting allows for natural regeneration of several tree species. In gaps with insufficient natural regeneration replanting adds economically desired tree species. Using non-native trees (e.g. hybrid larch (Larix $decidua \times kaempferi = L. \times marschlinsii$) can be controversial. Thinnings increase the light and water supply of the herb and shrub layers. Residues, i.e. tree tops, branches, and roots, remain on site.

Norway spruce forests are increasingly affected by disturbances (Fig. 2) (Gardiner et al., 2013; Hlásny et al., 2021b). Gaps created early in stand development (i.e. less than 50 years stand age) can be managed by sanitary cuts. The openings enable natural regeneration and foster the development of uneven-aged stands. For large scale disturbances at higher stand ages with few intact trees remaining promising management concepts are not available and damaged trees are salvaged. Shorter rotation periods reduce the risk of damages.

The relevance of secondary Norway spruce forests in Central Europe is declining. Yet, they are an iconic example of the debate between forest managers and nature conservationists. After World War II they replaced many mixed-species forests. Risks such as storm and bark beetle



Fig. 1. Common forest types in Central Europe. Beech stand in the Vienna Woods (a), Secondary spruce forest in Upper Austria (b), Douglas fir stand in Perchtoldsdorf, Lower Austria (c), floodplain forest in Moravia (d).

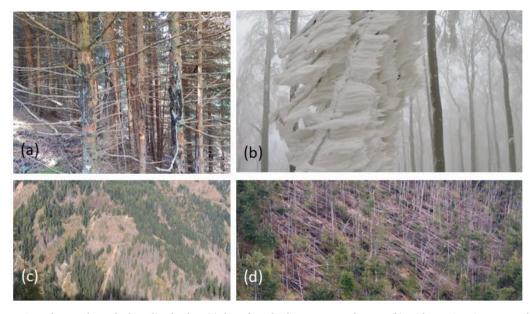


Fig. 2. Forest damages: Stem damage due to bark peeling by deer (a), hoar frost, leading to canopy damages (b), wide openings in a spruce-dominated mountain forest after a mass propagation of bark beetle (c), and storm damage (d).

damages, and ecological concerns were known, but were accepted with hindsight to high yield (Assmann, 1961). Triggered by a combination of windthrows and years with warm and dry conditions, waves of bark beetle attacks decimated these stands and caused dramatic losses to commercial forestry (Hlásny et al., 2021b; Jandl, 2020). However, many secondary spruce forests are still in a premature state and management concepts are sought to gradually increase their resilience in order to complete a production cylce. The management plan follows Table 2. Site conditions in low elevation offer more opportunities for the enrichment of the trees species spectrum than in mountain forests. Fencing can prevent bark peeling on young trees (Fig. 2 a).

2.3. Management of non-native Douglas fir stands

Central Europe has a limited range of commercially relevant coniferous tree species due to high extinction rates during the Neogene and Quaternary (Latham and Ricklefs, 1993; Svenning, 2003). Douglas fir is cultivated in Central Europe since 150 years. It is a potential alternative to native conifers due to its similar timber quality, high productivity and drought tolerance, and low susceptibility to bark beetle infestations (de Sauvage et al., 2023; Schüler and Chakraborty, 2021). It has similar site requirements as European beech. The mixture of both leads to overyielding as consequence of complementary light interception in the canopy (Thurm et al., 2016). Table 3 describes the replacement of a

Table 1Management cycle of a Central European beech forest.

Intervention	Narrative
Natural regeneration, age 0-15 Mixture control, until age 25	Beech is often vividly regenerating from previous stands that were managed in the shelterwood system. Fostering naturally regenerating hardwoods (oak, maple, wild cherry (Prunus avium L.). Grouping of species in small-scale management units. Maintenance of a high stand density. Trails for future management interventions are prepared.
Precommercial thinning, age 25-35	Selection of promising individuals at distances of approx 10 m, aiming at a final stand density of 60-100 stems ha ⁻¹ . Removal of competitors of target trees. Support of other hardwood species.
Commercial thinnings, age 35-80	Support of high-quality trees. Emphasis on correction of damages to avoid entrance of stem pathogens.
Canopy opening, age 80-100	Consecutive harvesting of pre-mature hardwoods. Additional growing space for remaining stand; shelterwood
Stepwise harvesting, age 100-150	Reduction of stand density, final stem diameter increase; natural regeneration; harvest prior to red heart formation.

Table 2Management cycle of Norway spruce in mountain areas.

Intervention	Narrative
Regeneration phase	Natural regeneration is supplemented with seedlings to an initial density of approx. 1600 plants ha ⁻¹ . Replanting after early mortality enriches the tree species composition according to management objectives. Trees with high initial growth rates and shade-tolerant trees can be combined. Weed control, protection against deer browsing and weevils is advised.
Thinnings, age 25-60	Reduction of stand density to approx. 800 plants ha ⁻¹ ; regulation of spatial distribution of high quality stems and tree species mixture. Low stand density increases the resilience against storm and snow damage. The revenue of the removed wood is already economically viable. The final thinning to approx. 400 stems ha ⁻¹ promotes high-quality stems and stimulates diameter growth.
Harvest, age 80- 180	Trees are extracted according to market opportunities and the expected resilience of the mature stand.

Table 3
Management cycle of Douglas fir.

Intervention	Narrative
Afforestation	Pure Douglas fir requires approx. 1500-2000 seedlings ha ⁻¹ . In mixed stands the spatial distribution needs to reflect the light demand, because Douglas fir has a high initial growth rate and outcompetes other tree species. Mixtures with native trees (e.g. European beech, Norway spruce, wild cherry, hornbeam (<i>Carpinus betulus</i> L.) are possible.
Tending	At a stand height of $6-12$ m approx. 200 target trees ha ⁻¹ are selected and pruned. At a stand height of 20 m competitors are removed and pruning is extended to 6 m.
Harvest	At a stand height of >30 m single stems are harvested. Gaps in the canopy are tolerated in order to foster a horizontally and vertically diverse stand structure and to allow natural regeneration.

secondary spruce forest with Douglas fir (Fig. 1 c).

Douglas fir is highly productive. Stem diameters of 25-50 cm are achieved within 30-60 years. Diameters of 60-80 cm require 50-100 years. The potential to replace poorly performing native conifers with Douglas fir is an economic incentive that may contrast with interests of nature conservation.

2.4. Case study floodplain forest

Flood plain forests are highly dynamic and harbor a rich biodiversity (Richardson et al., 2007). They can be narrow unmanaged strips of alders and willows along mountain brooks or extensive forests along rivers in low elevation with different frequencies of inundation. We describe an intensely managed plantation established from poplar clones (*Populus canadensis* (Foug.)) (Tuskan et al., 2006) with a rotation period of 30 years (Fig. 1 d, Table 4). Upon reaching a target stem diameter poplars are harvested and the remaining slower growing trees species are left on site (de Groot et al., 2022).

Poplars have high and narrow canopies. In the wide open space between individual poplars natural regeneration of many tree species occurs. The development of oak (*Quercus sp.* L.) and ash (*Fraxinus excelsior*

Table 4Managing a poplar plantation in a floodplain.

Intervention	Narrative
Stand establishment	Poplars are planted on a 4×4 m grid, already resembling the final spacing. Valuable tree species are fostered.
Pruning at age 10 and on demand Final harvest; age 30-40	Early pruning is advised because poplar retains dead branches, thereby reducing its timber value. Timber extraction is unproblematic on flat sites in lowlands.

L.) is supported. Both species have much longer life cycles than poplar and remain on site during consecutive production cycles of poplar, either as future target trees or as habitat trees. The abundance of dead standing and lying deadwood and the underbrush promotes biodiversity (de Groot et al., 2022).

3. Discussion

3.1. Biodiversity at the landscape level

The heterogeneous ownership structure often results in diverse land use patches, leading to the presence of various forest types side-by-side (Ammer et al., 2017; Pröbstl-Haider et al., 2017) (Fig. 3). Yet, biodiversity conservation benefits from responsive conservation planning tailored to local and regional circumstances. Effective strategies, such as ecological ecosystem connectivity, involve data-driven land use planning across multiple stakeholders in the landscape. This approach enables the conservation and restoration of wildlife corridors and stepping-stones, enhancing overall biodiversity.

3.2. Tree species richness and non-native trees

Climate change and ecological considerations have rekindled the interest in resilient multi-species and uneven-aged forests where complimentary functional traits promote synergies between biodiversity conservation and timber production. Assemblages of several economically relevant tree species are an alternative for mono-species stands (Dieler et al., 2017). In particular, Silver fir, European larch, and several broadleaved tree species are gaining ground in comparison to Norway spruce. Interventions follow species-specific schedules, rendering a random mixture of species impractical. A pragmatic approach is grouping tree species and age classes, respectively, in clusters thereby taking anticipated forest operations into account (Fig. 3, b, c, and Tables 1, 2, 3, 4). Active management can foster the establishment of multi-species forests, thereby increasing both the resilience and ease of tending interventions. Light-demanding oak and and shade-tolerant European beech are major tree species of temperate forests that form mixed stands. However, European beech systematically outcompetes oak. Canopy openings are insufficient to promote the natural regeneration of oak and competing European beech and hornbeam need to be actively removed (Ligot et al., 2013).

The role of non-native trees in forestry is controversial. Some are invasive, while others (e.g. White pine (*Pinus strobus* L.), Douglas fir, Red oak (*Quercus rubra* L.)) can increase the leeway of forestry when coping with climate change. They can occupy ecological niches due to higher drought and heat tolerance. Unintended ecological consequences need to be understood and mitigated. Foresters have devised comprehensive protocols to assess risks and opportunities (Bindewald et al., 2021; Kusbach et al., 2023). Yet, the vulnerability of non-native trees to pests and pathogens may become apparent once they are used on large areas. For example, White pine was very successful in Europe until it was heavily affected by a rust disease caused by *Cronartium ribicola* (von Tubeuf, 1928). Similar experiences cannot be ruled out for non-native candidate trees that are presently discussed and may compromise the positive outlook as presented in Table 3.

Climate change and forest management reduce the share of appropriate tree species. A bottleneck of available tree species has been described (Wessely et al., 2024). Endemic pests can further limit the spectrum of available tree species. Several waves of elm disease, caused by *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, and ash dieback due to the beetle *Agrilus planipennis* and the fungus *Hymenoscyphus pseudoalbidus* have affected dominant tree species of floodplain forests (Valenta et al., 2016). An unresolved issue are damages due to wildlife (Fig. 2 a). Ungulates selectively browse rare tree species and reduce the spectrum of options to conserve and increase the diversity in forests.



Fig. 3. Rural landscape in Upper Austria with a mix of forest, agricultural land, and settlements (a). A random mixture of tree species (b), and arrangements of species patches in a forest (c).

3.3. Length of the rotation period

Fig. 4 shows the development of a managed Norway spruce stand over 150 years. The accumulation of aboveground biomass saturates after approx. 130 years. The increase in the stem volume peaks early in stand life and is close to zero at 140 years. Optimal resource use defines the ideal harvest age when the current increment equals annual increment. The annual increment drops earlier but the average annual increment declines slowly. Consequently, forest managers have some flexibility: without substantial increment losses the rotation period can be elongated (gray Box in Fig. 4).

From the point of view of biodiversity and conservation of endangered species the economic risks due to disturbances at high stand ages are not compelling arguments. Some middle ground is reached in the concept of uneven-aged continuous cover forestry (Pommerening, 2023). Yet, when forest managers opt for a longer rotation period, regular stem extractions are required to stay within the tree-size dependent limits of maximum stand density (Pretzsch, 2010; Reineke, 1933). This option is described in the context of beech forests (Tables 1) where repeated reductions in stand density stimulate diameter increases in the remaining stand. Without stem extractions the mortality rate

increases. The elongation of the rotation period implies an increased risk of stand-devastating damages. Very long rotation periods of stands have only a slim chance of being achieved, even when individual trees can get very old (Binkley, 2023). Creating unique habitats at late seral stages of forest development is uncertain. Currently, disturbances frequently interrupt the expected stand development prematurely.

3.4. Dead organic matter

A characteristic of old forests is the abundance of dead organic matter. Woody debris such as decaying logs provides unique habitats for a variety of species and around 25% of forest species depend on it (Siitonen, 2001). Dead wood is essential for saproxylic beetles and wood-inhabiting fungi. Slowly decaying coarse woody debris is a nutrient source (Harmon et al., 2020).

From an economic point of view there is no compelling argument to leave felled stems on site. It requires case-by-case decisions whether the retention of decaying wood is beneficial. To best support biodiversity, dead wood should be continuously available in space and time, and derive from different tree species, decay stages, and diameter classes (Haeler et al., 2020). This diversity is not merely provided by tree tops,

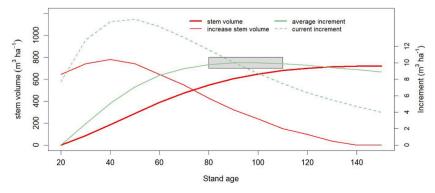


Fig. 4. Tree growth and biomass over age. Standing stem volume, increase in the standing stem volume (red lines), current and average annual increment (green lines). The gray box indicates the decadal leeway to compromise between economical interests and rotation period. Data from Yield Table Fichte Bayern 10 (Marschall, 1975).

stumps, and harvest residues (Brin et al., 2010; Grove, 2002; Heilmann-Clausen and Christensen, 2004).

How much deadwood is optimal in Central Europe is difficult to establish from limited reference data. However, the presently encountered deadwood is on the low end of estimates, particularly in intensively managed low-elevation forests (Müller and Bütler, 2010). Enriching forests with deadwood by management is surprisingly complex. Continuous cover forestry widens the distribution of age and diameters but do not necessarily increase the amount of coarse woody debris (Albrich et al., 2021; Neumann et al., 2023; Pommerening, 2024).

Fresh stems of Norway spruce are notoriuous breeding places for bark beetle that can lead to catastrophic mass propagations (Hlásny and Haas, 2023; Hlásny et al., 2021a; Kamińska et al., 2021; Marini et al., 2012). Routinely, the removal of lying stems has high priority (Fig. 2 c). Yet, debarking or bark scratching decreases bark beetle populations drastically, with the latter being more beneficial for other saproxylic insects (Hagge et al., 2018). Dead stems of other tree species can remain on site for decay, unless entomological advise otherwise.

3.5. Balancing between active forest management and biodiversity conservation

The biodiversity crisis in Europe is driven by land use, climate change and environmental pollution (European Environmental Agency, 2019). Protection of biodiversity in one region may increase the pressure on natural resources in others and can have negative net effects (Betts et al., 2021; Rosa et al., 2023). Forest management and biodiversity conservation cover common ground. Synergies exist due to the increase in the number of managed tree species, the establishment of uneven-aged forests, and small-scale harvesting operations in a range as they are common practice and are complying with Forest Acts (Dieler et al., 2017). Respective activities are currently implemented in the context of adaptation to climate change. Foresters have some leeway to extend the length of the rotation period (Fig. 4) and base their preference usually on market opportunities and the expected risk of disturbances.

Heterogeneity on the landscape level is common when forest owners simultaneously and adjacently implement widely different management concepts. Steping-stones and habitat trees ensure the connectivity of ecosystems. Thinning operations and selective cuttings emulate small-scale disturbances and diversify habitats in forests. There is no single concept fitting all situations. Synergies and tradeoffs between forest management and biodiversity conservation deserve to be analyzed on a case-by-case basis and require the adoption of knowledge-based compromises.

4. Conclusions

- Central European forests are sustainably managed and certain measures can contribute to biodiversity conservation.
- Forest management and biodiversity conservation have different objectives and a lot of common ground. In recognition of the biodiversity crisis forest managers have several options. It is essential to prioritize specific conservation targets to ensure high carbon sequestration rates, tree species richness, and biodiversity.
- Biodiversity of many, but not all taxonomic groups is increased due
 to active forest management operations such as thinning and treespecies mixtures. Structural heterogeneity, abundance of deadwood, step-stone biotopes, veteran trees and defragmentation of the
 landscape can be created by active forest management.
- Harmonized monitoring concepts on biodiversity in forests ecosystems are not yet implemented. Conclusions on biodiversity are derived from case studies, where many site peculiarities matter and generalizations are not yet widely accepted.

 Sustainable multipurpose forestry is a valid concept for Central Europe that supports many but not all objectives of biodiversity conservation.

CRediT authorship contribution statement

Robert Jandl: Writing – original draft, Supervision, Investigation, Conceptualization. Elena Haeler: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. Georg Kindermann: Writing – original draft, Investigation. Katharina Lapin: Writing – original draft, Investigation. Janine Oettel: Writing – original draft, Investigation. Silvio Schüler: Writing – original draft, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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