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A synthesis of multi-taxa management experiments to guide forest biodiversity conservation in Europe

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ABSTRACT

Most European forests are used for timber production. Given the limited extent of unmanaged (and especially primary) forests, it is essential to include commercial forests in the conservation of forest biodiversity. In order to develop ecologically sustainable forest management practices, it is important to understand the management impacts on forest-dwelling organisms. Experiments allow testing the effects of alternative management strategies, and monitoring of multiple taxa informs us on the response range across forest-dwelling organisms. To provide a representative picture of the currently available information, metadata on 28 multi-taxa forest management experiments were collected from 14 European countries. We demonstrate the potential of compiling these experiments in a single network to upscale results from the local to continental level and indicate directions for future research. Among the different forest types, temperate deciduous beech and oak-dominated forests are the best represented in the multi-taxa management experiments. Of all the experimental treatments, innovative ways of traditional management techniques (e.g., gap cutting and thinning) and conservation-oriented interventions (e.g., microhabitat enrichment) provide the best opportunity for large-scale analyses. Regarding the organism groups, woody regeneration, herbs, fungi, beetles, bryophytes, birds and lichens offer the largest potential for addressing management–biodiversity relationships at the European level. We identified knowledge gaps regarding boreal, hemiboreal and broadleaved evergreen forests, the treatments of large herbivore exclusion, prescribed burning and forest floor or water manipulations, and the monitoring of soil-dwelling organisms and some vertebrate classes, e.g., amphibians, reptiles and mammals. To improve multi-site comparisons, design of future experiments should be fitted to the set-up of the ongoing projects and standardised biodiversity sampling is suggested. However, the network described here opens the way to learn lessons on the impact on forest biodiversity of different management techniques at the continental level, and thus, supports biodiversity conservation in managed forests.

1. Introduction

Forests cover 35 % of Europe's land area and are home to a major part of Europe's terrestrial biodiversity, whose conservation represents an increasing challenge and responsibility (European Commission, 2021). Moreover, forests are significant for the economy and society, as they provide timber and many other economically valuable goods and ecosystem services (Forest Europe, 2020).

Despite the recent increase in forest cover, millennia of human land use in Europe have considerably decreased forest cover and structural and compositional heterogeneity in extant forests (Kaplan et al., 2009). Although 24 % of Europe's forests are protected (Forest Europe, 2020), most of these are also managed for timber production. Only about 3 % of Europe's forests (excluding Russia) retain their primary condition (FAO, 2020). Notwithstanding the indisputable value of primary forests (Bruun and Heilmann-Clausen, 2021; Schall et al., 2021), their limited area points to the crucial role of close-to-nature forest management and forest restoration in the conservation of Europe's terrestrial biodiversity (Bauhus et al., 2013).

Forest management influences the levels of biodiversity basically by changing habitat structure, habitat availability and abiotic circumstances. Hence, exploring the effects of management and the alteration of stand structure and abiotic conditions on biodiversity is essential for the elaboration of sustainable timber production that integrates conservation and economical aspects (Kraus and Krumm, 2013). Revealing these relationships is also necessary for the development of conservation-oriented forest management, which aims at increasing forest biodiversity without timber production purposes (Bauhus et al., 2013).

Relying on a diverse group of taxa, rather than on single indicators has a key role in assessing the biodiversity sustainability of forest management since it increases representativeness of the forest biota (Burrascano et al., 2018), and may help to counter the taxonomic bias in conservation research (Clark and May, 2002). Multi-taxa studies are more likely to include taxa that are highly species-rich and hold great significance for forest ecosystem functioning such as fungi and arthropods (Halme et al., 2017), or taxa with a high share of species of high conservation concern, such as saproxylic beetles (Cálix et al., 2018) or several groups of vertebrates (EEA, 2010). Moreover, linking the diverse range of responses of multiple taxa to environmental changes sheds light on various ecosystem processes (Aubin et al., 2013). In this view, numerous multi-taxa studies have been published regarding the management effects on forest biodiversity in Europe in recent years (Seibold et al., 2015; de Groot et al., 2016; Schall et al., 2018; Lelli et al., 2019).

Experiments allow for disentangling the correlating factors and isolating single effects and thus are useful tools in identifying underlying mechanisms, and multi-taxa forestry experiments are key complements to observational studies of the management–biodiversity relationships (Burrascano et al., 2020). The starting point for the present study is that there are several such experiments at the local or national levels across Europe, but no overview of these have been published yet, however, their joint analyses would allow for generalising the results of individual studies at the European scale. Such compiled evidence could help enhance the development of European-level guidelines for sustainable and conservation-oriented forest management.

We aim to provide an overview of recent experimental field studies in Europe dealing with the effects of various forestry treatments on multi-taxa biodiversity. Here, we describe them by reporting on i) geographical and habitat representation; ii) broad treatment types; iii) representation of different taxonomic groups; and iv) environmental variables. We aimed to:

1) map the information from multi-taxa forestry experiments regarding forest categories, treatments and organism groups;
2) explore the potential of the existing information for addressing management-related questions at the European level;
3) identify knowledge gaps (issues not covered by the existing experiments) concerning the forest and management type and biodiversity coverage.

2. Methods

2.1. Data collection

We compiled information on experiments according to the following criteria: i) experiments were established in European closed forests (i.e., pre-treatment canopy cover >40%); ii) experiments included both manipulation and control sampling units; iii) treatments comprised interventions that changed the forest structure (canopy, understory, or microhabitats) or influenced the forest floor or water conditions. Interventions could have commercial and/or conservation-oriented purposes. iv) Minimum of three replicates per treatment were applied; v) a minimum of three taxonomic groups were sampled, representing at least two of the kingdoms Plantae, Fungi and Animalia; vi) detailed information on study design, treatments, sampling protocols and coordinates of sites was available.

The search for experiments followed multiple pathways. It was initiated in the framework of the BOTTOMS-UP COST Action (https://www.bottoms-up.eu/en/) involving forest ecologists from 28 European countries who searched for appropriate experiments within their network and country. Besides, we scanned the list of LIFE projects (https://ec.europa.eu/environment/life/project/Projects/index.cfm) related to forests and searched for relevant publications on the Web of Science (https://www.webofscience.com, applied search strings: "forest", "experiment", "biodiversity", "Europe"). Experiments in the metadatabase by Bernes et al. (2015) about the effect of conservation-oriented forest management on biodiversity fitting the above criteria were also incorporated. Projects that were merely in the planning stage were also included.

At first, we collected detailed structured descriptions of the projects. The description forms were filled by one or several custodians associated with each experiment, providing general information about the experiment, metadata about the sites, description of the applied treatments, investigated taxa, environmental variables, functions and processes (see the blank form and instruction guide in Appendix 1).

2.2. Data standardisation and interpretation

In order to make the highly heterogeneous setups of the experiments comparable, several terms were defined and applied consequently across the projects, even if it resulted in some simplifications. The lowest level of analysis, even within complex sampling procedures were defined as 'experimental units'. 'Blocks' were determined as areas for replicates of the complete set of treatments. 'Sites' were determined as homogenous geographical areas to which discrete abiotic (topography, macroclimate and bedrock) and homogeneous stand structural parameters were assigned. Sites were delimited by the experiment custodians, and their spatial scale highly varied between the different projects, thus – contrary to the terms 'experimental unit', 'number of replications' and 'block' – this term could not be handled uniformly across the experiments. The experimental units and replicates of an experiment could be located in different sites or within one site.

Several variables of the experiments, where standardisation was possible and meaningful, were merged into two metadata tables at the experiment- and site levels separately. Since the experiments varied widely in their spatial scale and data accuracy, in many cases, only ranges were available for numerical characteristics of the sites (e.g., altitude, stand age, or canopy openness), or just the same approximate value was given for all sites. Forest compositional categories and types were defined based on the EEA classification (EEA, 2007); in many cases, more than one compositional type was assigned to a single site.

We defined six main intervention categories with subcategories (hereafter 'types', Table 1). For cuttings, we separated types according to the approach of the canopy opening. If cutting was based on an individual tree or stem selection, we called it 'thinning', while aggregated cuttings based on a defined size area were categorised as 'gap cutting' or 'clearcutting'. We defined the area threshold between 'gap cutting' and 'clearcutting' as 2000 m^2, based the separation on their potential effect on site conditions, even if the boundary between them would not be sharp (Muscolo et al., 2014). In some cases, an experiment could include more than one treatment category and/or type.

The definition of organism groups was based on their taxonomic categories; however, the studied groups spanned across different taxonomic levels (family and higher). Some taxonomically identical groups were considered as two independent groups, typically 'woody regeneration' and 'herbs'. Likewise, 'Carabidae' were often studied independently from other groups of beetles ('Coleoptera'), thus we handled them separately. Similarly, 'Chiroptera' were treated separately from the other mammals ('Mammalia'). On the other hand, taxa with ecologically similar functions were merged (Bryophyta and Marchantiophyta into 'bryophytes', lichenised fungi, as a paraphyletic, but morphologically and functionally well-isolable group to 'lichens'). Our 'Fungi' group covers mainly macrofungi detected by the naked eye, but in some cases, it also contains a wide range of fungi determined by environmental DNA sequencing. Notwithstanding the heterogeneous ranks and the multiple exceptions, for the sake of simplicity, thereafter we call all groups 'taxa'. In many projects, only subgroups of a given taxon were sampled. In such cases, the list of subgroups was also provided. Occasionally, these were taxonomic groups, but they often covered functional groups or groups that can be collected by special sampling methods. The nomenclature for high-rank taxonomic groups follows Roskov et al. (2019).

Arthropod traps collected numerous taxa, among which only a few have been identified and analysed in a given project. However, the other collected taxa have the potential to be identified and used in the future; therefore, besides the investigated taxa, the applied collecting methods for arthropods were also listed.

Figures were created in R 3.6.1. (R Development Core Team, 2019) with the package ggplot2 (Wickham, 2016).

3. Results

3.1. General description of the experiments

The established network comprised 28 experiments conducted over 14 European countries (Fig. 1, Table 2), each with a comprehensive list of metadata (Appendices 2 and 3) and a detailed textual description (Appendix 4).

The experiments covered not only a broad latitudinal and longitudinal range but also varied greatly in altitude (5–1850 m above sea level). Overall they covered 29 EEA forest compositional types from 12 compositional categories (EEA, 2007). Comparing the frequency of the compositional categories in the network to their total area in Europe (Barbati et al., 2014), Mesophytic deciduous forests, Beech forests and Mountainous beech forests were overrepresented among the experiments, as well as Mediterranean coniferous forests. Some relatively common compositional categories as boreal and hemiboreal forests and the other categories were underrepresented (Fig. 2).

The experimental design and spatial scale of the survey were rather variable across projects, with a broad range of both in terms of number (1–89) and the area of sites (0.16–30 000 ha) per experiment. The number of experimental units varied as well (15–272, and an exception, where 1170 logs were the experimental units). The replication number of the treatments ranged from three to 90. A block design was applied in 18 out of the 28 experiments. Before-After-Control-Impact design was implemented in 25 projects, while the other three experiments had only a Control-Impact design. After-treatment data collection was heterogeneous regarding the total number of samplings and the temporal frequency of the samplings of different taxa.

3.2. Treatments

Cutting was the most commonly applied experimental treatment (52 %), but microhabitat enrichment and large herbivore exclusion were also applied in several projects (26 % and 9 %, respectively) (Fig. 3). Forest floor manipulation and prescribed burning were scarce, and water manipulation was performed only in one experiment. Thinning and gap cutting were the most common cutting

Table 1
The applied treatment categories and types in the collected experiments.

Treatment category	Category abbreviation	Treatment type	Type abbreviation
Cutting	CUT	Clearcutting	CC
		Forest-open field mosaic creation	FOM
		Gap cutting	GC
		Green tree retention	GTR
		Thinning	THI
		Undergrowth removal	UGR
Exclusion of large herbivores	EXC	Exclusion of large herbivores	EXC
Forest floor manipulation	FLO	Fertilisation	FRT
		Litter raking	LR
		Mechanical damage of ground layer	MCH
Microhabitat enrichment	MH	Deadwood enrichment	DW
		Habitat tree manipulation	HT
Prescribed burning	BUR	Prescribed burning	BUR
Water manipulation	WAT	Ditch filling	DF

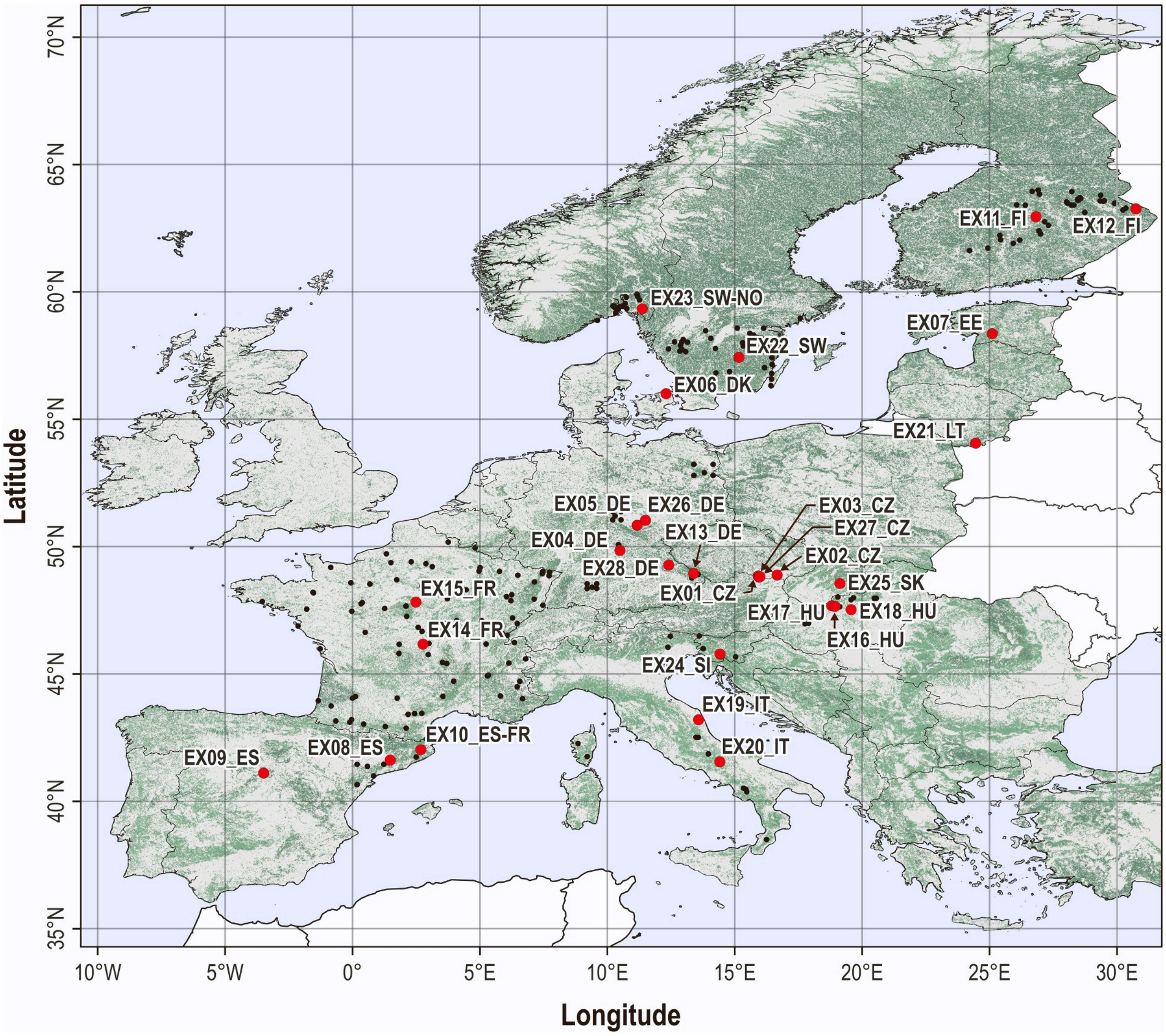


Fig. 1. The location of the multi-taxa forest management experiments analysed in this study. Black dots: sites; red circles: centroids of experiments with multiple sites, or positions of experiments with only one site (labels: experiment ID reported in Table 2). Green background: forest areas (EEA and Copernicus Land Monitoring Service, 2021).

types, while the most frequent microhabitat treatment was deadwood enrichment. The median number of treatment types within an experiment was two, ranging from one to five different treatment types. The number of temporal repetitions of the interventions varied between one and 10.

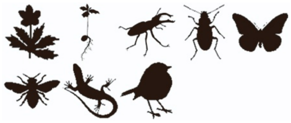
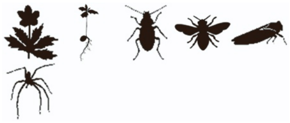
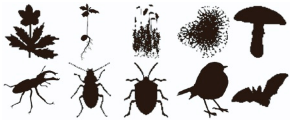
3.3. Investigated taxa

Altogether a total of 29 taxa were studied in the analysed experiments (Fig. 4). The median number of taxa per experiment was seven, ranging from three to 16. Woody regeneration and herbs were studied in almost all experiments (27 and 26 cases, respectively). Fungi, Coleoptera, bryophytes, Carabidae and Aves were sampled in more than 10 experiments. In the case of Fungi, Coleoptera, Hymenoptera, Diptera, Hemiptera, Annelida and Mammalia, only various subgroups within the higher taxon were sampled in most of the experiments. In most cases, arthropods were sampled by flight interception trap (17 projects) and pitfall trap (14 projects), while soil coring was used in five cases.

3.4. Structural and environmental co-variables

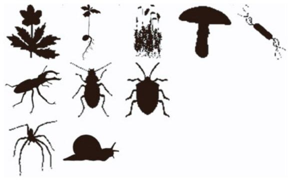
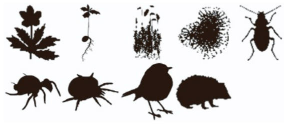
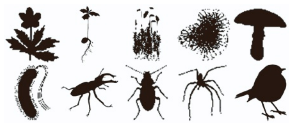
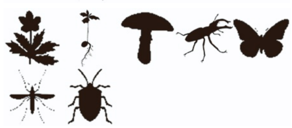
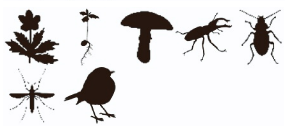
Stand structural data were available for all experiments although their quality and range were variable (Fig. 5). Tree diameter and species were determined in most of the experiments (in 25 projects), and data on basal area, tree height, standing or lying deadwood,

Table 2
Overview of the analysed experiments: forest compositional categories (EEA, 2007), number of replications and experimental units, treatment categories and investigated taxa.

Experiment ID	EEA codes	Replications	Experimental units	Treatments	Taxa
EX01_CZ	5	6	36	CUT	
EX02_CZ	5	5	15	CUT	
EX03_CZ	5	15	45	FLO	
EX04_DE	6	various	69	MH	
EX05_DE	2, 5, 6, 7	29	116	CUT, MH	
EX06_DK	6	5	25	CUT, MH	
EX07_EE	11	8	64	CUT, WAT	
EX08_ES	10	various	272	CUT, BUR, MH	
EX09_ES	7	12	24	CUT, EXC	
EX10_ES-FR	5, 9, 10	5–14	24	CUT, MH	
EX11_FI	1	6–12	43	CUT	
EX12_FI	1	3	24	CUT, BUR, MH, EXC	

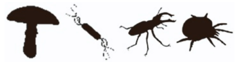
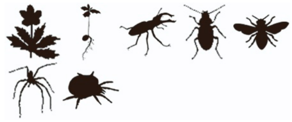
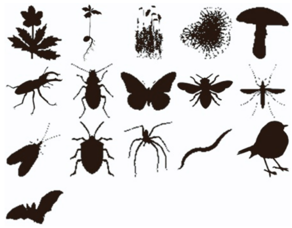
(continued on next page)

Table 2 (*continued*)

Experiment ID	EEA codes	Replications	Experimental units	Treatments	Taxa
EX13_DE	7	5	190	CUT, MH	
EX14_FR	2, 3, 5, 6, 7, 10, 14	89	178	EXC	
EX15_FR	6	3	33	CUT, EXC	
EX16_HU	5	6	36	CUT	
EX17_HU	5	6	30	CUT, EXC	
EX18_HU	5, 8	8–14	22	CUT, MH	
EX19_IT	3, 6, 7, 8	3–11	49	CUT, MH	
EX20_IT	7	various	33	CUT, MH, EXC	
EX21_LT	1, 2	NA	70	CUT, FLO, MH, BUR	
EX22_SW	2	25	50	CUT	
EX23_SW-NO	2	26	52	CUT	
EX24_SI	7	9	27	CUT	

(*continued on next page*)

Table 2 (*continued*)

Experiment ID	EEA codes	Replications	Experimental units	Treatments	Taxa
EX25_SK	5	5	40	CUT, FLO	
EX26_DE	2, 6, 7	90	1170	MH	
EX27_CZ	4	10	20	CUT	
EX28_DE	6	8	72	CUT, MH	

Experiment ID: identification number of the experiment and the code of the country. EEA codes: 1. Boreal forest, 2. Hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest, 3. Alpine coniferous forest, 4. Acidophilous oak forest, 5. Mesophytic deciduous forest, 6. Beech forest, 7. Mountainous beech forest, 8. Thermophilous deciduous forest, 9. Broadleaved evergreen forest, 10. Coniferous forest of the Mediterranean, Anatolian and Macaronesian regions, 11. Mire and swamp forest, 14. Plantations and self-sown exotic forests.
Treatments: BUR = prescribed burning, CUT = cutting, EXC = exclusion of large herbivores, FLO = forest floor manipulation, MH = microhabitat enrichment, WAT = water manipulation.

Taxa: Acari, Amphibia, Annelida, Araneae, Aves, Bacteria, Bryophyta, Carabidae, Chiroptera, Collembola, 9Coleoptera (except Carabidae), Diptera, Fungi, Herbivorous insects, Hemiptera, Herbs, Hymenoptera, Isopoda, Lepidoptera, Lichens, Mammalia (except Chiroptera), Mollusca, Myriapoda, Nematoda, Neuroptera, Protista, Pseudoscorpiones, Reptilia, Woody regeneration.

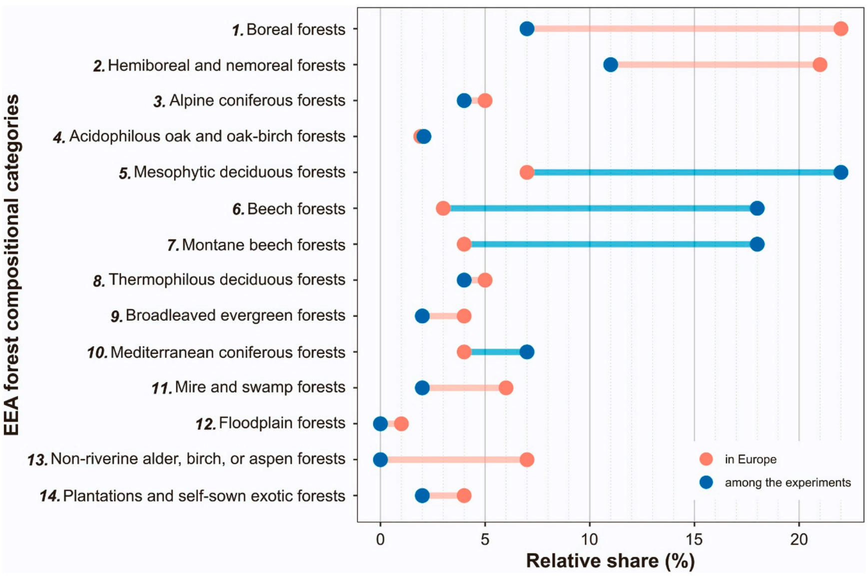


Fig. 2. Frequency of the experiments according to forest compositional categories (EEA, 2007), compared to the respective share of the area of these categories in Europe. One experiment may contain forests of multiple categories.

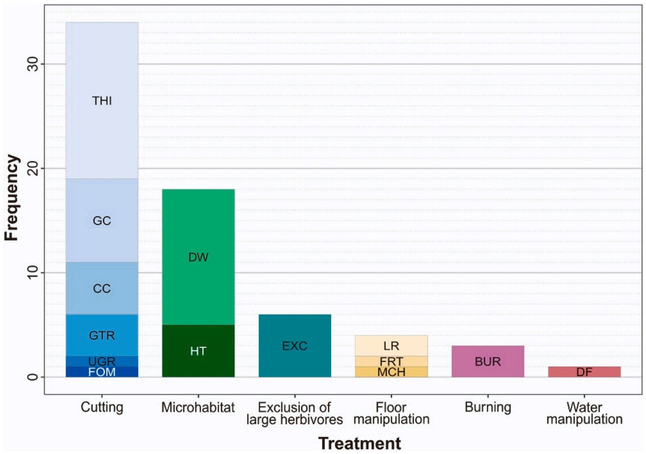


Fig. 3. Frequency of the different treatment categories and types in the experiment network. Cutting: CC = clearcutting, FOM = forest–open field mosaic creation, GC = gap cutting, GTR = green tree retention, THI = thinning, UGR = undergrowth removal. Microhabitat: DW = deadwood enrichment, HT = habitat tree enrichment. Exclusion of large herbivores: EXC = exclusion of large herbivores. Floor manipulation: FRT = fertilisation, LR = litter raking, MCH = mechanical damage of ground layer. Burning: BUR = prescribed burning. Water manipulation: DF = ditch filling.

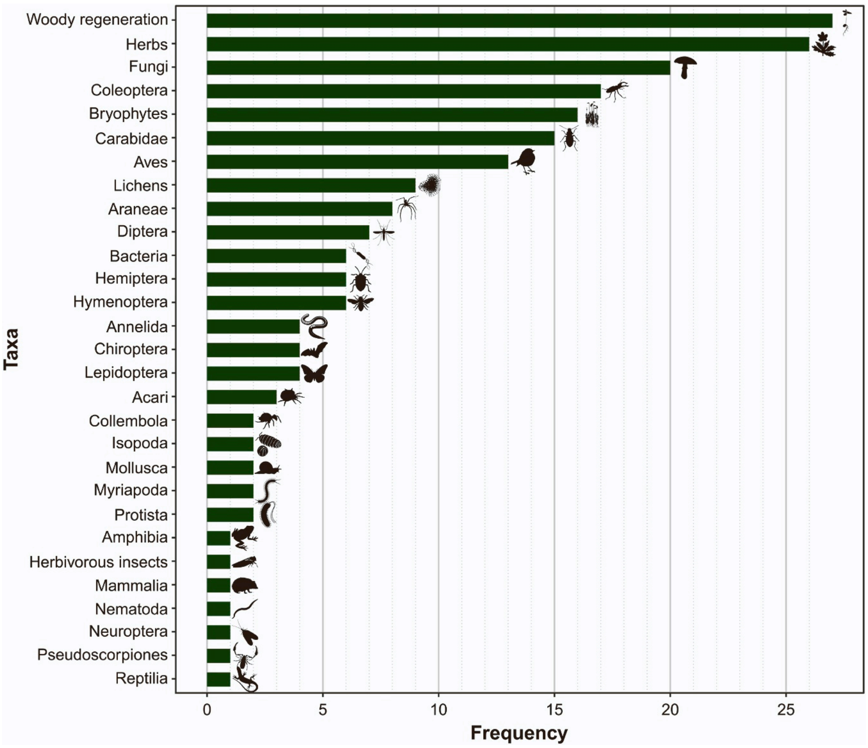


Fig. 4. Frequency of studied taxa in the experiment network.

stem number, canopy openness and tree volume was accessible in > 15 projects. Regeneration density data were available in 12 projects.

Among the environmental variables, light data were collected with high frequency (in 20 cases, Fig. 6), mainly by hemispherical photos (13 cases). Soil components, pH and temperature, air temperature and humidity were also measured in at least 10 projects. Litter data were collected in seven experiments.

In 19 experiments, biodiversity-related functions or processes were also measured (Table 3), among which the most frequent ones were browsing by large herbivores and decomposition.

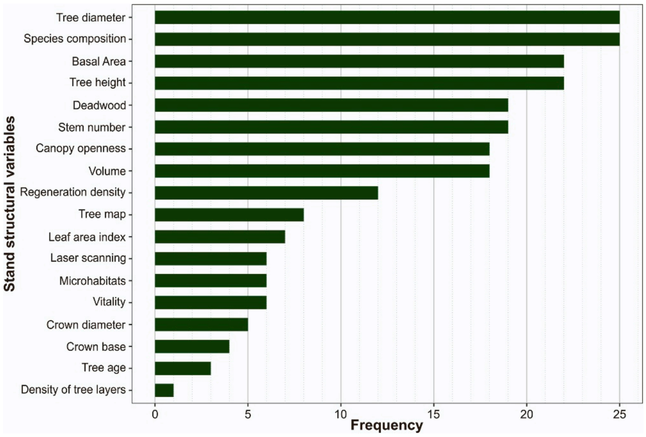


Fig. 5. Frequency of measured stand structural variables in the experiment network.

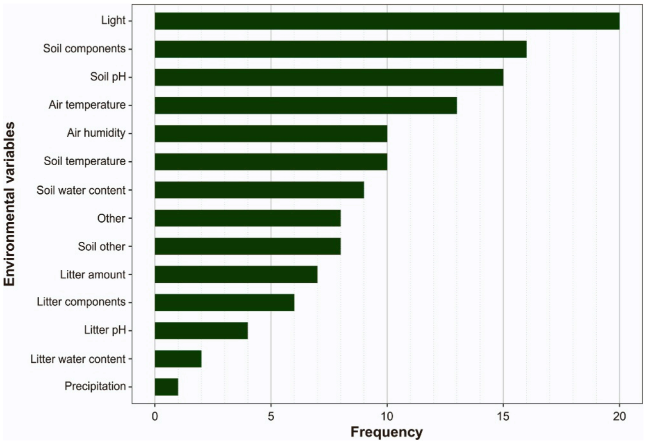


Fig. 6. Frequency of measured environmental variables in the experiment network.

4. Discussion

4.1. Distribution of multi-taxa experiments across forest compositional categories

Compared to their cover in Europe (Barbati et al., 2014), Mesophytic deciduous forests, Beech forests and Mountainous beech forests are the best represented among the multi-taxa experiments, similar to observational multi-taxa studies (Burrascano et al., 2020). Only an intermediate number of experiments was found in the huge area of the boreal and hemiboreal regions. Although there are many forestry experiments conducted in this region (http://noltfox.metla.fi; Koivula and Vanha-Majamaa, 2020), the relative number of multi-taxa experiments is low. Coniferous forests of the Mediterranean region, Thermophilous deciduous forests and Acidophilous oak and oak-birch forests are well-represented compared to their share in Europe. In Broadleaved evergreen forests, Mire and swamp forests and Plantations and self-sown exotic forests only one experiment per forest category was found, thus, the management-biodiversity relationships in these forests have not been adequately explored. Involving Floodplain forests and Non-riverine alder, birch or aspen forests in multi-taxa experiments is an important recommendation for future studies.

4.2. Applied treatment types

Thinning, gap cutting, deadwood enrichment and herbivore exclusion are broadly applied in forestry practice in Europe (Matthews, 1991; Pommerening and Murphy, 2004; Seibold et al., 2015; Bernes et al., 2018), thus they are well-studied in multi-taxa experiments as well. Other treatments are relevant only in certain regions and are studied only on a few sites. Hereafter, we discuss individually those treatments that occurred in more than five projects, and then shortly the rarer treatment types.

4.2.1. Thinning

A total of 15 experiments studied different types of thinning, covering the main regions and compositional categories of Europe.

Thus, the effect of thinning on forest biodiversity in different forest types (e.g., in coniferous vs. broadleaved, or in stands of shade-tolerant vs. intolerant tree species) would be a potential research avenue. Evaluating the biodiversity responses to thinning in different climatic zones might help to understand the effect of canopy openings facing climate change.

In practice, thinning is often implemented in rotation forestry system (as preparation cutting), but it is also a widely used tool of continuous cover forestry system (selection cutting) (Matthews, 1991), furthermore, it is applied in conservation-oriented forest management as well (Bernes et al., 2015). Thus, thinning experiments are established with two different goals, to find either ecologically sustainable management techniques for commercial forestry or potential tools for improving forest habitats.

Similarly to the diversity of the applied thinning methods in forestry practices, the thinning experiments are also heterogeneous in their implementation. There are two different methods applied in thinning experiments: systematic and selective thinning (to promote target trees). In the latter case, thinning can be part of various multifunctional management systems, with numerous conservation-oriented considerations. Thinning is always paired with uncut controls, but in some cases, it is also compared to gap cutting or clearcutting. Thinning intensity ranges from 10% to 61%, and two projects compare different thinning intensities.

The differences in the applied thinning (e.g., in intensity or extent) might influence the outcomes of the multi-taxa monitoring. Thus, thinning treatments should not be compared across experiments as the same kind of intervention but may allow exploring the effect of various thinning intensities on forest taxa. This is definitely true for more sessile groups like plants and soil-dwelling organisms. However, more motile taxonomic groups like some groups of insects and birds, are more affected by the surrounding stands and are therefore more dependent on the context (i.e., forest type) (de Groot et al., 2016). In these cases, all thinning treatments could be compared, e.g., across forest types.

4.2.2. *Gap cutting*

Sustainable forest management can be implemented not only by tree-based thinning but also by area-based gap cuttings (Pommerening and Murphy, 2004), which mimics the fine-scale forest dynamics (Standovár and Kenderes, 2003). We found eight multi-taxa experiments studying this method. Although natural gap dynamics are also characteristic of hemiboreal, boreal and alpine coniferous forests (Kuuluvainen et al., 2012; Janda et al., 2017), gap studies are concentrated in the broadleaved deciduous forests of the temperate regions. The number of available projects allows for comparing the effects of gap cutting between stands dominated by the shade-tolerant beech and the light-demanding oak.

Similarly to thinning experiments, the effect of gap cutting on multi-taxa forest biodiversity is studied under two different approaches, i.e., to develop sustainable management techniques for commercial forestry, or as an element of conservation-oriented management.

Gap size and gap shape strongly influence the environmental conditions and biogeochemical processes within the gap, and thus affect biodiversity and natural regeneration (McNab et al., 2021; Muscolo et al., 2014). Due to the differences in the gap sizes of the collected experiments (150–1600 m^2) they cannot be compared as a uniform intervention across projects but could represent a size gradient for European-level studies focusing on gap size–forest biodiversity relationships. The irregular but near-circular or near-elliptical shape of natural gaps (Schliemann and Bockheim, 2011) is approximated in silvicultural practice usually with circular, elliptical or squared gaps (Muscolo et al., 2014), but sometimes the optimal light and soil water conditions, and thus proper regeneration is ensured by elongated shape (Streit et al., 2009). In the collected experiments, the shapes of the gaps are typically circular, squares were created only in two cases and elongated in one. Therefore, exploring the effects of gap shape under various circumstances needs the involvement of additional experiments.

The biodiversity response to gap cutting can be studied at various spatial scales, which might strongly influence the results (Schall et al., 2018), making the comparisons challenging. In six experiments, gaps and adjacent closed parts of the stand are the treatment levels, enabling the comparison of these projects. In the other two cases, stands with and without gaps are compared.

Table 3
Other functions and processes measured in the experiments.

Function/process	Frequency
Browsing	9
Decomposition	7
Seed fall	3
CO_2-efflux	2
Fire prevention	2
Large wild ungulates activity	1
Wild boar activity	1
Development of transplanted bryophytes	1
Incidence of oak mildew and ash dieback	1
Development of transplanted sedge	1
Nature sounds	1
Seed recruitment of herbs	1
Socio-economic evaluation	1
Seed predation	1
Tree growth	1
Tree phenology	1
Windthrow	1

Besides comparing gaps to uncut parts of the forest, in three projects, gap cutting is compared to thinning and/or clearcutting as well. Two projects are focusing on the details of the implementation of gap cutting with the comparison of different gap types: isolated gaps vs. gaps connected to open areas, or gaps with different sizes (small vs. large), shapes (circular vs. elongated) and creation modes (one or two steps) are compared.

4.2.3. Deadwood enrichment

Deadwood manipulation is an important intervention of conservation-oriented management, increasingly applied across Europe (Lacaze, 2000). It can also be used in commercially managed forests to enhance biodiversity.

Deadwood manipulation was performed in 13 experiments. The temperate and boreal regions have so far been core areas for deadwood experiments (Seibold et al., 2015; Sandström et al., 2019) but only a few have focused on multiple taxa (Cornelissen et al., 2012; Thorn et al., 2016). According to Seibold et al. (2015), the Mediterranean represented a major gap concerning multi-taxa deadwood experiments. Most of our multi-taxa deadwood projects are located in the temperate region, with only one experiment in the boreal region. We also found some projects in the western Mediterranean, filling the mentioned gap; while the eastern Mediterranean remained underrepresented. Overall, the collection of experiments covers 18 EEA forest compositional types.

All but one study follows an experimental unit-based approach, while one follows a deadwood object-based approach that is challenging to compare with the experimental unit-based studies. The effects of deadwood enrichment might depend on the used reference (e.g., intensively managed or structurally diverse natural forests). In the collected experiments, usually only one of them occurs within one project, therefore, in the case of comparative studies across projects, we suggest that the control experimental units should be excluded from the analysis.

The manipulation of deadwood is implemented usually by on-site deadwood creation (cutting, girdling, or burning) but in some cases, deadwood is brought to the sites. In one case, the experiment also includes the preservation of existing deadwood. The amount of deadwood is standardised in a few instances (against the stand volume or by standardising the number of created items), while in most experiments it is only measured. These heterogeneities in the designs allow only for partial comparison between datasets. Six experiments also include habitat trees, with various origins (retention or creation).

Deadwood decomposition offers a variety of habitats, promoting a succession of various organisms (Gossner et al., 2016). Therefore, the period of an experiment is crucial to evaluate its full potential as a habitat, but similarly to the findings of Seibold et al. (2015), most of our collected experiments offer only short-term data.

4.2.4. Exclusion of large herbivores

Large herbivores (such as deer and wild boar) are functionally important components in European forests. Their high density hampers forest regeneration (Ramirez et al., 2018) and modifies the understory communities (Boulanger et al., 2018), which in turn may influence other taxa either directly or through trophic and other functional interactions (Bernes et al., 2018). Excluding large herbivores by fencing is a common methodology to study their effects on biodiversity, but this approach suffers from several constraints (e.g., site legacy, zero vs. unknown/uncontrolled ungulate densities, Bergström and Edenius, 2003).

Herbivore exclusion is applied in six out of 28 experiments, and the effect of browsing is studied altogether in nine projects. In all but one project, herbivore exclusion is an additional treatment to cuttings. Although these experiments have an overall multi-taxa approach concerning the main treatment, the biodiversity survey against exclusion rarely constitutes more than a few taxa. Three experiments study only the woody regeneration in both control and exclusion units, while in one experiment regeneration and herbs are also studied. There are only two projects, where other taxa (bryophytes, fungi, lichens and several animal groups) are surveyed about exclusion treatment. Thus, studying the indirect effects of herbivore exclusion on various components of forest biodiversity requires the extension of samplings to additional organism groups.

Besides the general exclusion of large herbivores, only two experiments have selective exclosures for different species. To better explore the effects of various herbivore guilds, more selective exclusion experiments are needed. Finally, the relatively small size of exclusion units (0.004–0.6 ha) makes it possible to study only the exclusion effects on sessile organisms or motile species with narrow home ranges. We, therefore, appeal to the scientific community to install large-scale exclosures or other experimental set-ups where large herbivores' density is controlled over larger areas compatible with studying the effects of herbivores on different taxa with varying spatial requirements, including trophic cascades (Cardinal et al., 2012).

4.2.5. Other treatments

Some of the investigated treatments that are relevant only in a certain region or forest compositional categories are studied only in a few experiments. Although hydrological restoration by ditch filling or ditch blocking is relevant in several moist lowland forest types (Mazziotta et al., 2016), we found only one experiment to consider this in a conifer-dominated mire forest.

Litter raking was a traditional practice across Central Europe (Bürgi, 1999); however, as it retreated, currently it is scarcely studied. We found two experiments investigating this treatment, both from Sessile oak–hornbeam forests.

Prescribed burning is widely used in boreal and Mediterranean forests to mimic natural low-intensity fires (Silva et al., 2010), but this treatment is underrepresented in the multi-taxa experiments.

Clearcutting is less frequently used in experiments than thinning and gap cutting (only five studies), although it can be considered as an endpoint of the thinning intensity or gap size gradients. Green tree retention is underrepresented with its three projects, even though studying its effect on biodiversity would be advantageous. Retention is often considered an ecologically sustainable method (Gustafsson et al., 2010) as compared to simple clearcutting, but its positive effect on biodiversity is taxon-specific (Rosenvald and Lõhmus, 2008).

4.2.6. Combinations of treatments

Among the collected 28 experiments, 16 studies investigated treatment combinations. All of them contain at least one type of cutting, while other intervention types have been added subsequently. This can be explained by the fact that cutting is the most common forestry intervention; moreover, it substantially changes the environmental conditions potentially influencing the effect of other treatments on biodiversity (Hyvärinen et al., 2009; Hjältén et al., 2012). Ten out of the 12 microhabitat enrichment experiments, five out of the six large herbivore exclusions, all three burning treatments and the water-manipulation treatment are combined with cutting.

4.3. Investigated taxa

Numerous treatment types (such as cutting, herbivore exclusion, burning, or forest floor manipulation) have a strong influence on woody regeneration and herbs (Cugunovs et al., 2017; Boulanger et al., 2018; Tinya et al., 2019). Plants can be easily observed and determined and woody regeneration is of silvicultural interest as well. Thus, it is anticipated that these taxa are the most frequently sampled (in 27 and 26 experiments, respectively), enabling common analyses at a wide range of forests. Fungi, Coleoptera, bryophytes, Carabidae and Aves have also been sampled in more than 10 studies, allowing us to study their response to various forestry treatments across the network. However, in the case of Fungi and Coleoptera, it must be considered that in different experiments sampling is limited to various subgroups. Soil invertebrates, Diptera, Hymenoptera and other vertebrates than birds are underrepresented in the experiments. Numerous taxa are related to deadwood (Stokland et al., 2012), among which herbs, regeneration, bryophytes, wood-inhabiting fungi, Carabidae, saproxylic beetles and birds are often studied in deadwood enrichment experiments (more than five experiments out of 13), while bacteria, lichens and bats constitute research gaps.

The heterogeneous sampling methods strongly hamper the comparability of the different projects, especially in the case of the insect groups. To increase comparability in future experiments, more standardised samplings are suggested (Burrascano et al., 2021). The comparability of the existing biodiversity data (collected with different methods, sampling intensities and in different geographical regions) can be increased if not the absolute value of the community variables (such as species richness and abundance) are compared, but a per-dataset standardised effect size of differences in the investigated variables between control plots and intervention plots is used. Similarly, for species composition, not the raw species, but community dissimilarity indices and traits should be compared across the various projects. To compare experiments collecting data on different elements of forest biodiversity, multidiversity indices can be calculated for each project and effect of a given treatment on multidiversity can be compared across projects.

4.4. Stand structural and environmental co-variables

Most of the studies also collect environmental and stand structural attributes as explanatory variables for biodiversity. Basic stand structural variables (species composition, tree diameter, stand basal area and tree height) are available for most of the projects. However, other structural, microclimatic and soil variables are collected in very heterogeneous ways.

Light, which is the abiotic factor most directly influenced by the cutting treatments (Kovács et al., 2020) is studied in most of these experiments. The broad use of hemispherical photography makes the data comparable. Canopy cover may influence the decay process and colonisation of organisms on deadwood (Seibold et al., 2016), however, it is considered only in half of the deadwood enrichment experiments, with quite heterogeneous methodologies.

Soil conditions are influenced not only by cuttings and burning but also by forest floor and water manipulations (Sayer, 2006; Agbeshie et al., 2022), thus soil components and pH are studied in numerous experiments (altogether, in 18 cases).

Air temperature and humidity are measured in much fewer projects; however they may also vary after different cuttings (De Frenne et al., 2021), and can be important explanatory variables for deadwood enrichment studies as well (Seibold et al., 2016). Although their longer-term simultaneous data collection needs some effort, some affordable and user-friendly instruments could make these measurements feasible in more projects.

Among ecological processes and functions, besides the numerous occasionally studied topics, only browsing and decomposition are widely investigated and comparable across projects.

5. Conclusions

5.1. Research agenda for European-level analyses

The multi-taxa experiments conducted as a part of this study cover major parts of Europe and investigate a considerable share of forestry interventions that are relevant for sustainable or conservation-oriented forest management, and a large number of taxa. The experiments significantly differ not only in their spatial scale, type, intensity and extent of interventions but also in their sampling methods. Despite their heterogeneity, there are several general questions that can be investigated with meta-analyses across a relative broad pool of the experiments. Regarding these general questions, the commonalities of the scientific results of the local studies can be tested, as well as their variability across regions or forest types. Besides, there are some specific questions that are investigated by only one or few experiments (e.g. to compare different implementation types of the given treatment, such as various gap types or deadwood enrichment in shady plots vs. on sunlight). These questions cannot be upscaled to European level, but some plots of these projects (e.g. their most typical treatment types) can be involved to answer the above-mentioned general questions at a continental level, even if the original aim of the experiment was more specific.

Although there are many forestry manipulation experiments in Europe involving biodiversity investigations (Bernes et al., 2015; Seibold et al., 2015), most of them are single-taxon studies. Using a multi-taxa approach in our study is a relevant step towards getting more comparable information across experiments regarding the management–biodiversity relationships (Sabatini et al., 2016).

The most important similarities among multi-taxa forest management experiments are gap cutting, thinning, deadwood manipulation and large herbivore exclusion among the treatments, and the most frequently studied taxa include herbs, tree regeneration, fungi, beetles, bryophytes and birds. The data from these allow us to make the broadest generalisations, however, their application width depends on the given issue. Besides, numerous other treatments and taxa have the potential for common analyses on the scale of two or more experiments.

We pose several questions directly related to sustainable forest management that could be upscaled to the European level based on the generalised results of the considered experiments (Fig. 7):

1. During timber production forestry, how do various close-to-nature management techniques (such as gap cutting and thinning) affect forest biodiversity? Which are the best available forestry methods for conserving biodiversity?
2. How can the different conservation-oriented interventions (deadwood enrichment, habitat tree enrichment, or canopy openings) improve forest biodiversity?
3. How does the cutting intensity (size of gaps, intensity of thinning) influence forest biodiversity?
4. How does the forest type (coniferous/mixed/broadleaved; shade-tolerant/light-demanding dominant species) influence the effect of management? Understanding the management impacts in various climatic zones may help to predict the biodiversity response to treatments and to find those methods that better conserve forest biodiversity in managed forests under climate change.

Besides these questions, others have prominent relevance for ecology (Sutherland et al., 2013, Fig. 7):

5. Are the responses of different biodiversity components to disturbances such as forestry interventions congruent across taxa? How are the taxa of different trophic levels influenced by treatments?
6. What are the effects of forest management disturbances on the functional diversity of the taxa?
7. How do the forest specialist and generalist species respond to treatments?
8. How are the abiotic conditions (microclimate, soil characteristics) influenced by management and how do they affect forest biodiversity? Does forest management impose changes on environmental filters that determine the assembly of ecological communities?

5.2. Knowledge gaps

Hereby, we describe those issues that are not well covered by the existing multi-taxa forestry experiments and need additional

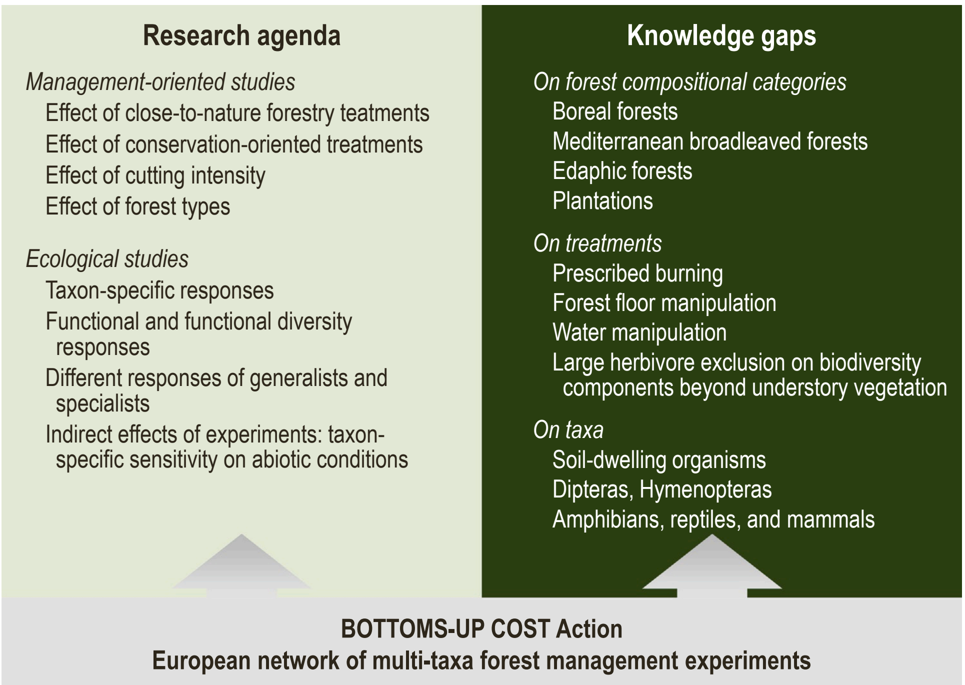


Fig. 7. Research agenda and knowledge gaps based on the existing multi-taxa forestry experiments in Europe.

experiments (Fig. 7). More representation of boreal and Mediterranean broadleaved forests would increase the spatial representativeness of the results and our knowledge about the management effects on biodiversity. Zonal forests are usually well studied, while the – primarily water-determined – edaphic forests are less known with knowledge gaps. Despite the lower conservation value of plantations, their high contribution in terms of the total area in Europe urges their more intensive investigation.

Tree cuttings – which usually have economical relevance – are well studied. However, forest management and conservation also operate with other interventions like prescribed burning, forest floor or water manipulation. The effects of these interventions are relatively less explored and thus more evidence is essential to formulate best practices. Large herbivore exclusion is widely applied in large areas and for the long term, thus it would be especially relevant to understand its effect not only on the well-studied understory but also on other components of forest biodiversity.

Soil-dwelling organisms are extremely species-rich components of forest ecosystems, with important ecological functions such as decomposition. To better assess the management effects on these processes, the inclusion of soil organisms in experiments is highly recommended. In the same context, Diptera and Hymenoptera are rarely studied species-rich groups, because of their complex identification. However, metabarcoding may facilitate their inclusion in experiments in the future. Amphibians, reptiles and mammals, as characteristic vertebrate elements of forest biota, also constitute knowledge gaps.

We think that the current overview would promote fitting the design of future experiments to the set-up of these projects and using standardised biodiversity sampling (see Burrascano et al., 2021) to enable multi-site comparisons and generalisation of results on a transregional scale.

CRediT authorship contribution statement

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Data Availability

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02553.

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