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Environmental Evidence

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What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review

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Abstract

Background: Forest harvesting changes forest habitat and impacts forest dependent species. Uneven-aged management is often considered better for biodiversity than even-aged management, but there is an ongoing discourse over the benefits and disadvantages of different silvicultural systems. This systematic review contributes to the public discussion and provides evidence for policy making by synthesising current evidence on impacts of even-aged and uneven-aged forest management on biodiversity in boreal forests of Fennoscandia and European Russia. In this review even-aged and uneven-aged forest management are compared directly to each other as well as to natural forest to provide a broad basis for public discussion.

Methods: Both peer-reviewed and grey literature were searched in bibliographical databases, organizational webpages and internet search engines in English, Finnish, Swedish and Russian. Articles were screened for relevance by their title/abstract and again by full text. The inclusion of studies was assessed against pre-defined criteria published in an a priori protocol. A narrative synthesis and meta-analysis were conducted to describe the evidence base and to compare species richness and abundance between differently managed forests. The influence of habitat specialism, taxon, years since harvesting, deadwood availability and harvesting intensity on species richness and abundance were also tested.

Review findings: Searching identified 43,621 articles of which 137 articles with 854 studies had independent data and were included in the narrative synthesis. Of those, 547 studies were included in the meta-analysis. The most studied taxa were arthropods, vascular plants, bryophytes, fungi, and lichens. Results showed that forests with less disturbance (uneven-aged and mature even-aged) host more forest dependent species than young even-aged forests (< 80 years old) although the difference was only marginally significant for mature even-aged forests (> 80 years old). Uneven-aged forest had similar number of species and individuals than natural forest whereas even-aged forest had less species than natural forest. Open habitat species and their individuals were more numerous in young even-aged forests and forests undergone retention harvest. Effect sizes found were mostly large indicating strong and uniform impact of forest management based on species' habitat preferences. In addition to habitat specialism, years since harvest explained some of the differences found in species richness and abundance due to increase of open habitat

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species in the early successional stages and forest dependent species in late successional stages. Taxon had limited explanatory power.

Conclusions: Habitat preferences determine species' response to different harvesting methods and the magnitude of effect is large. Less disturbance from harvesting is better for forest dependent species whereas opposite is true for open habitat species. Uneven-aged and mature even-aged forests (> 80 years old) are important to maintain biodiversity in boreal forests. However, the results also highlight that natural forests are needed to ensure the future of forest dependent species in Fennoscandia and European Russia. Given that a broader set of biodiversity aspects are to be protected, best overall biodiversity impacts for a variety of species at landscape level can be achieved by ensuring that there is a mosaic of different forests within landscapes.

Keywords: Clearcut, Selection system, Continuous cover forestry, Species richness, Abundance

Background

Forests cover around 75% of land area in Finland, 68% in Sweden, 50% in European Russia and 41% in Norway and are mainly used for wood production [1, 2]. Consequently, harvesting and management of forests on an industrial scale is the most important factor driving forest degradation in boreal forests of Fennoscandia and European Russia [3–5]. There are many studies on the impacts of forest harvesting on different species groups in Fennoscandia [e.g. 6, 7], and long-term monitoring shows declines of biological communities, for example in many forest bird populations [8, 9], lichens [10], and deadwood associated (saproxylic) beetles [11] although some insect groups have shown positive trends lately [12]. Also, species assemblages may not be maintained in protected areas if they are embedded in heavily managed landscapes [13, 14]. Under these circumstances the management of production forests is a key aspect for maintaining biodiversity.

A common forest management regime in the whole boreal zone has long been even-aged management (Table 1) [15]. In Finland, for example, even-aged management was the primary management regime in forestry enacted by the private Forest Act of 1928 [16] until 2014, when uneven-aged management regime was enabled again. The law was changed to give forest owners more control over their own forests and in recognition of the different values forests have besides timber production. In Sweden, uneven-aged management was the most common management approach until the beginning of 20th century. It was practiced until 1948 when a new law with detailed regulations regarding regeneration of forests was declared and from 1950 selective logging was forbidden in state owned forests [17]. In 1993 a new law enabled practices like natural regeneration and selective logging again [18]. In Norway, clearcutting is the common management practice although forest owners have relatively greater freedom to manage their forests according to their own objectives within the legal framework [19]. In European Russia, most final fellings are clearcuts and uneven-aged forestry with selective logging method is more widely used only in the western parts of the country in Murmansk and Leningrad regions [20].

As boreal forests in their natural state are usually heterogenic with trees and stands of different species, ages and sizes, even-aged management simplifies the forest structure with negative consequences for forest biodiversity [21]. To lessen the impact of harvesting on forest dependent species, even-aged forest management regimes have evolved from clearcuts where all trees are removed to management systems where some aspects of structural diversity are retained. Retention forestry is a method of even-aged management where some old trees, dead or living, or small stands of trees are retained during harvest to create structural diversity (Table 1) [22, 23]. Seed tree and shelterwood methods are included in the even-aged forest management system although the shelterwood system can also be used to create an uneven-aged forest structure if some of the shelter trees are maintained over a long regeneration period [21]. In the shelterwood cutting more trees are retained than in the seed tree cutting as the purpose is to provide shelter for existing seedlings alongside with seed material for a new tree generation.

A further step towards increased structural diversity has been uneven-aged forest management. It denotes a silvicultural system where the stand has several age classes and as a result, higher structural diversity than in even-aged stands. Uneven-aged forest management aims for more heterogeneous stand structure and to have less impact on forest biodiversity than clearcuts (Table 1) [24, 25]. Trees are harvested by a single-tree or group selection where mature trees or tree groups are selected for harvesting and younger trees are left to grow. In single-tree selection, only small gaps are created when individual trees are removed [21]. In group selection, gaps are bigger and disturbance from harvesting is concentrated into certain areas.

Even though even-aged forest management is still the most common harvesting method in Finland, Sweden and Norway, public interest towards uneven-aged forest

Table 1 Definitions of different forest management regimes excluding unmanaged forests. Common synonyms are also given

Forest management regime	Synonyms	Definition
Even-aged forest management	Clear-cutting, clear-felling	Management method that produces relatively homogenous forest structures. Forest regeneration is achieved by natural regeneration, sowing or planting and stand development controlled by thinnings and regeneration felling. During the regeneration felling in the clear-cutting method most trees in the area are removed[a]. In case of natural regeneration, individual seed trees are left in the area (i.e. seed tree cutting is performed)
	Leaving retention trees	Management method almost similar to clear-cutting, but some individual trees (dead or alive) or tree groups are left standing during the regeneration fell. Leaving retention trees aims at maintaining some of the key structures of native forest ecosystems to enhance the structural diversity of the harvesting area and provide habitat continuity for species
Even-aged or uneven-aged forest management	Shelterwood cutting	During shelterwood cutting large number of mature trees are left in the area to regenerate the area naturally and to provide shelter (less harsh environmental conditions) for the new growth. It involves cutting trees in a series of cuttings to allow existing seedlings to grow and new ones to establish themselves before mature trees are removed. Mostly used to create even-aged stands but shelterwood system can be used to create uneven-aged stands if some of the shelter trees are maintained over a long regeneration period
Uneven-aged forest management	Continuous cover forestry, selection system, selective cutting/felling, selection cutting/felling, partial cutting/felling, gap cutting/felling, patch cutting/felling	Management method where some of the trees are removed in one harvest. Forest regenerates through the trees left standing. The forest structure is maintained heterogenous over time by harvesting. This can be achieved by single-tree selection (selective felling) or group selection (gap felling)

[a] Leaving retention trees became more common in the end of 1990s, and nowadays it is common practice in Finland, Sweden and Norway

management has increased in the last decades [26–30]. Recent scientific studies suggest that uneven-aged forest management provides higher values for some biodiversity aspects while even-aged forest management is better for other [15, 31]. Therefore, it is not surprising that there is no overall consensus between stakeholders on the impacts of these two forest management regimes on biodiversity [32]. This review addresses the need to have a synthesis of the current evidence on the impacts of different forest management systems on biodiversity.

Stakeholder engagement

The topic originated from discussions with representatives of the Finnish forest industry and was further discussed at a stakeholder workshop [33]. 13 individuals from 12 stakeholder organisations participated in the workshop (see protocol [33] for full details). At the workshop, research questions, initial theory of change, PECO-based search terms, and factors creating heterogeneity were presented and discussed. Based on the discussion with the participants and in response to comments in the peer-review, the topic was narrowed to two research questions. The workshop participants also suggested sources of grey literature and potential sources for unpublished data. Comments and suggestions of the participants were integrated into the protocol before submission and subsequent publication of the protocol [33].

Objective of the review

The objective of the review is to systematically review and synthesise results of studies comparing the impacts of even-aged and uneven-aged forest management on biodiversity, including species of different habitat specialisations, different taxa and at different time scales. Uneven- and even-aged forest management systems will be compared to each other but also to natural forests to provide a comprehensive picture of their role in maintaining biodiversity. Natural forests are defined to include unmanaged forests with no signs of past management and semi-natural forests with only a few signs of past management, e.g. some cut stumps from past cuttings.

Normally these forests are old but sometimes they can be young as a result of natural disturbance such as fire.

According to the protocol of this review [33] the aim was to conduct reviews on both stand and landscape level biodiversity impacts. However, during the review process it became clear that there was not enough data for landscape level analysis. Hence, this review concentrates on stand level only. The research question is:

What are the stand level effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia?

As both of the management types will be compared not only to each other but also to unmanaged forests, there are two exposures and multiple comparators for the study question (Fig. 1). Hence, the question components are:

Population: Boreal forests in Fennoscandia and European Russia.

Exposures: Even-aged and uneven-aged forest management.

Comparators: Natural and semi-natural forests, comparison between the two exposure types.

Outcomes: Indicators of species richness and abundance.

Methods

This review follows methods described in the a priori systematic review protocol [33]. All deviations from the protocol are reported and explained in the next section. The review is conducted according to the guidelines for systematic reviews by the Collaboration for Environmental Evidence [34] and complies with the ROSES reporting standards (Additional file 1).

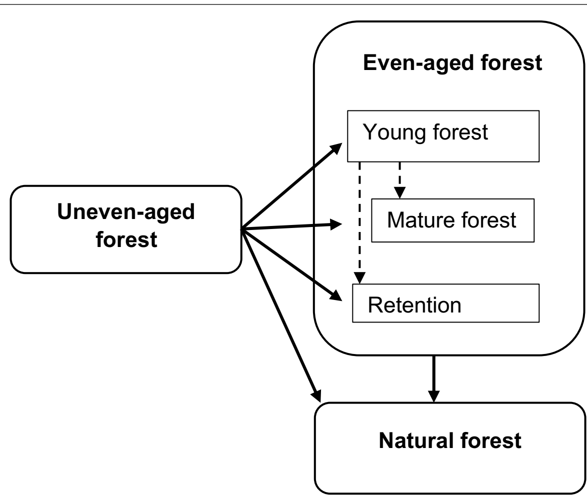

Fig. 1 Different comparisons included in the review. Solid arrows show comparisons between differently managed forests and dashed arrows show comparisons within even-aged forest management regime

Deviations from the protocol

The search in Google Scholar was not limited only to "title, at least one of the words", instead the search was conducted with no limitations other than excluding citations and patents. During article screening, the title and abstract of an article were screened together instead of separate stages as stated in the protocol. Combining the title and abstract stages was deemed necessary to have more reliable screening results in relation to time spent. Full text screening differed also from what was written in the protocol [33]. Due to time limitations and the high number of articles included by title/abstract, each article was screened by one person only. To ensure consistency of decisions, an additional consistency check was performed at this stage (details given later in the text). Additional assessment of a random set of 20 Russian articles was not conducted contrary to what was specified in the protocol [33] because consistency assessment had been conducted in the full set of articles.

Data were extracted largely by AJ due to changed circumstances after the protocol was published. Team members did not extract data together from a set of studies. Instead, SS cross-checked data extracted from all uneven-aged articles and MH and AJ cross-checked data extracted from even-aged articles. There was also one important addition to eligibility criteria compared to the protocol: mature even-aged forest was added as a comparator because most articles reported results for young (< 80 years old) and mature (> 80 years old) even-aged forests separately. During the synthesis of the results, studies that fulfilled any of the criteria in the category 'high' (e.g. effect modifiers not considered) were not excluded from the synthesis as was written in the protocol [33]. Instead, their effect on results was tested by excluding them from the quantitative analysis as part of the sensitivity analyses.

Search for articles

Search string

Search strings were formulated based on discussions in the stakeholder meeting and known literature on the topic. A scoping exercise of alternative search terms was conducted before the protocol [33] was submitted to a peer-review and again after it was modified during the peer-review stage but before submission of the final protocol. The performance of the search strings was tested in CAB Abstracts, Scopus and databases included in the Web of Science Core Collection [Science Citation Index Expanded (1945-present), Social Sciences Citation Index (1956-present), Arts & Humanities Citation

Index (1975-present), Conference Proceedings Citation Index- Science (1990-present), Conference Proceedings Citation Index- Social Science & Humanities (1990-present), Emerging Sources Citation Index (2015-present) (hereafter treated as one for simplicity)] with a test list of 20 articles that can be found as an additional file of the published protocol [33]. All the articles in the test list were located during testing. Further details on the performance of the tested search strings can be found in the protocol of this review [33].

Searches were undertaken between March and September 2019. Details of the search strings used, exact dates and the number of articles found are given in Additional file 2. The search string in English is summarised below (in Web of Science format):

#1 TS=((Boreal NEAR/5 (forest* OR zone OR tree*)) OR taiga OR spruce* OR picea OR pine* OR pinus OR birch* OR aspen* OR populus).

#2 TS=(Finland OR Finnish OR Swed* OR Norw* OR Russia* OR Fennoscan* OR Scandin* OR "north* europ*" OR "nord* countr*") and TS=(forest* OR tree*).

#3 TS=(clear-cut* OR clearcut* OR clearfell* OR clear-fell* OR "clear fell*" OR even-aged OR uneven-aged).

#4 TS=(forest* NEAR/5("continu* cover*" OR "natural* regenerat*" OR multiage* OR alternativ* OR "common* sens*" OR unmanaged OR managed OR sustainabl*)).

#5 TS=(silvicult* NEAR/5("continu* cover*" OR "natural* regenerat*" OR multiage* OR alternativ* OR "common* sens*" OR unmanaged OR managed OR sustainabl*)).

#6 TS=(Regenerat* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(select* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(partial* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(alternat* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(retent* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(conserv* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(gap* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(patch* NEAR/5 (cut* OR fell* OR harvest* OR log*)) OR TS=(dispers* NEAR/5 (cut* OR fell* OR harvest* OR log*)).

#7 TS=(biodiversi* OR fauna OR flora OR fungi OR eukaryot* OR vertebrat* OR invertebrat* OR animal* OR plant* OR arthropod* OR lichen* OR insect* OR bird* OR mammal* OR vegetat* OR bryophyte* OR amphibian* OR reptile*).

#8 TS=(species NEAR/5 (divers* OR rich* OR assemb* OR abund*)).

#9 #2 OR #1.

#10 #6 OR #5 OR #4 OR #3.

#11 #8 OR #7.

#12 #11 AND #10 AND #9.

The search string was translated to other search languages (Additional file 3). It was simplified by reducing the number of search terms to search organizational websites and to conduct internet searches (Additional file 2). Boolean operators were used to combine main search terms whenever the search engine allowed it (Additional file 3). To detect articles published between the database search and data analysis, a search alert was set in two bibliographic databases (Russian Science Citation Index on the Web of Science (RSCI) and Scopus) and in the Web of Science Core Collection (WoS). Search alerts were on from 29th March 2019 to 29th August 2019.

Languages

The systematic review includes studies published in English, Finnish, Swedish, and Russian. The selection of languages was based on the geographical scope of the systematic review and limited by the language skills of the review team. Organisational websites and bibliographic databases were searched in the primary language the website/database is published except websites in Norwegian, which were searched in English. If a publications section or library catalogue included unique studies published in more than one of the review languages (e.g. main website language is Swedish but there are also unique publications in English), the search was conducted in all languages. The searches in search engines were conducted in all four languages.

Bibliographic searches

The searches in CAB Abstracts, RSCI, Scopus and WoS were conducted using Helsinki University institutional subscriptions and the full search strings (English and Russian) were used. For the rest of the databases no subscriptions were needed, and simplified search strings were used. For the full search details see Additional file 2.

The following bibliographic searches were conducted:

- CAB Abstracts (https://www.cabi.org/); Keyword search from 1973 onwards, no further limitations
- Directory of Open Access Repositories (https://doaj.org/); 'Search all' field was used with not further limitations.
- Digital Dissertations Library of Russian State Library (http://diss.rsl.ru/), Search made in the front page
- Doria (https://www.doria.fi/); Search made with "entire Doria" option
- Helka—University of Helsinki Catalogue (https://helka.finna.fi/); All fields were searched with no further limitations.
- Jultika—University of Oulu repository; All fields were searched with no further limitations.

- JYX—Publication archive of the University of Jyväskylä (https://jyx.jyu.fi/); All fields were searched with no further limitations
- Russian Science Citation Index on the Web of Science (https://clarivate.com/); Topic search, access from 2005 onwards.
- Russian Scientific Electronic Library (https://elibrary.ru/); title, abstract and key word search with no further limitations
- Scopus (https://www.scopus.com/home.uri); Title, abstract, and keyword search with no further limitations
- Swedish University Dissertations (http://www.avhandlingar.se/); All fields were searched with no further limitations
- UTUPub—University of Turku repository (https://www.utupub.fi/); All fields were searched with no further limitations
- Web of Science Core collection (https://clarivate.com/); Topic search covering all years within Science Citation Index Expanded (1945-present), Social Sciences Citation Index (1956-present), Arts & Humanities Citation Index (1975-present), Conference Proceedings Citation Index- Science (1990-present), Conference Proceedings Citation Index- Social Science & Humanities (1990-present), Emerging Sources Citation Index (2015-present).

Search engines

Internet searches were conducted in 'private' mode to prevent the influence of previous browsing history and location on search results. The search was conducted with no limitations other than excluding citations and patents. The searches were conducted in all four study languages using simplified search strings (Additional file 2). The results were organised by relevance. After the first 50 hits, results were checked until relevant articles were no longer retrieved as advised in Livoreil et al. [35]. One hundred irrelevant hits were deemed sufficient before the search was terminated. The maximum number of hits screened was 1000 as this was the maximum number of hits displayed in Google and Google Scholar (an error message was displayed after 100th page and further pages could not be viewed even when the number of hits shown in the first page was more than 1000). The final number of hits screened is reported in Additional file 2.

The following search engines were searched:

- Google Scholar (https://scholar.google.com/)
- Google (https://www.google.com/)

Organisational websites

Searches were conducted in the publication section of a website if available. If not, the search was conducted using the 'search' function of the front page. Search strings were adjusted to each website separately based on the properties of the 'search' function. If an organisation publishes a journal, the site of the journal was searched if the journal was not already included in some of the bibliographic databases searched. Russian websites were manually searched due to the low performance of the 'search' function to find relevant hits during scoping exercise. Some other websites were also manually searched in the case of no 'search' function was found or in the case when the 'search' function was not working properly. Full details of the searches are given in Additional file 2.

Supplementary searches

Citation chasing was undertaken to supplement the search. Citations were checked in the following articles:

- Five most relevant review-articles that were excluded at full text stage (Additional file 4). Relevance was defined based on the proximity of their topic to this review's research question.
- Five most recent even-aged management articles.
- The most recent article within every group (see data coding and extraction) of uneven-aged management articles.
- Five most recent individual (not belonging to a group) uneven-aged management articles.

In addition, a call for unpublished data was published on the website of the Evidence-Based Forestry in Finland project (http://npmetsa.fi/en/frontpage/) and sent directly to stakeholder organisations that may have unpublished data on the topic.

Article screening and study eligibility criteria

Screening process

Articles were screened at two stages: title/abstract and full text stage. Before screening was started, a random set of 100 articles (from CAB Abstracts, Scopus or WoS) was independently screened by each of the three screeners. Two sets of 100 articles (200/43,523 articles) were needed before the agreement level of ≥ 95% was achieved between the three screeners (AJ, MH, SS). All screening decisions that differed were discussed among the screening team to facilitate consistency. If a screener was unsure whether to include an article, it was moved to the next stage.

Full texts of articles included at title/abstract stage were retrieved from the internet, the Helsinki University

Library, the Jyväskylä University Library and by interlibrary loans. If an article was not found from these sources, it was classified as unretrievable. Due to time limitations and the high number of articles included by title/abstract, each article was screened by one person only. To ensure consistency of decisions an additional consistency check was performed at this stage. A random set of articles (5 percent of the articles included by title/abstract; 38 articles in total) was screened by each of the three screeners. An agreement level of ≥ 95% was achieved during the check after which screening process began. If a screener was unsure whether to include an article, it was discussed with other screeners.

Articles found in CAB Abstracts, Scopus and WoS were exported into Colandr application [36]. Colandr is developed for conducting systematic reviews and it utilizes artificial intelligence to sort articles by their relevance based on former decisions of the screeners to include or exclude articles. Screening by title/abstract in Colandr was terminated after 1000 consecutive articles presented by Colandr were determined ineligible. At that point 60% of the articles had been screened. To test the reliability of the decision to terminate the search, we searched Colandr for peer-reviewed articles located from other sources, e.g. Google Scholar and citation chasing, that the algorithm may have missed. No articles included in the review were found among the unscreened articles.

At the full text stage all articles were screened. Articles retrieved from other databases were manually screened at both stages of the screening. Articles in Russian were screened by only one person. All unsure cases were discussed within the group. Additional assessment of a random set of 20 Russian articles was not conducted because consistency assessment had been conducted in the full set of articles. Inclusion of articles authored by authors of this review was jointly determined by the other research group members in accordance with the eligibility criteria.

Eligibility criteria

The eligibility criteria were based on PECO components, study design and geographical location of the studies (Table 2). Studies located in Finland, Sweden, Norway and European Russia were eligible for this review. The criteria were specified in more detail after publication of the research protocol [33] to ensure consistency in screening decisions after it became clear that each article will be screened by a single person only.

Study validity assessment

All studies included after full-text screening were critically appraised. Critical appraisal of study validity was based on study design, sampling, accounting for potential effect modifiers and data analysis methods as these were deemed by the review team to be key variables related to reliability and generalisability of study findings. The criteria relate both to internal validity (risk of bias and confounding factors) and external validity (generalisability) of results. They include, for example, appropriate and representative replication, suitable outcome measuring methods, possibility of researchers to control baselines differences, measures taken to address potential baseline differences (e.g. accounting for spatial heterogeneity), and information about potential confounding factors) (Table 3). Following the appraisal, studies were categorised as 'low', 'medium' or 'high' risk of bias. If information was inadequate to make an assessment, the study was labelled as 'unclear'. Studies in 'low' and 'medium' categories were deemed to have sufficient quality to provide reliable evidence base in terms of quantitative synthesis and hence, the categorisation was used mainly in the narrative synthesis. The effect of studies with high risk of bias on the results was tested by including/excluding them from the quantitative analyses.

Due to time limitations, each study was assessed by one person (MH or AJ) and not by two as was stated in the protocol [33]. At the beginning of the critical appraisal, a consistency check was conducted with 100 studies included after full-text screening. AJ and MH assessed the studies independently and the assessment results were compared for consistency. There was a high agreement between AJ and MH on which articles to include as decisions differed in less than 5% of the studies (calculated as different decisions per 100 studies). The differences related to appraisal criteria on study design and sampling, which were clarified when decisions were discussed to improve consistency. Any uncertain decisions during the critical appraisal were discussed and the risk of bias determined jointly by the research group members. The validity of studies written by authors of this review was jointly determined by the other research group members in accordance with the critical appraisal criteria. The results of the assessment are given in Additional files 5 and 6. Where necessary, details of the reasoning are given next to the critical appraisal category.

Data coding and extraction strategy

Basic publication details and data on exposure, comparator(s), outcome, study subject (species), study year, study location and a description of the sampling method were extracted (Additional files 5 and 6). For being able to analyse responses of species specialised in different habitat types, the preferred habitat was categorised as 'forest', 'open habitat', 'generalist' or 'soil'. If the study subject included both forest and open habitat species, it was categorised as 'both'. None of the study subjects were categorised into more than one category.

Table 2 The eligibility criteria for article screening

Question elements	Eligibility criteria
Populations	*Included*: Boreal forests in Fennoscandia and European Russia (the dominating tree species in the study area must be spruce or pine)
Exposure	*Included*: Even-aged forest management Uneven-aged forest management Excluded: Thinning (studies where the objective is to study precisely the effects of thinning, thinned even-aged forests were included) Retention (articles where the objective is to study precisely the effects of retention)[a] Management where the stems and all cutting biomass were left in the forest (restoration, not for production purposes)
Comparators	*Included:* Young even-aged forest, age ≤ 80 years Mature even-aged forest, age ≥ 80 years Natural or near-natural forests, including protected forest areas, national parks Retention felling (only included in the case of experimental studies where traditional clearcut (i.e. all the trees are removed) is one of the treatments; otherwise even-aged forests where retention felling had been done were included as even-aged forest) *Excluded*: Non-forest lands, e.g. agricultural areas, parks in urban areas Tree plantations not considered to be forest, e.g. Christmas tree plantations Forested peatlands
Outcomes	*Included*: Species richness Abundance (counts or coverage) *excluded*: All data on non-terrestrial species and bacteria Data on tree species Amount of dead wood (is treated as an effect modifier) Community composition indices Species biomasses Visiting frequency/habitat occupancy/breeding success etc. Number of nests/grouse leks/ant mounds etc.
Study design	*Included:* Control-intervention field studies *Excluded*: Simulation/modelling studies (even partly simulated/modelled) Studies where exposure/comparator and outcome data are from different sources (combining the data of two different field data) Habitat selection studies Edge effect studies (But included if there are separate areas, for example, clearcut interior/edge area/forest interior. In addition, interior areas should be located far enough from the edge relative to the species in question so that edge effects do not compromise the results) Studies, where the study subject (often lichen) is transplanted to the exposure/comparator area
Language	*Included:* English Finnish Swedish Russian

[a] There has been a recent meta-analysis on the impact of retention on biodiversity [19]

Approximately 80% of the even-aged and over 90% of uneven-aged articles included information about preferred habitat of studied species. National species databases were searched to find information of habitat preferences when none were given in the publication [38, 39]. If there was uncertainty under which category the study subjects belonged to, it was classified as 'both' to avoid bias of misclassification.

Multiple articles from one study site (i.e. linked articles) were appraised as a group to avoid inclusion of duplicate data following Frampton et al. [37]. Within each group data on different taxa were extracted. If there were several articles on the same taxon (e.g. from different years or regarding different outcome measures), only independent outcome data and study site information were extracted from the articles and combined in the data set. No duplicate data were collected. If there were results of several independent studies in one article (e.g. from multiple taxa), data were extracted

Table 3 Critical appraisal criteria to assess individual studies in the full text stage

Factor	Low	Medium	High
Study design	Experimental studies (includes also quasi-experimental studies)	Observational studies (intervention is not under the control of the researcher)	Case studies (descriptive study of a particular case)
Sampling	Large sample size relative to outcome measure and species in question (high confidence that replication is appropriate and representative) Sampling method suitable for the population of interest[a] Randomisation of the study areas accounts for spatial heterogeneity Random sampling of study subjects Control and exposure areas matched based on their ecological characteristics	Small to medium sample size relative to outcome measure and species in question (medium level of confidence that replication is appropriate and representative) Sampling method suitable for the population of interest[a] Control and exposure areas comparable based on their ecological characteristics	Sampling method not suitable for collecting data on the population of interest[a]
Accounting for heterogeneity and potential effect modifiers	Potential biologically important effect modifiers that could influence the study findings identified, and data collected on them. The context in which the study took place clear	Potential biologically important effect modifiers that could influence the study findings identified and considered in relation to the results. The context in which the study took place clear even when there was no direct data collection	Effect modifiers not identified or considered. The context of the study is unclear
Data analysis methods	Methods appropriate[b]	Methods appropriate[b]	Methods not appropriate[b]

Studies that fulfilled any of the criteria in the category 'high' (e.g. effect modifiers not considered in an observational study with medium sample size) were considered 'high risk'

[a] Suitable sampling method refers to the use of methods that are known to work for the population in question based on published studies, e.g. flying insects are sampled by trapping or fogging, not by cutting branches

[b] Appropriate methods refer to the use of statistical methods that consider data characteristics such as sample size and distribution. For example, non-parametric statistical tests are used for data that does not follow normal distribution

from each of them separately. Data were recorded in an Excel spreadsheet (Additional file 5 and 6).

Data on sample sizes, outcome means, standard deviations (SD), and standard errors (SE) were extracted. WebPlotDigitizer [40] was used to extract data from figures. If data on outcome mean, SD or SE were not available, data on test statistics that could be converted into effect size metrics were collected. Data on effect modifiers and potential sources of heterogeneity were extracted to enable statistical exploration of the relationship between outcomes and sources of heterogeneity. Authors of the articles were contacted by e-mail to retrieve any missing information or data.

One article could include more than one suitable exposure (uneven-aged: selective felling and gap felling, even-aged: different aged even-aged forests). In the case of uneven-aged management selective felling was chosen as the primary exposure because it was the exposure in the majority of the included studies. Seven studies (3 articles) included data from both selective and gap felling in which case gap felling was excluded as an exposure. In the case of comparisons between different even-aged forests, sapling stand (about 10 years old) was selected as the primary exposure which was compared to other even-aged forest stands (retention and mature forest). If data for sapling stand was not available, then exposures were selected in the following order: clearcut (0–5 years old) → young forest (20-40 years old) → middle-aged forest (40–80 years old). If even-aged forest was compared to natural forest, also mature even-aged forest (over 80 years old) could be selected as an exposure. If both exposure and comparator had stands of different ages, data from all were extracted and same age classes were compared to each other in the analyses.

There were some studies where the forest was described as almost natural with some signs of logging. In these cases, the forest was classified as uneven-aged only when it was said to be selectively cut. If the forest was described as mainly untouched with few signs of past removal of trees, it was classified as natural. There were also studies, where retention comparator was divided into two: areas where the retention trees were standing and the clearcut area surrounding it. In these cases, data on the retained area were extracted.

If studies had data from multiple years (i.e. same study conducted in different years), only data from the last year of the study were extracted to avoid temporal dependence between samples. The only exception was when there had been at least two decades between sampling occasions. In this case the data were deemed to be independent (i.e. not more similar to each other than to other data in the data set) based on the ecology of the studied species. When extracting data on studies with BACI study design, only data on CI-comparisons were extracted.

Abundance data of single species were extracted only for mammals. Articles where studies concentrated on one species (apart from mammals) were included in the narrative synthesis if they fulfilled the eligibility criteria. Data concerning tree species richness/abundance were not extracted.

Data were extracted mainly by AJ. Therefore, in deviation from the protocol [33], team members did not extract data together from a set of studies but instead data were cross-checked by SS or MH. AJ checked data extracted by MH. At the beginning of the data extraction process AJ, SS and MH discussed data extraction in the context of the first ten articles to ensure that they have a shared understanding of how variables are coded and that the data extraction sheet captures all important information. As a result of the discussions, three effect modifiers were added to the data extraction sheet. Any uncertainties on what data to extract later in the data extraction stage were discussed among the group.

Potential effect modifiers and reasons for heterogeneity

To understand variation in effect sizes, possible effect modifiers were extracted from the studies. The list was compiled based on the authors' subject expertise and in consultation with the stakeholders who participated in the stakeholder meeting. It was peer-reviewed and published in the protocol of this review [33]. Three effect modifiers were added to the list after the protocol was published: the amount of dead wood, intensity of harvesting and the age of the forest. For uneven-aged forest, age was recorded either as range or as the age of the oldest tree class depending on the information given in the article. The full list of potential effect modifiers is following:

- Geographic location (country, latitude-longitude)
- Climatic conditions (description including temperature, rainfall and other details if given)
- The year(s) the study was conducted
- Time since the exposure started
- The length of the study
- Size of study area (ha)
- Forest type and soil type (dominant tree species and soil type, potential soil treatment)
- Differences in management type (details of intervention/comparator and history of management)
- Certification (yes/no, certification system if mentioned)
- Owner of the study site(s) (private, company, state)
- Harvesting of energy wood (includes stumps, branches)
- Amount of dead wood (m^3/ha)
- Age of the forest (for uneven-aged forest recorded either as range or as the age of the oldest trees depending on the information given in the article)
- Intensity of harvest (% of area harvested or % of tree volume removed).

Data synthesis and presentation

A narrative synthesis of data from all the included studies was produced. Linked articles were included at the full text stage but only studies that had independent data on the outcomes were included in the narrative synthesis. The narrative synthesis describes the evidence-base with tables and figures, including description of exposures and comparators, study locations and designs, and studied taxa. All the information described in the narrative synthesis can be found in Additional files 5 and 6.

In addition to the narrative synthesis, a quantitative synthesis, i.e. meta-analysis, was conducted to assess the effects of forest management on biodiversity outcomes at stand level. Studies that provided quantitative data on outcome measures were included in the meta-analysis. Studies that had incomplete or missing information that could not be retrieved were excluded from the meta-analysis.

Meta-analysis

Standardised mean difference (Hedges' d) was used as a measure of the effect size for species richness and abundance:

$$d = \frac{(\bar{X}_e - \bar{X}_c)}{s} J$$

where $\bar{X}_e$ and $\bar{X}_c$ were the means of the exposure and control groups, s is the pooled standard deviation and J is a correction term mitigating for small sample size bias.

The pooled standard deviation was calculated as

$$s = \sqrt{\frac{(n_e - 1)SD_e^2 + (n_c - 1)SD_c^2}{n_e + n_c - 2}}$$

where n_e *and* n_c are the sample sizes of the exposure and control groups and *SD* is the standard deviation.

Correction term *J* was calculated as

$$J = 1 - \frac{3}{4(n_e + n_c - 2) - 1}$$

Variance for Hedges' d was calculated as

$$var = \frac{n_c + n_i}{n_c n_i} + \frac{d^2}{2(n_c + n_i)}$$

If there were non-independent cases within a study (i.e. uneven-aged forest was compared to both production and natural forest), a corrected overall sample size, $N_{corrected}$ was calculated to avoid double counting the exposure sample size following the method described in Gleser and Olkin 2009 [41]:

$$N_{corrected} = n_e + \sum_{1}^{i} n_c$$

where n_e is the sample size of the exposure and n_c are sample sizes for the controls.

$N_{corrected}$ was then used to calculate corrected S_{pooled}, *J*, *Hedges' d* and its variance for studies with non-independent cases:

$$S_{pooled.corrected} = \sqrt{\frac{(n_e - 1)SD_e^2 + (n_c - 1)SD_c^2}{N_{corrected} - 2}}$$

$$J_{corrected} = \left[1 - \frac{3}{4(N_{corrected} - 2) - 1}\right]$$

$$var_{corrected} = \frac{1}{n_c} + \frac{1}{n_e} + \frac{d^2}{2(N_{corrected})}$$

If information on means or SDs was missing, available test statistics were used to either calculate SDs or to convert available test statistics to Hedges' d. Imputation was used to calculate missing SDs:

$$SD = \bar{X}_j \left(\frac{\sum_e^K SD_e}{\sum_e^K \bar{X}_e} \right)$$

where $\bar{X}_j$, is the observed mean of the study with missing information, and *K* is the number of j^{th} studies with complete information.

To estimate overall effect sizes, random effects model with restricted maximum-likelihood estimator (REML) was used to account for between and within study variance. Inverse-variance weights were used in the model, i.e. weights were equal to $w^i = (v_i + \tau^2)^{-1}$. Cochran's Q-test [42] was used to test whether variability in the observed effect sizes is larger than would be expected based on sampling variability alone. A significant test indicates that the true effects are heterogeneous. To test the effects of moderators (i.e. effect modifiers) mixed-effects model with REML was used. Q-test was used to test for residual heterogeneity (QR), i.e. variability in effect sizes that was not accounted for by the moderators whereas the test of moderators (QM) was used to test whether at least one of the regression coefficients (not including the intercept) is different from zero.

Data were analysed in two hierarchical steps. First, an analysis of the overall effect size per forest management category was conducted for both outcome measure (species richness and abundance) (Table 4). At this stage, potential publication bias was explored by producing funnel plots and conducting trim and fill-tests [43]. The influence of grouped studies (i.e. studies from the same study site) and logging intensity was tested for comparisons between uneven-aged forest and comparator forest areas. Also, sensitivity analyses were conducted by excluding studies with imputed SDs and studies included in the 'high risk of bias' category in the critical appraisal. Influence of potential outliers was also tested at this stage. In addition, possible influences of the type of publication (academic or grey literature), country, study year or sampling method on effects sizes were tested.

At the next stage, differences in outcome measures were tested between exposure and comparators. First, differences in species richness and individual abundance between different comparator forests were investigated. To test for differences in effect sizes between exposure and comparators, a mixed-effects model was used when the amount of residual heterogeneity within each subgroup (defined by a comparator) did not differ significantly across subgroups [44]. The mixed-effects model has a single variance component for the amount of residual heterogeneity and hence, assumes that the amount of heterogeneity within subgroups is the same. If significant differences were found, separate analyses were performed for each exposure-comparator pair. A likelihood ratio test (LRT) was used to examine whether there were significant differences in residual heterogeneity.

Second, potential effect modifiers linked to species richness and abundance were analysed (Table 4). The number of effect modifiers were limited to those that based on literature [e.g. 45] are most likely to influence species responses to avoid losing statistical power due to too many moderators in relation to the number of studies in the analysis. Taxa were pooled at the order level or higher to have enough responses per category. Studies that had only one case per comparator forest were excluded from the analysis. Not all studies included in the meta-analysis had information on both forest attributes and therefore, subsets of studies were used in the analyses. The influence of forest or species attributes was not tested if there were less than five studies. All statistical tests were conducted in R version 3.6.3. [46] using the *rma.mv* and *rma.uni* functions in the *metafor* package [47].

Table 4 Variables used in the data analysis. Excludes intensity of harvest, which was tested only for uneven-aged forests

Category	Variable	Description
First stage of analysis: At the forest management level (uneven-aged or even-aged)		
Publication bias	Effect size	
Effect modifiers related to study attributes	Country	
	Study year	
	Sampling method	
	Literature type	Academic or grey literature
Comparator	Management type	Natural, young even-aged forest, mature even-aged forest or retention forest
Second stage of analysis: At comparator forest level		
Species attributes	Taxa	Taxa that had at least two studies per comparator were analysed
	Habitat specialism	Forest dependent species, generalist, open habitat species, soil inhabiting species
Forest attributes	Deadwood	Volume of deadwood Uneven-aged management: Volume of deadwood in comparator forest when the comparator was young even-aged forest or retention; volume of deadwood in exposure forest when the comparator was mature even-aged or natural forest. Even-aged management: Volume of deadwood in exposure forest in the case of all comparators
	Years since harvest	How many years ago the forest was harvested Uneven-aged: time since exposure forest was harvested was used when comparator was natural forest or mature even-aged forest; time since comparator forest was harvested was used when comparator was young even-aged forest or retention Even-aged: time since exposure forest was harvested was used with all comparators

Review findings

Review descriptive statistics

Searches in bibliographic databases CAB Abstracts, Scopus and Web of Science were conducted in March 2019. The rest of the bibliographic databases were searched during May–July 2019. Searches in the first three databases resulted 27 252 hits and in the other databases 2 314 hits (total 29,566; Fig. 2; Additional file 3). Search alerts were on from 29th March 2019 to 29th August 2019 and resulted 271 hits.

Search engine searches were conducted in July–September 2019 and resulted 8077 hits. Organisational websites were searched March–May 2019 and returned 5 609 hits. Russian websites were manually searched, and 64 potentially relevant articles were found. A call for data resulted in 34 articles from four researchers. Citation chasing was conducted in September 2019. Altogether 25 articles were checked for citations. All search dates and the number of hits are summarized in Additional file 3.

In the end, 667 full text articles were screened and 178 of these were included in the review (Fig. 2). In addition, seven articles found through citation chasing and one article found outside the pre-determined sources were included at the full text stage, and hence, the final number of articles included was 186. All articles excluded at the full text stage and the reason for exclusion are listed in Additional file 4. The most common reasons for exclusion at the full text stage were study design (for example, review articles, simulations, habitat selection studies or edge effect studies), comparator (for example, lack of comparator or too little information about the comparator to ensure eligibility), population (for example, not eligible country, not boreal forest) and exposure (for example, poor description of the exposure or the exposure was not eligible) (Fig. 2).

124 of the 186 articles included in the review belonged to a group (i.e. they were linked articles that share a common study site). Of these, only 75 reported independent data. Articles commonly reported outcomes from more than one study. For example, outcomes were reported for several taxonomic groups separately or article included outcome data from multiple comparisons. Altogether 854 studies from 137 articles had independent data (Fig. 2) and were included in the narrative synthesis. Furthermore, 547 studies from 88 articles had suitable data for meta-analysis.

Three articles included at the full text stage were authored by one of the authors of this review (MM). The inclusion and critical appraisal of these articles were

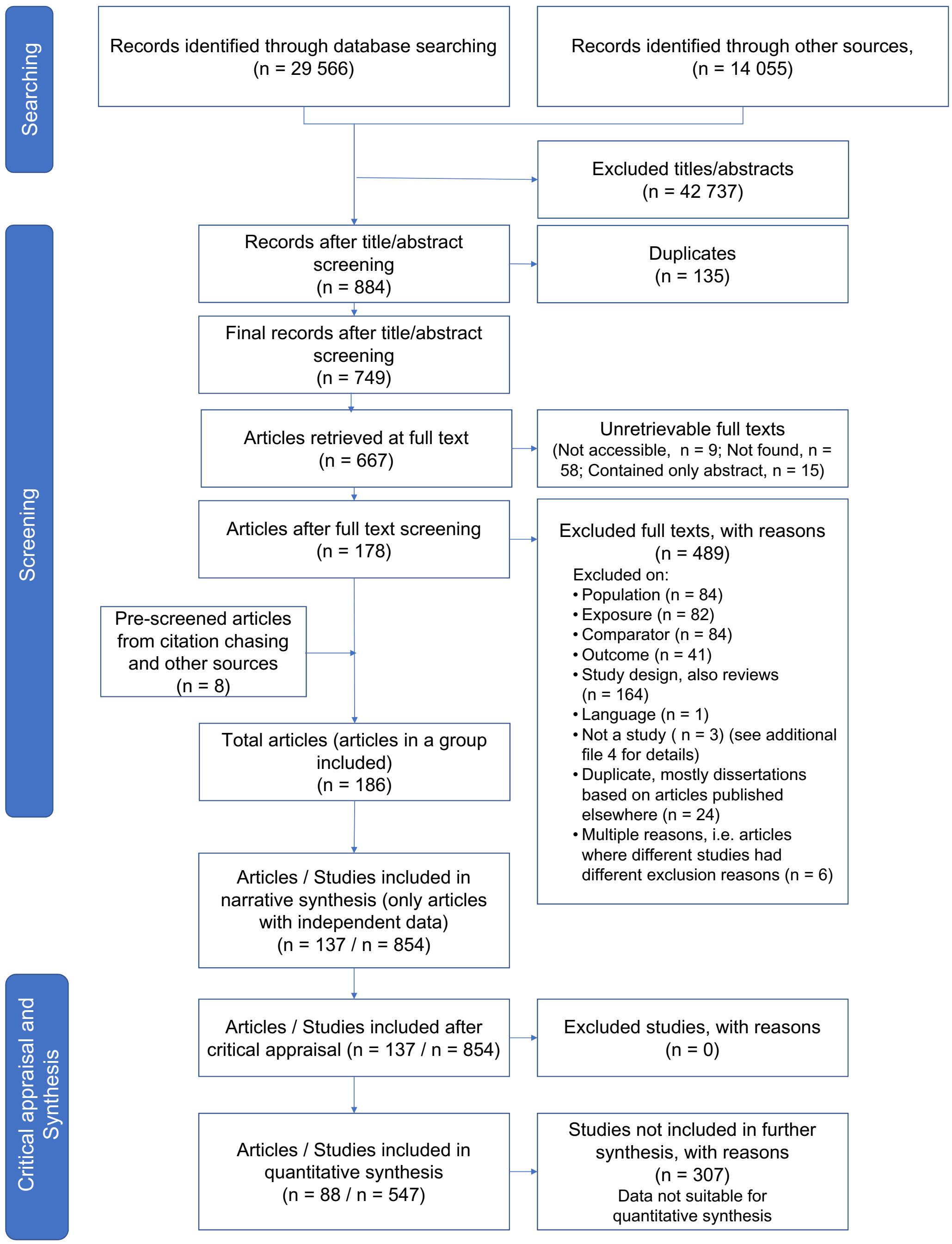

Fig. 2 Flow diagram adapted from ROSES [48] showing literature sources and inclusion/exclusion process. Note that duplicate removal after searches was not fully successful and some duplicates were removed only after title/abstract screening. Excluded articles include also duplicates but the exact number cannot be reported as automatic duplicate removal did not function as desired in the software used

assessed by SS, MH and AJ following the eligibility and critical appraisal criteria determined in the protocol [33] and taking into account the subsequent modifications stated in this review.

Sources of articles included in the narrative synthesis

Majority of the articles included in the narrative synthesis were found in CAB Abstracts, Scopus or Web of Science databases (110 articles, 80.3%). Through other bibliographic searches five (3.6%) articles were found. Other searches resulted in the following number of articles: search engines nine (6.6%), citation chasing four (2.9%), search alerts four (2.9%), organisational websites three (2.2%), call for data one (0.7%) and other sources (found outside the predetermined sources) one (0.7%). The three articles found in organisational websites were from Russian sources.

Narrative synthesis including validity assessment

Management types

Of the 137 articles included in the narrative synthesis, 99 studied even-aged, 10 uneven-aged and 28 both forest management regimes. In the case of articles where exposure could have been either uneven-aged or even-aged forest management, uneven-aged management was chosen as the exposure. This choice was made because uneven-aged management was the less-studied management type. In the end, there were 603 even-aged management studies and 251 uneven-aged management studies. Details of the studies and data included in the narrative synthesis can be found in Additional files 5 and 6.

Table 5 Articles included in narrative synthesis by language

Forest management regime	English	Russian	Finnish	Swedish
Uneven-aged	33	3	1	1
Even-aged	88	7	4	0

Literature type

Six types of literature were included, but majority were peer-reviewed journal articles (129 articles). In addition, there were one book chapter, two master's theses, one bachelor's thesis, one dissertation article, one report and two monographs. Most of the articles were written in English (Table 5, Additional files 5 and 6).

Publication year

Majority of the articles were published after year 2000, especially those on uneven-aged management (Fig. 3).

Locations

Most of the studies were conducted in Finland or Sweden. There were more studies on uneven-aged than on even-aged forest management conducted in Norway. In the case of other countries, the number of studies considering even-aged management was higher (Table 6, Additional files 5 and 6). 15 of the 38 uneven-aged articles (39.5%) included in the narrative synthesis were from a project called MONTA, which focused on biodiversity impacts during the regeneration of production forests in Finland between 1996 and 2006. Of the 198 studies included in meta-analysis 98 (49.5%) were MONTA studies.

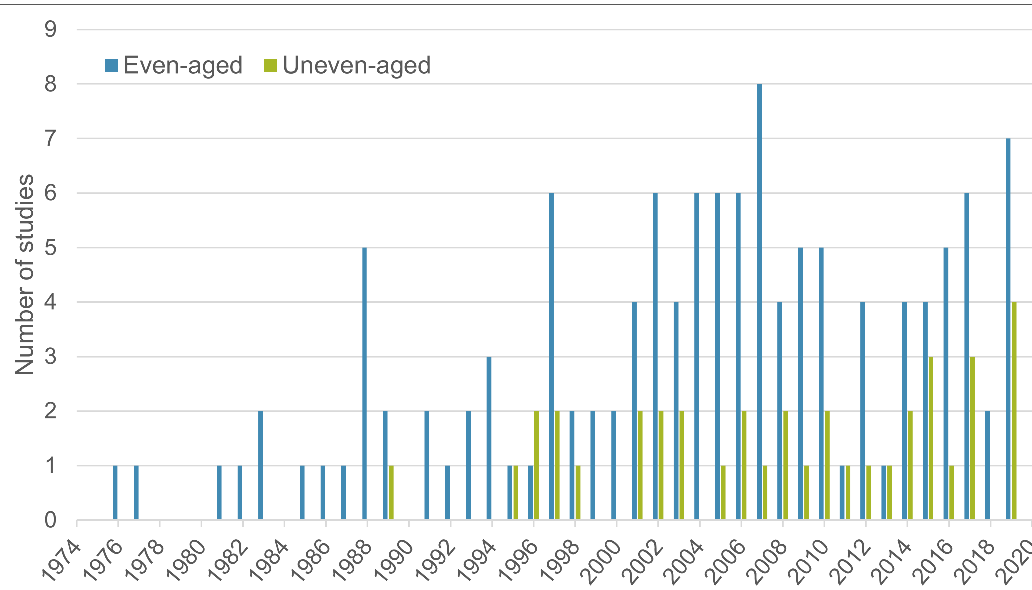

Fig. 3 Articles included in narrative synthesis by year of publication

Table 6 Articles and studies included in narrative synthesis by study country

Forest management regime	Finland	Sweden	Norway	Russia	Finland + Russia (article contained study sites in both countries)
Uneven-aged articles	15	12	6	3	2
Uneven-aged studies	126	64	51	8	2
Even-aged articles	40	37	10	10	2
Even-aged studies	355	145	27	40	36

Study designs

A total of 597 studies presented control-intervention (CI) data, 253 before-after-control intervention data (BACI), and 4 before-after (BA) data (Additional files 5 and 6). Of the uneven-aged management studies 142 presented CI data, 109 BACI data and 0 BA data. Of the even-aged management studies 455 presented CI data, 144 BACI data and 4 BA data.

Exposures

As defined, there were two exposure classes: uneven-aged and even-aged forest management and there were 251 and 603 studies of them, respectively. Uneven-aged management was either selective felling (single-tree or small tree groups) or gap felling, in few cases also strip felling and one experimental study on shelterwood cutting (for details see Additional file 5). The intensity of tree removal varied between studies. In some, selective felling meant removing the largest trees (for example [49]) whereas in others up to 54% of the tree volume was removed (for example [50]). Gap felling typically meant that 60-66% of tree volume was removed. In two articles, one on gap felling [51] and another on shelterwood cutting [52], almost 70% of the tree volume was removed. In experimental studies the actual time of felling was usually known. In other studies, the time of felling was estimated, or the forest was defined as selectively cut by the stand structure or the number of stumps visible. Time of felling was more or less evenly distributed across the data set.

Even-aged management was clearcut, sometimes with retention trees. The youngest even-aged forests were cut only few months before the study (for example [53]) whereas the oldest were approximately 100 years old (for example [54]). Further details are provided in Additional file 6.

Comparators

The most common comparators were natural forest followed by mature even-aged forest (Table 7, Additional files 5 and 6). Most natural forests were relatively old, from 100 to 300 years, but also some younger post-fire semi-natural forest comparators existed (for example [51]). Mature even-aged forests were by definition at least 80 years old, and the oldest ones were approximately 200 years old over-mature even-aged forests [54]. When the exposure was uneven-aged management, young even-aged forest was a common comparator. These were between 0 (right after clearcut) and 80 years old.

Table 7 Studies included in the narrative synthesis by comparator

Forest management regime	Young even-aged forest	Retention felling	Mature even-aged forest	Natural forest
Uneven-aged	95	30	50	76
Even-aged	–	26	193	384

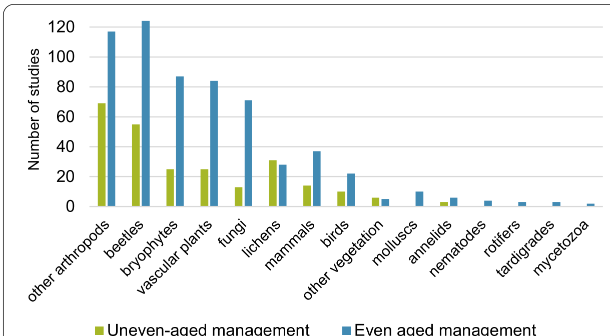

Fig. 4 Taxa studied in the studies included in the narrative synthesis. Other arthropods = all arthropods except beetles. Other vegetation = for example, the studies where the study subject was the whole field layer

Outcomes

Two biodiversity outcomes were included in the review: species richness and abundance. Of the uneven-aged management studies, 96 contained data on species richness and 155 on abundance (Additional files 5 and 6). Of the even-aged management studies, 262 contained data on species richness and 341 on abundance.

The studies on uneven-aged management contained data on nine different taxa and studies on even-aged management on fourteen different taxa (Fig. 4). The most studied taxa in both management types were arthropods, around half of which were beetles. They were followed by lichens, bryophytes and vascular plants in articles on uneven-aged management and by bryophytes and vascular plants in articles on even-aged management.

Potential effects modifiers and sources of heterogeneity

Reporting of the potential effect modifiers and sources of heterogeneity varied. Geographic location, years when the study was conducted, and forest type were reported in almost every article. Climatic conditions, size of the sampling area, soil type and amount of dead wood were reported in some of the articles. The least reported effect modifiers were certification, owner of the study site and harvesting of energy wood. Soil moisture (drained vs. non-drained) and connectivity were dropped as effect modifiers because they were hardly reported at all. Further details can be found in Additional files 5 and 6.

Table 8 Studies included in the narrative synthesis by their study validity assessment statuses

Forest management regime	Low risk	Medium risk	High risk	Unclear
Uneven-aged	83	160	0	8
Even-aged	42	546	4	11

Study validity assessment

For each included study, a validity assessment was conducted. If an article contained more than one study, all studies were assessed separately. In the summary table presented in Additional files 5 and 6, results of the validity assessment are presented per study. Studies within articles differed in their assessments only in two articles ([55], id 139, medium + high, some of the studies did not report sample size; [56], id 155, medium + low, in some of the studies sampling methods did not meet the criteria for 'low risk of bias' category). No studies were excluded after the critical appraisal was completed.

Most of the studies were appraised as having a medium risk of bias (706 studies). 125 studies were assessed to have a low risk of bias and 4 studies were assessed to have a high risk of bias (Table 8, Additional files 5 and 6). The reason for the high risk of bias were unsuitable analysis methods. 19 Russian studies were assessed as 'unclear' because their methods were inadequately described (sampling method or sample size not told). The low number of studies with low risk of bias was partly a result of high number of observational studies that were classified as having a medium risk of bias because researcher has no control over the exposure.

Data synthesis

Description of the articles included in meta-analysis

In total 88 articles with 547 studies had suitable independent data for meta-analysis (Fig. 5). Uneven-aged

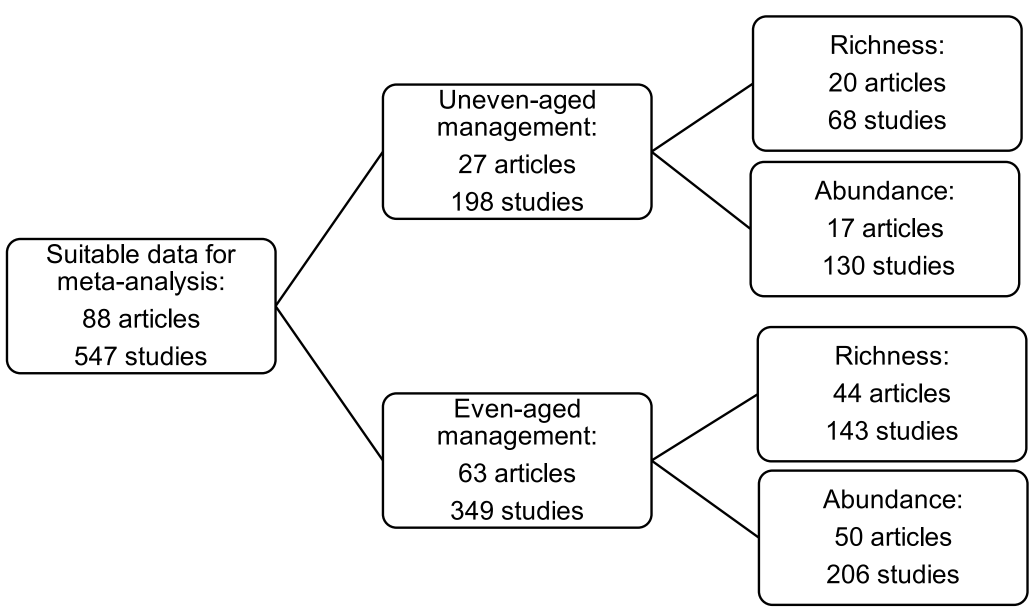

Fig. 5 Articles and studies including suitable data for meta-analysis classified by management regime and outcome. The sum of uneven-aged management articles and even-aged management articles is not the sum of all articles because two articles had independent data on both uneven-aged and even-aged management

Table 9 Studies included in meta-analysis by country

Forest management regime	Finland	Sweden	Norway	Russia	Finland + Russia
Uneven-aged	120	48	28	0	2
Even-aged	161	110	17	26	35

Table 10 Studies included in meta-analysis by comparator

Forest management regime	Young even-aged forest	Retention felling	Mature even-aged forest	Natural forest
Uneven-aged	75	30	37	56
Even-aged	–	18	104	227

management was the exposure in 198 studies (27 articles) whereas even-aged management was the exposure in 349 studies (63 articles). The sum of even-aged and uneven-aged management articles is not equal to the total number of the articles included in the meta-analysis because two articles had independent data on both exposures [45, 57]. At the study level, 80 studies on uneven-aged management were assessed as having a low risk of bias, 118 medium and 0 a high risk of bias. Of the even-aged management articles 112 were assessed as having a low risk of bias, 227 medium and 10 a high risk of bias (Additional files 5 and 6).

Majority of the studies were conducted in Finland (Table 9) (Additional files 5 and 6). When the exposure was uneven-aged management, the most common comparator was young even-aged forest (Table 10) (Additional file 5). For even-aged management it was natural forest (Additional file 6). Majority of the studies concentrated on forest dependent species (Table 11). The most studied taxa were arthropods (especially beetles and in the case of uneven-aged management also spiders) (Additional files 5 and 6). The other common species were lichens and vascular plants (uneven-aged management) and bryophytes and vascular plants (even-aged management).

Logging intensity (percentage of tree volume removed) in the uneven-aged forest was recorded in 35 studies on species richness and in 55 studies on abundance (Table 12) (Additional files 5 and 6). Age of the oldest

Table 12 Level of logging intensity of the uneven-aged forest in the studies included in the meta-analysis. Not all studies had recorded logging intensity

Studied biodiversity outcome	Logging intensity 60–70%	Logging intensity 40–50%	Logging intensity 30–40%
Species richness	23	2	10
Abundance	18		37

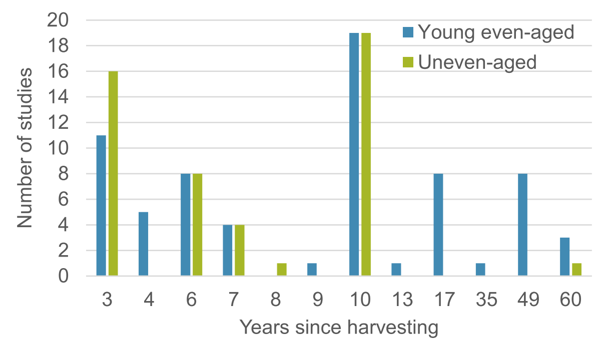

Fig. 6 Years since harvesting for uneven-aged and young even-aged forests

tree class in the uneven-aged forests varied from 25 to 287 years but was commonly between 40-130 years. Also, years since harvesting ranged from recently cut to more than 200 years but were similar between uneven-aged forests and young even-aged forests (Fig. 6). Deadwood volumes varied between different comparator forests. Uneven-aged forest had 8–47 m^3/ha, even-aged forest 4–11 m^3/ha, and natural forest 17–73 m^3/ha of deadwood. Detailed information is given in Additional file 5.

In the following sections the results of meta-analyses are given by exposures (uneven-aged and even-aged forest management) and outcomes (species richness and abundance). Overview of the results is presented in Table 13. During each four overall analyses, sensitivity analyses were conducted by excluding studies with imputed SDs. Results were consistent with or without studies with imputed SDs for all exposures except when species richness was the outcome variable and even-aged forest the exposure (for results see Additional file 7). In

Table 11 Studies included in meta-analysis by habitat specialism of the studied species

Forest management regime	Forest dependent species	Open habitat species	Generalists	Soil inhabiting species	Multiple species with different specialisms
Uneven-aged	85	16	33	25	39
Even-aged	172	9	33	9	126

Table 13 Summary of the meta-analysis results

Exposure	Comparator	Overall effect	Forest dependent species	Open habitat species	Taxa	Years since harvesting	Deadwood
Species richness							
Uneven-aged forest	Young even-aged forest		++	–			
	Retention			–			na
	Mature even-aged forest	++				*	na
Young even-aged forest	Retention		na	na			na
	Mature even-aged forest		–	++	**	**	
Uneven-aged forest	Natural forest				*		na
Even-aged forest		–	–			**	
Abundance							
Uneven-aged forest	Young even-aged forest	++	+	–			*
	Retention			–			na
	Mature even-aged forest			+	**	**	na
Young even-aged forest	Retention		na	na	na	na	
	Mature even-aged forest		–		**		na
Uneven-aged forest	Natural forest	+					na
Even-aged forest							

Top row shows outcome variable and effect modifiers. Excludes intensity of harvesting, whose influence on overall effect sizes was tested only for uneven-aged forest. Key: ++ significantly more species/individuals in the exposure, – significantly more species/individuals in the comparator, ± marginally significant effect. For taxa, years since harvesting, and deadwood ** denotes significant influence and * marginally significant influence on effect sizes. Empty cells denote no effect and na is used when effect could not be tested for the lack of data

that case, removing studies with imputed SDs caused publication bias based on the trim and fill-test. Hence, studies with imputed SDs were included in all of the analyses. Ten studies included in the meta-analysis were deemed as 'high risk'. They were all comparisons of individual abundance between even-aged and natural forest. Sensitivity analyses were conducted by excluding those studies and the results are reported in the text and in Additional file 8.

Uneven-aged forest management compared to even-aged forest management

Species richness Uneven-aged forests had higher overall species richness, but the effect was not statistically significant ($d = 0.229$, $p = 0.345$, $n = 68$) (Fig. 7). There was considerable heterogeneity as expected due to different comparator forest areas and species ($Q = 587.908$, $p < 0.0001$). Publication bias was not visually detected, and trim and fill-test confirmed that adjustment to the effect size was not needed (Additional file 9). None of the effect modifiers related to study attributes (country, year when data were collected, literature type and sampling method) had systematic impact on the effect sizes ($QM = 1.957$, $p = 0.744$). No significant differences in species richness were detected between studies from the MONTA project that were all conducted in the same area and other studies from different areas ($QM = 0.085$, $p = 0.771$). Also, intensity of harvesting (percentage of tree volume removed) had no impact on species richness ($QM = 0.35$, $p = 0.554$, $n = 35$).

Residual heterogeneity within subgroups differed significantly across subgroups ($p < 0.001$) and therefore, pairwise comparisons were performed to compare species richness between subgroups. When uneven-aged forest was compared to young even-aged forest (clearcut harvest < 80 years ago), overall species richness did not differ significantly ($d = -0.059$, $p = 0.919$, 95% CI -1.190, 1.072, $n = 26$) (Fig. 8). There were more forest dependent species in the uneven-aged forest than in the young even-aged forest ($d = 2.470$, $p = 0.0033$, 95% CI 0.821, 4.118, $n = 26$) but opposite was true for open-habitat specialists ($d = -6.235$, $p < 0.0001$, 95% CI -8.828, -3.641, $n = 26$). Habitat specialism explained 70% of the variation in effect sizes. There was enough data for beetles, spiders and plants (including mosses and vascular plants) to test the effect of taxon but no association was found ($QM = 0.847$, $p = 0.655$, $n = 21$). Neither of the forest attributes, the amount of deadwood in the young even-aged forest and years since it was harvested, was significant (deadwood: $QM = 0.142$, $p = 0.706$, $n = 12$; years since young even-aged forest logged: $QM = 1.468$, $p = 0.226$, $n = 26$).

When uneven-aged forests were compared to forests undergone retention harvest, overall species richness

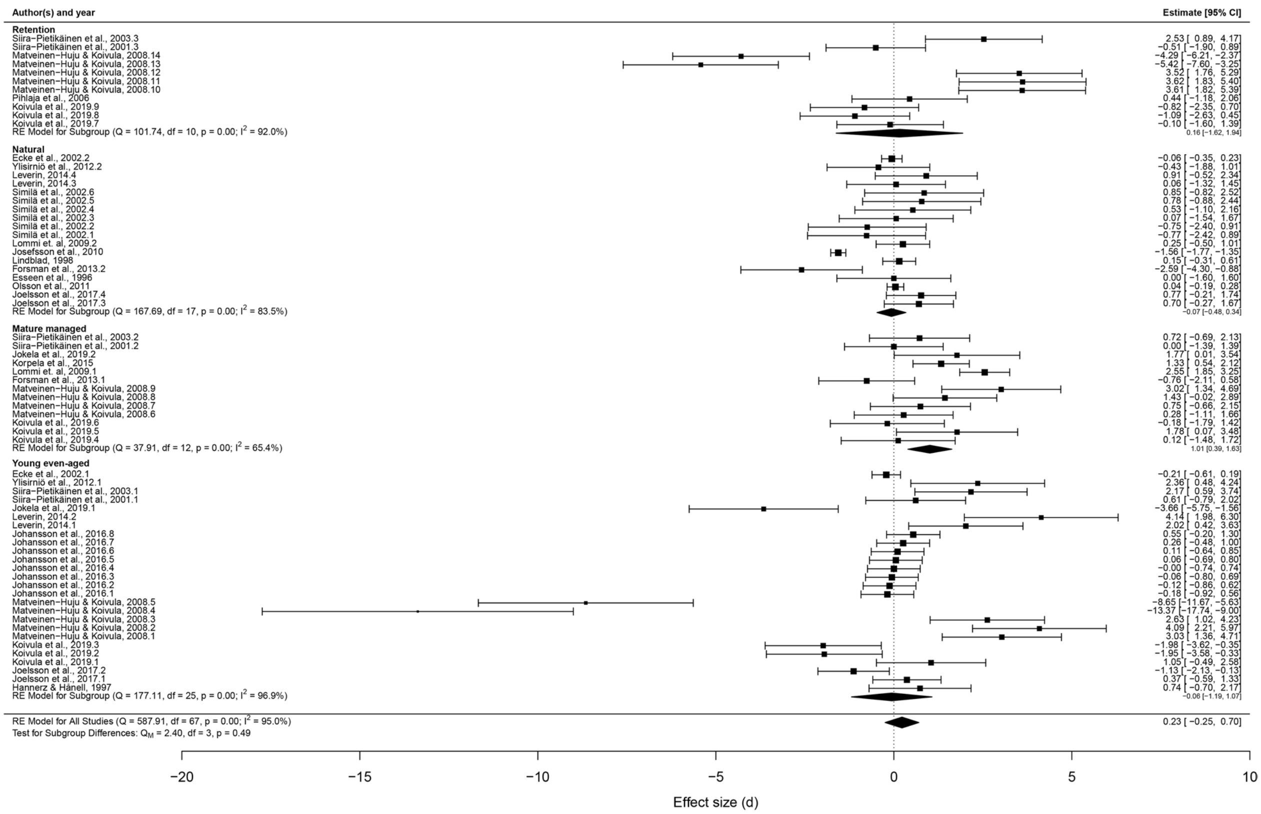

Fig. 7 Forest plot of effect sizes for species richness between uneven-aged forest and comparator forest areas. Effect sizes to the right of zero mean uneven-aged forest has more species than comparator forest. The grand mean noted by a diamond at the bottom is the summary effect of all the individual effect sizes. Diamonds within the forest plot note subgroup means. The error bars represent 95% confidence intervals

did not differ significantly ($d = 0.157$, $p = 0.862$, 95% CI -1.621, 1.936, $n = 11$) (Fig. 9). Habitat specialism explained 43% of variation in the effect sizes. There were significantly more open habitat species in the retention forest ($d = -5.772$, $p < 0.0001$, 95% CI -6.943, -2.660, $n = 10$). The impact of taxa was tested for spiders and beetles. No effect of taxa was found ($QM = 0.001$, $p = 0.973$, $n = 10$), which is not surprising as there were both forest dependent and open habitat species and hence, effects in different direction within taxa. Time since retention forest was logged did not influence the effect sizes ($d = -0.165$, $p = 0.575$, 95% CI -0.743, 0.412, $n = 11$). There was no data on deadwood volumes so its impact could not be tested.

Uneven-aged forest had significantly more species than mature even-aged forest ($d = 1.012$, $p = 0.001$, 95% CI 0.393, 1.631, $n = 13$) (Fig. 10). The result was driven by two studies with comparatively large sample sizes, one on lichens and another on insects, and relatively low, although still significant, heterogeneity between studies ($Q = 37.913$, $p = 0.0002$). Neither habitat specialism nor taxa explained differences in species richness as mean standardised differences in individual studies were mainly non-significant but it should be noted that data sets were small in both cases (habitat specialism: $QM = 1.689$, $p = 0.793$, $n = 13$; taxa: $QM = 0.52$, $p = 0.471$, $n = 9$, groups included in the analysis: beetles, spiders). Years since harvest explained 34% of the heterogeneity but was only marginally significant ($d = 0.024$, $p = 0.061$, $n = 12$). There was not enough data to test the impact of deadwood volumes on species richness.

Abundance Overall abundance (i.e. number of individuals) was higher in uneven-aged forest than in comparator forests, but the effect was only marginally significant ($d = 0.255$, $p = 0.091$, $n = 130$). There was substantial heterogeneity in the effect sizes ($Q = 1327.247$, $p < 0.0001$). Neither country, literature type, the year when the study was started, or sampling method explained the variation ($QM = 2.926$, $p = 0.570$). Publication bias was not visually detected, and trim and fill-test confirmed that adjustment to the effect size was not needed (Additional file 9). Individual abundance in studies from the MONTA project was similar to the other studies ($QM = 0.099$, $p = 0.753$).

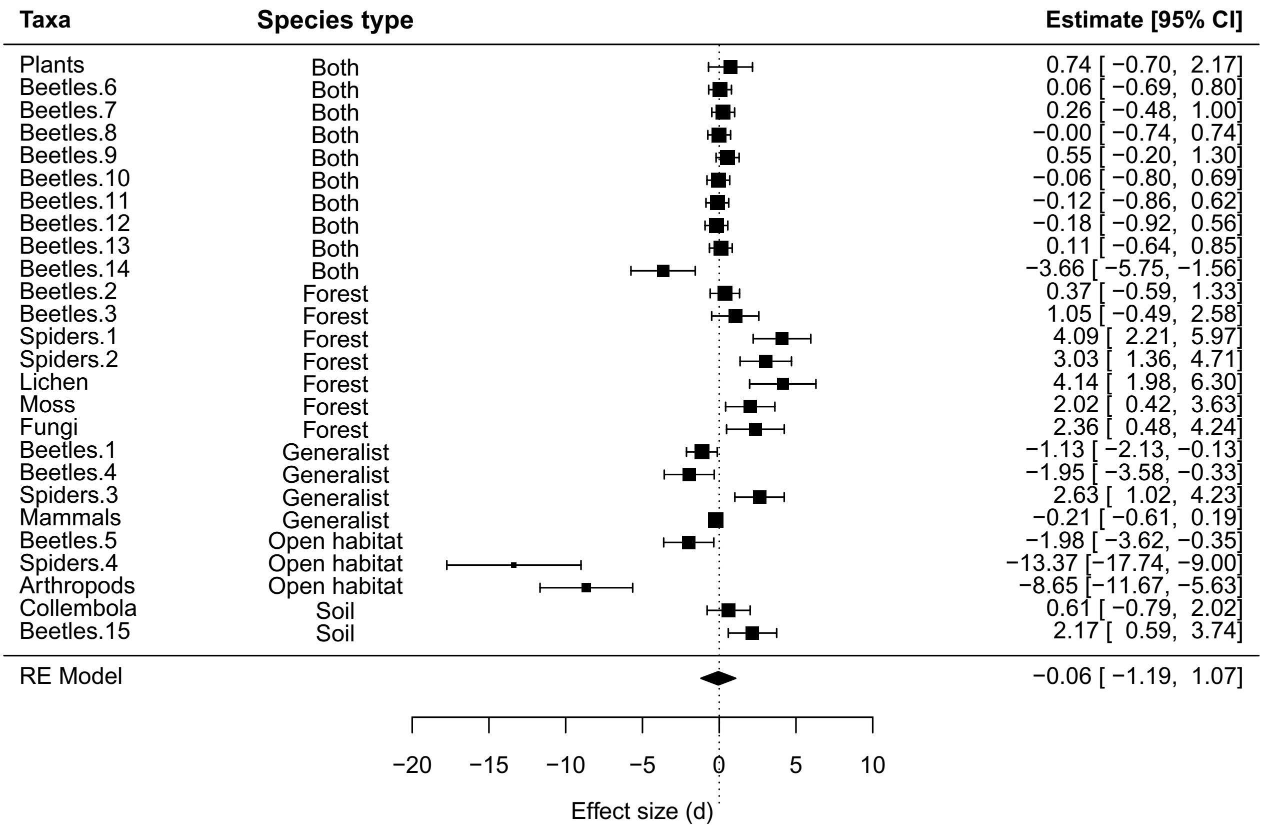

Fig. 8 Forest plot of effect sizes for species richness (mean standardized difference between uneven-aged and young even-aged forest). Effect sizes to the right of zero mean uneven-aged forest has more species than young even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond is the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

Harvesting intensity (% of tree volume removed during harvesting of the uneven-aged forest) had no impact on individual abundance (QM = 0.069, p = 0.793, n = 55).

A mixed-effects model was used to test differences between exposure and comparators as the amount of residual heterogeneity within each subgroup did not differ significantly (p = 1.00). There were significantly more individuals in uneven-aged forests than in young even-aged forests (d = 0.498, p = 0.038, 95% CI 0.027, 0.969, n = 130). Investigation of potential effect modifiers revealed that the number of individuals belonging to species categorised as open habitat species was higher in young even-aged forests than in uneven-aged forests and the effect was statistically significant (d = −5.541, p = 0.0004, 95% CI −8.628, −2.455, n = 49) (Fig. 11). The abundance of forest dependent species was higher in uneven-aged forests that in young even-aged forests, but the effect was only marginally significant (d = 1.082, p = 0.077, 95% CI −0.118, 2.281, n = 49). There were no significant differences between taxa (beetles, bryophytes, lichens, mammals, spiders, soil arthropods, vascular plants) (QM = 3.627, p = 0.727, n = 48). Years since harvest of the young even-aged forest did not influence individual abundance (d = 0.01, p = 0.673, 95% CI = −0.035, 0.054, n = 43). The volume of deadwood in the young even-aged forest had marginally significant impact on effect sizes (d = 0.174, p = 0.082, 95% CI −0.022, 0.371, n = 43) suggesting importance of deadwood for individual abundance.

When uneven-aged forest was compared to retention forest, no differences in individual abundance was found (d = 0.0443, p = 0.925, 95% CI −0.873, 0.961, n = 130). Habitat specialism explained 26% of heterogeneity. There were significantly more individuals in retention forest belonging to species in the open habitat category than in uneven-aged forest (d = −3.572, p = 0.032, 95% CI −6.828, −0.316, n = 18) but for other habitat categories (forest, generalist, soil) the effect was not significant (Fig. 12). Years since the forest was harvested or taxa had not impact on individual abundance (years since harvesting: QM = 0.17, p = 0.681, n = 19; taxa: QM = 2.395, p = 0.664, n = 18). Taxa included in the analysis were

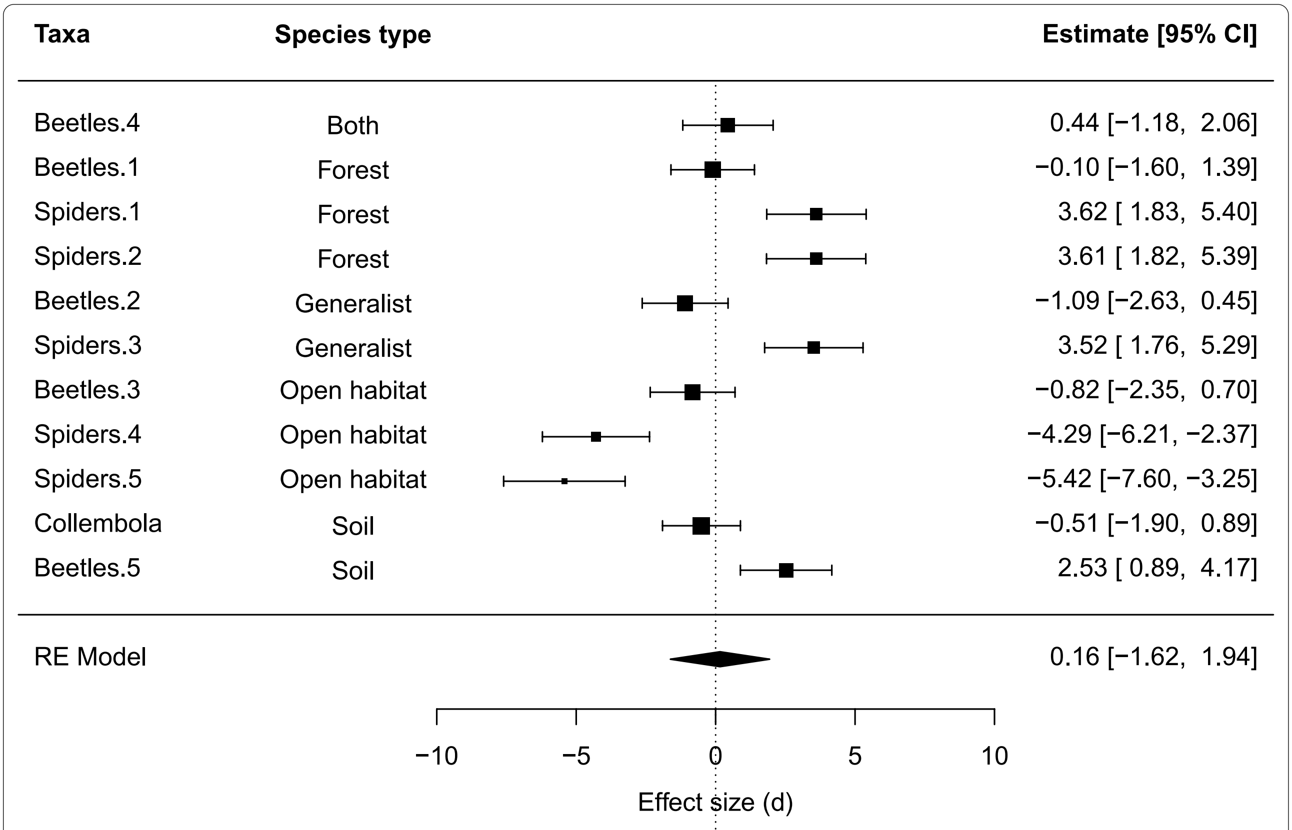

Fig. 9 Forest plot of effect sizes for species richness (mean standardized difference between uneven-aged and retention forest). Effect sizes to the right of zero mean uneven-aged forest has more species than retention forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond is the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

spiders, soil arthropods, beetles, bryophytes, and vascular plants. There was not enough data to test the effect of deadwood volume.

When uneven-aged forest was compared to mature even-aged forest, no significant differences in individual abundance were found (d = 0.294, p = 0.490, 95% CI − 1.131, 0.542) (Fig. 13). Years since uneven-aged forest was harvested explained 65% of heterogeneity in effect sizes and had statistically significant impact on the effect sizes (d = − 0.155, p = 0.0004, 95% CI − 0.241, − 0.069, n = 24). Up to 7 years after logging, individual abundance was significantly higher in the uneven-aged forest after which it started to decrease compared to the mature even-aged forest (Fig. 14). This pattern during the early years was driven by the increased number of individuals belonging to species in the open habitat category but the effect was only marginally significant (d = 0.876, p = 0.087, 95% CI − 0.127, 1.88, n = 23). At species level, spiders were more abundant in the uneven-aged forest than in the mature even-aged forest (d = 2.009, p = 0.0002, 95% CI 0.946, 3.073, n = 23) and the results were similar for flower visiting insects, a category that included bumble bees and butterflies (d = 1.056, p = 0.01, 95% CI 0.252, 1.859, n = 23). There were less beetles in the uneven-aged forest than in the mature even-aged forest, but the effect was only marginally significant (d = − 0.957, p = 0.094, 95% CI − 2.076, 0.162, n = 23). There was not enough data to test the effect of deadwood volume.

Managed forests compared to natural forest

Species richness Overall species richness did not differ between uneven-aged forest and natural forest (d = − 0.068, p = 0.745, 95% CI − 0.475, 0.34, n = 18) (Fig. 15). Species attributes had no significant impact on effect sizes [habitat specialism: QM = 2.41, p = 0.121, n = 18; taxa: QM = 3.626, p = 0.163, n = 15 (fungi, lichens and beetles)]. However, for fungi the effect was marginally significant (d = − 0.819, p = 0.084, 95% CI − 1.747, 0.109). Time since the uneven-aged forest was harvested did not explain heterogeneity and had no statistically significant influence on effect sizes (QM = 0.004, p = 0.952, n = 10).

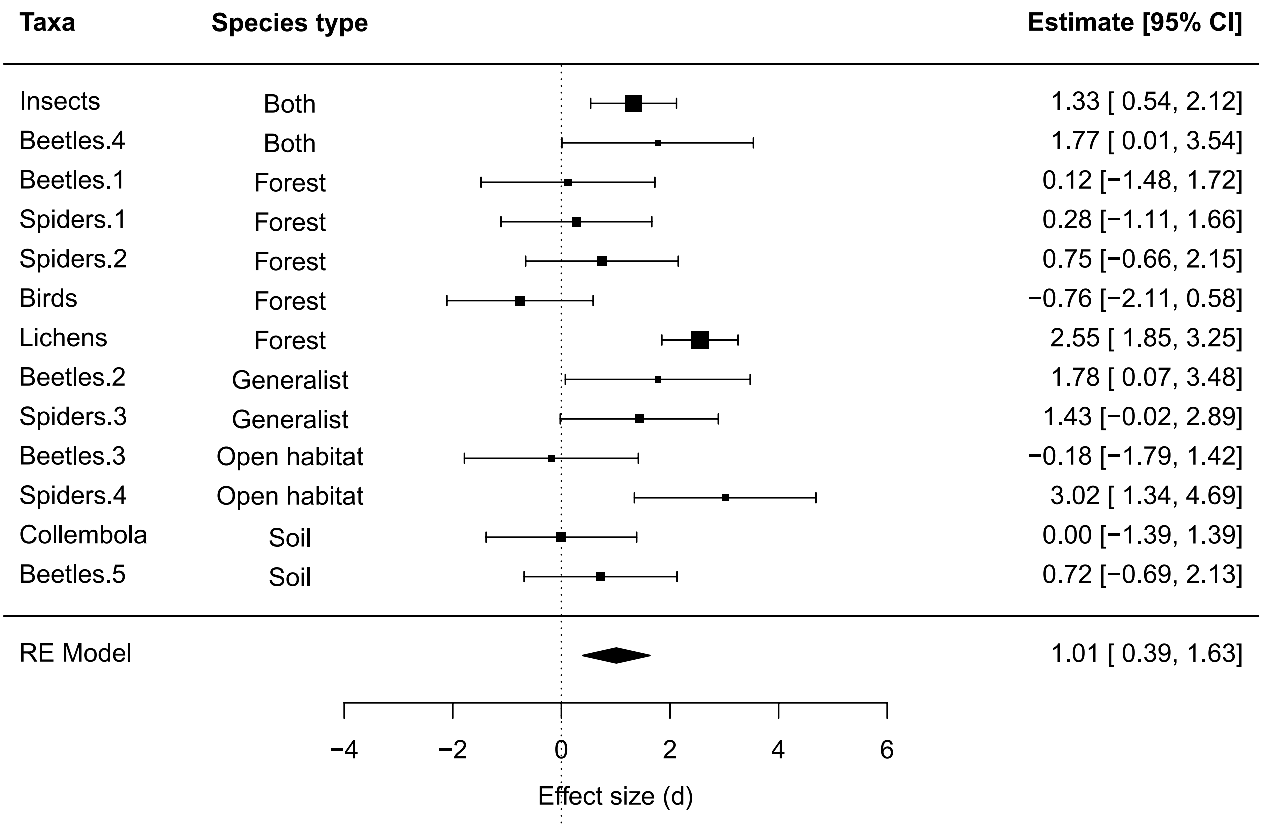

Fig. 10 Forest plot of effect sizes for species richness (mean standardized difference between uneven-aged and mature even-aged forest). Effect sizes to the right of zero mean uneven-aged forest has more species than mature even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond is the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

There were only four studies that had recorded deadwood volumes in the uneven-aged forest, so we did not test its influence on effect sizes.

Natural forest had more species than even-aged forests, (d = − 0.322, p = 0.041, 95% CI − 0.630, − 0.014) (Fig. 16). Natural forest had also significantly more forest dependent species than even-aged forests (p = − 0.955, p = 0.008, 95% CI − 1.661, − 0.249, n = 93) and habitat specialism accounted for 14% of heterogeneity. The effect was not significant for any particular taxa (QM = 4.097, p = 0.769, n = 89). Taxa investigated were beetles, bryophytes, birds, fungi, diptera, lichens, snails and vascular plants. Years since harvesting influenced species richness (d = − 0.008, p = 0.032, 95% CI − 0.015, − 0.001, n = 93) although it explained only 5.5% of variation. Based on the regression model, natural forest becomes significantly more diverse than even-aged forest 50 years after the harvest of even-aged forest (d = − 0.31, 95% CI − 0.611, − 0.008) (Fig. 17). Deadwood was not an important effect modifier (QM = 1.666, p = 0.197, n = 52).

Abundance There were more individuals in natural forest compared to uneven-aged forest, but the effect was only marginally significant (d = − 0.659, p = 0.070, 95% CI − 1.372, 0.054, n = 130) (Fig. 18). No statistically significant differences were found in species attributes between uneven-aged and natural forest (habitat specialism: QM = 2.75, p = 0.253, n = 38; taxa: QM = 7.26, p = 0.298, n = 35). Taxa investigated included plants, beetles, other insects (insect larvae and all insects > 4 mm), birds, lichens, bryophytes and mammals. There was not enough data to explore potential effect of deadwood volume. Years since the uneven-aged forest was logged did not have a significant impact on effect sizes (QM = 0.077, p = 0.782, n = 18).

Because residual heterogeneity was significantly different between subgroups (p = 0.001), even-aged forest was compared to natural forest at the subgroup level. No differences were found in individual abundance between even-aged and natural forests (d = − 0.246, p = 0.200, 95% CI − 0.621, 0.130) (Fig. 19). Furthermore, neither of the species attributes was significant (taxa: QM = 7.981,

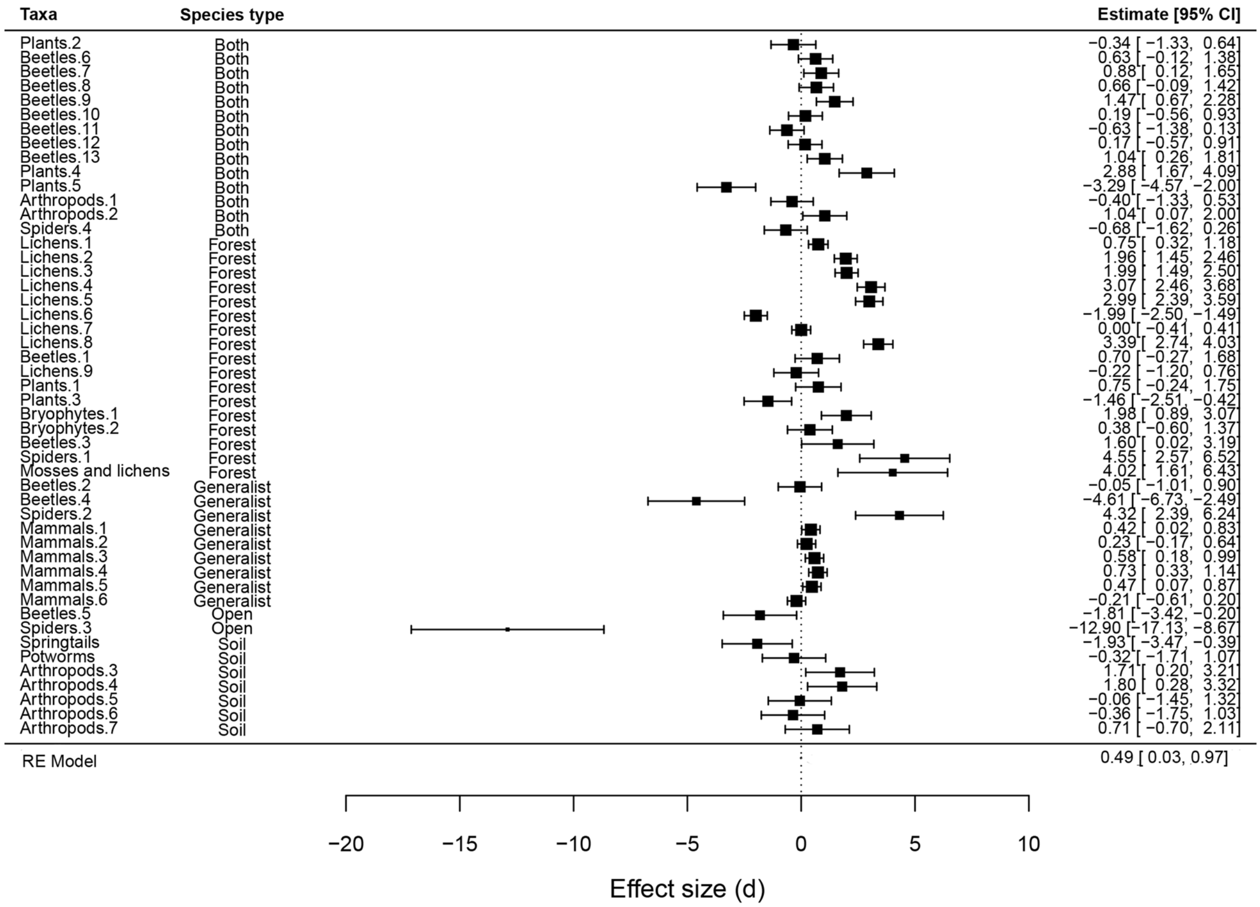

Fig. 11 Forest plot of effect sizes for individual abundance (mean standardized difference between uneven-aged and young even-aged forest). Effect sizes to the right of zero mean uneven-aged forest has more individuals than young even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The error bars represent 95% confidence intervals. Effect size below the bottom line on the right is the overall effect with 95% confidence intervals

$p = 0.631$, $n = 129$; habitat specialism: $QM = 1.527$, $p = 0.466$, $n = 134$). Taxa tested included birds, bryophytes, beetles, fungi, diptera, hymenoptera, lichens, mammals, nematodes, snails, and vascular plants. Similarly, neither of the forest attributes influenced abundance (deadwood: $QM = 0.826$, $p = 0.366$, $n = 74$; years since harvesting: $QM = 0.595$, $p = 0.441$, $n = 81$). As all the studies in the 'high risk of bias' category were comparisons between even-aged and natural forest, we tested their influence by removing them from the data set. Their exclusion did not change the results (Additional file 9).

Comparisons of different types of even-aged managed forests

Species richness Overall, there were less species in young even-aged than in the comparator areas but the difference was not statistically significant ($d = -0.142$, $p = 0.385$, 95% CI -0.464, 0.179, $n = 143$). There was significant heterogeneity in the effect sizes ($Q = 1015.233$, $p < 0.0001$). Visual inspection showed rather balanced spread of effect sizes indicating lack of publication bias and trim and fill-test confirmed it (Additional file 9). Effect modifiers related to study attributes (country, sampling method, study year, literature type) explained less than 2% of heterogeneity, and none of the effects was significant ($QM = 7.131$, $p = 0.129$, $n = 142$).

Because residual heterogeneity was significantly different between subgroups ($p < 0.001$), we conducted further analyses at subgroup level. Overall, there was no difference in species richness between retention forest and young even-aged forest ($d = -0.47$, $p = 0.388$, 95% CI -1.535, 0.596) (Fig. 20). Retention forest and young even-aged forests were logged at the same time, apart from one study. Years since harvest had no statistically significant impact on species richness ($QM = 0.022$, $p = 0.882$, $n = 12$). As the data set was small and all

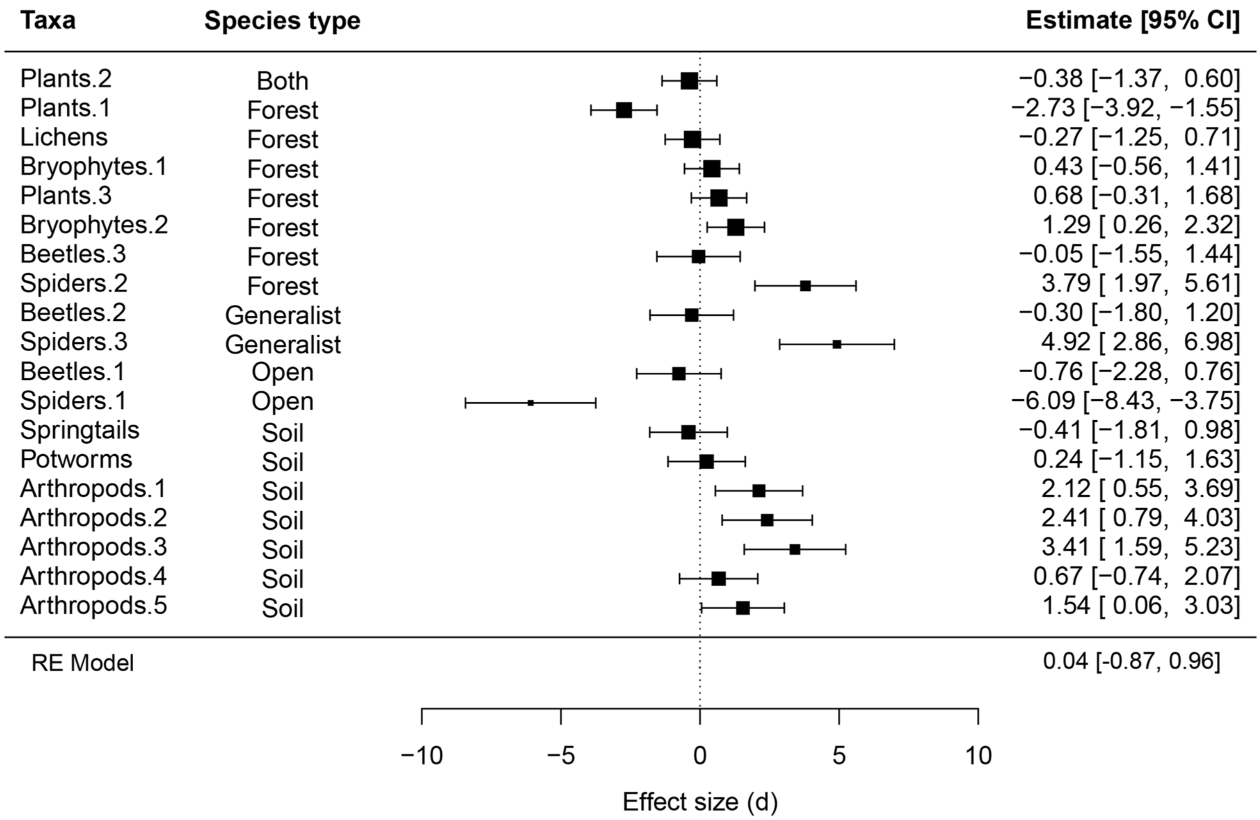

Fig. 12 Forest plot of effect sizes for individual abundance (mean standardized difference between uneven-aged and retention forest). Effect sizes to the right of zero mean uneven-aged forest has more individuals than retention forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The error bars represent 95% confidence intervals. Effect size below the bottom line on the right is the overall effect with 95% confidence intervals

except two studies were on forest dependent species in the data set, we did not test the effect of habitat specialism. Taxa did not explain heterogeneity on effect sizes (QM = 0.882, p = 0.643, n = 10). Taxa investigated were beetles, lichens and birds. There was no data on deadwood volumes so their effect could not be tested.

No statistically significant difference was detected in species richness between young and mature even-aged forest (d = 0.446, p = 0.340, 95% CI − 0.471, 1.364, n = 38) (Fig. 21). There were more forest dependent species in mature even-aged forest than in young even-aged forest, but the effect was only marginally significant (d = − 1.560, p = 0.064, 95% CI − 3.214, 0.093, n = 36). Young even-aged forests had significantly higher species richness of open habitat species than mature even-aged forest (d = 4.73, p < 0.0001, 95% CI 2.907, 6.553, n = 36). The difference was driven by vascular plants as there were significantly more plant species in young even-aged forest (d = 3.452, p = 0.0008, 95% CI 1.438, 5.466, n = 31). Significant differences were not found the other taxa (beetles, birds, bryophytes, collembola, fungi, mites). Years since the young even-aged forest was harvested had impact on species richness explaining 26% of heterogeneity in the effect sizes (QM = 10.999, p = 0.0009, n = 36). Further investigation showed that there are more open habitat species in the young even-aged forest during the first two years. Deadwood volume did not explain heterogeneity in effect sizes (QM = 1.246, p = 0.264, n = 6).

Abundance Overall, there were less individuals in young even-aged forests than in comparator forests, but the effect was not statistically significant (d = − 0.237, p = 0.083, 95% CI − 0.506, 0.031, n = 206). There was also significant amount of heterogeneity (Q = 1798.347, p < 0.0001). When high risk studies were removed and the analysis rerun, the overall mean effect size became significantly negative (d = − 0.292, p = 0.032, 95% CI − 0.559, − 0.025, n = 196) and remained significantly heterogenetic (Q = 1677.0346, p < 0.0001). Visual inspection of the funnel plot showed symmetrical distribution of the effect sizes with and without high risk studies and trim

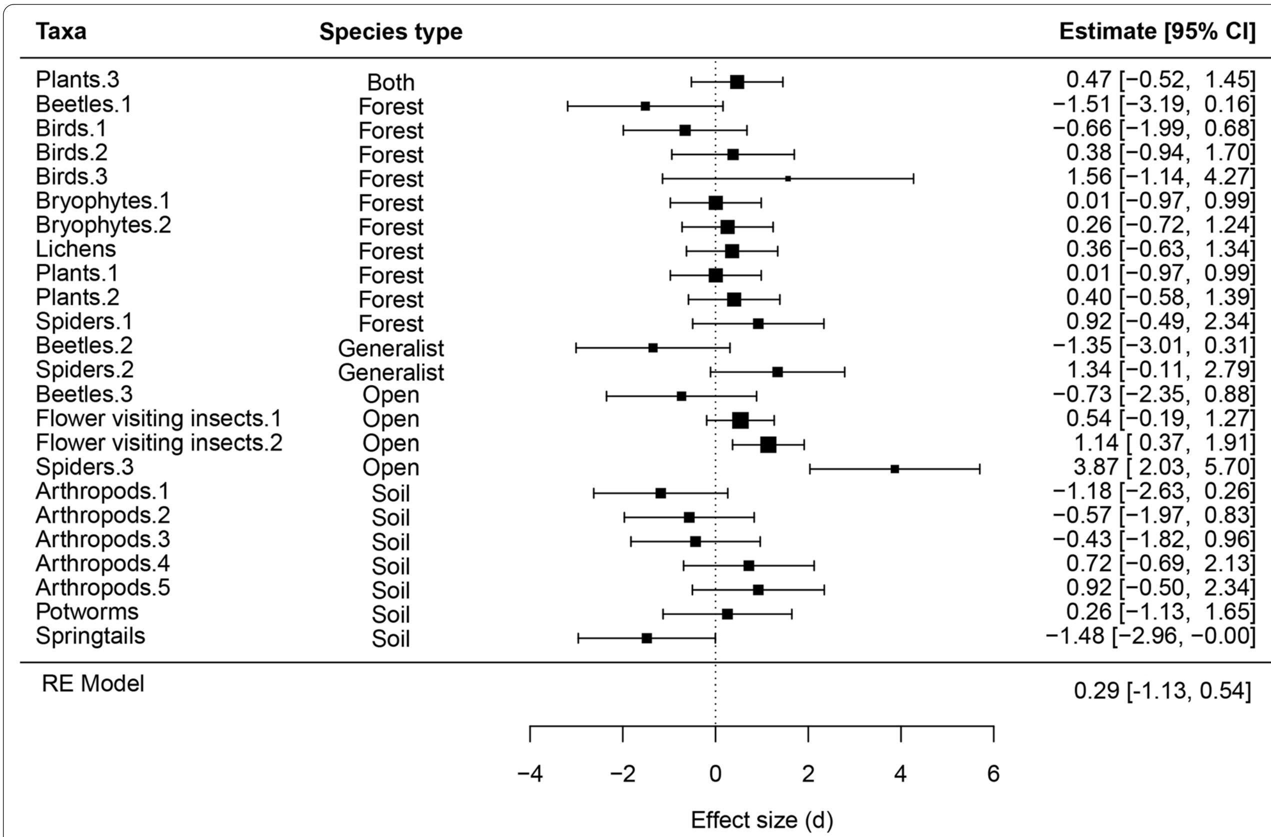

Fig. 13 Forest plot of effect sizes for individual abundance (mean standardized difference between uneven-aged and mature even-aged forest). Effect sizes to the right of zero mean uneven-aged forest has more individuals than mature even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The error bars represent 95% confidence intervals. Effect size below the bottom line on the right is the overall effect with 95% confidence intervals

and fill-test showed no publication bias (additional files 8 and 9). We investigated the influence of effect modifiers related to study attributes and found that none of them were significant in explaining heterogeneity in effect sizes (QM = 5.111, p = 0.276, n = 206; excluding high risk studies: QM = 5.959, p = 0.202, n = 196).

Because residual heterogeneity was significantly different between subgroups (p = 0.001), we conducted further analyses at subgroup level. Individual abundances did not differ significantly between young even-aged forest and retention forest (d = −0.013, p = 0.978, 95% CI −0.968, 0.942, n = 6) (Fig. 22). As there were no more than six studies, we only tested the impact of years since harvesting on effect sizes, which was not significant (QM = 0.062, p = 0.803).

When young even-aged forest and mature even-aged forest were compared, no significant differences in abundance were found (d = −0.209, p = 0.248, 95% CI −0.563, 0.145) (Fig. 23). Both species attributes, habitat specialism and taxa, were significant effect modifiers. There were significantly more individuals of forest dependent species in the mature even-aged forest than in the young even-aged forest (d = −0.796, p = 0.045, 95% CI −1.574, -0.018, n = 65). Taxon level investigation showed that the mature even-aged forest had significantly higher number of individuals of fungi (d = −2.781, p = 0.024, 95% CI −5.189, −0.374, n = 63) and snails (d = −2.269, p = 0.027, 95% CI −4.281, −0.256, n = 63), and approached significance for bryophytes (d = −1.181, p = 0.078, 95% CI −2.495, 0.132, n = 63). Young even-aged forest had significantly higher abundance of vascular plants (d = 1.202, p = 0.020, 95% CI 0.187, 2.217, n = 63). Years since the young even-aged forest was logged had no impact on abundance (QM = 0.015, p = 0.903, n = 65). There were not enough studies to test the influence of deadwood.

Evidence of effects

The evidence presented here on the impacts of different forest management approaches on species richness and abundance relate to stand level only. There were few significant differences in overall species richness and

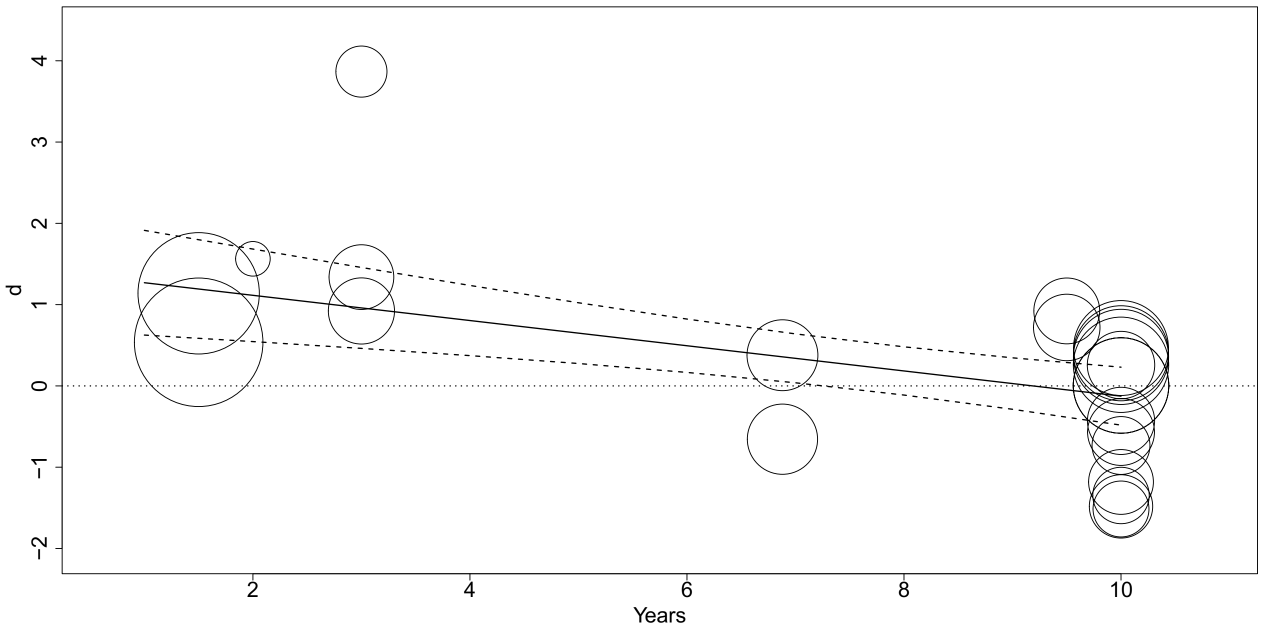

Fig. 14 Changes in individual abundance between uneven-aged and mature even-aged forest plotted against the years since uneven-aged forest was harvested. Positive effect size means more individuals in uneven-aged forest. Circles show individual studies. Their radius is proportional to the inverse of the standard errors meaning that larger circles are for more precise studies. A solid line for predicted average individual abundance is added with 95% confidence intervals. When the 95% confidence intervals do not cross the dotted line, the effect is statistically significant

individual abundance between uneven-aged and even-aged forests. Uneven-aged forest had more species than mature even-aged forest, which was mainly result of two studies with comparatively large sample sizes, one on insects and other on lichens (Fig. 10). Further, uneven-aged forest had more individuals than young even-aged forest (Fig. 12). When managed forests were compared to natural forest, the only significant result was that natural forests had higher species richness than even-aged forests (Fig. 16). The lack of significant results in overall species richness and individual abundance in the majority of comparisons is a result of effects in different directions and stems from varying habitat requirements.

Results of the meta-analysis suggest less disturbance from harvesting is better for forest dependent species and their abundance at stand level when different forest management regimes are compared. Uneven-aged forests had more forest dependent species and their individuals than young even-aged forests although the difference in abundance was only marginally significant (Fig. 8). No difference in species richness and abundance of forest dependent species was found when uneven-aged forests were compared to forests undergone retention harvests. However, the data sets were small: only three studies on species richness and seven studies on individual abundance had data on forest dependent species. A previous meta-analysis has shown that positive effects of retention harvests on species richness of forest species increase with proportion of retained trees and time since harvest, but interior forest species are negatively impacted by them [23]. Furthermore, the evidence suggests that uneven-aged forests can be as favourable habitats for forest dependent species as mature even-aged forests or natural forests, at least for the taxa included in this review (Figs. 13, 15). Even though species richness did not differ between uneven-aged forest and natural forest, species assemblages between these often vary [45, 58, 59]. The same forest dependent species may not occur in uneven-aged and natural forest depending on their specific environmental requirements [60].

The importance of natural and mature even-aged forests for forest dependent species was supported by the comparisons of these two types to young even-aged forests. Species richness and abundance of forest dependent species were higher in mature even-aged forests compared to young even-aged forests (Fig. 21). This is not surprising concerning the more open structure of young even-aged forests. There were more species overall and also more forest dependent species in natural forests than in even-aged forests even though age of the even-aged forests ranged from zero (recently performed harvesting) to 185 years (Figs. 16, 17). However, no differences in the overall abundance or the abundance of forest dependent species were detected (Fig. 19). This may partially stem

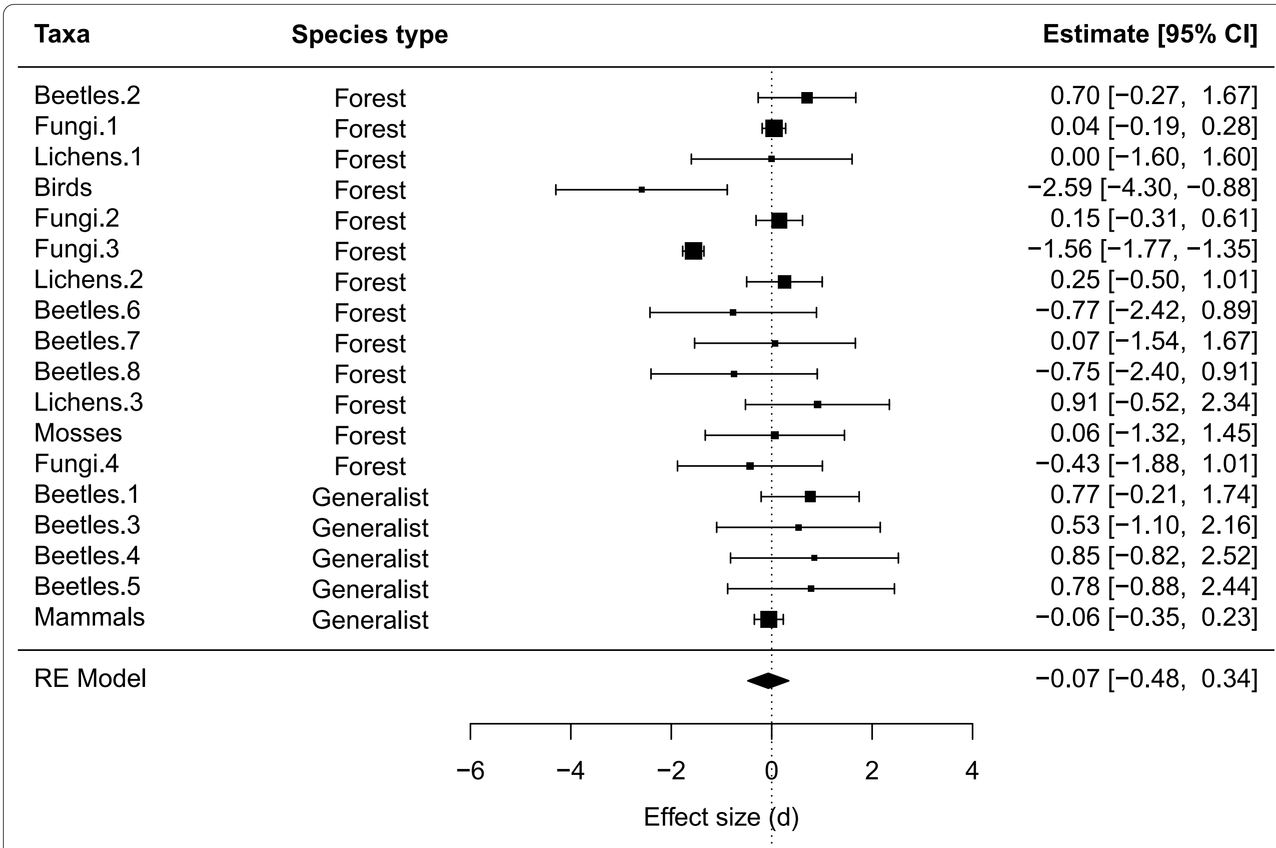

Fig. 15 Forest plot of effect sizes for species richness (mean standardized difference between uneven-aged and natural forest). Effect sizes to the right of zero mean uneven-aged forest has more species than natural forest. Different habitat specialisms of the taxa are given. The grand mean noted by a diamond is the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

from our categorisation of habitat specialism as forest species were not limited to old-forest specialists. Old-forest specialists most likely caused differences in species richness as they have specific habitat requirements that are not present in young even-aged forests [e.g. 61]. The abundance of other forest species that are adapted to broader range of forest conditions may not decrease as much as the abundance of old-forest specialists or recovers over time.

The evidence shows that open habitat species and their individuals were more common in young even-aged forests and forests undergone retention harvests than in uneven-aged forests (Figs. 11, 12). This is hardly surprising because the layered structure of the uneven-aged forest offers less suitable habitats for species preferring or tolerating open habitats. No differences in the number of open habitat species were found when uneven-aged and mature even-aged forests were compared suggesting similarity of environmental conditions in these forests (Fig. 13). However, there were more individuals of open habitat species in uneven-aged forests than in mature forests, but the difference was only marginally significant. As expected, there were also more open habitat species in young than mature even-aged forests (Fig. 23). A more detailed analysis revealed that there were more species and individuals of vascular plants in young than mature managed forests. This can be a result of emergence and intensive spreading of species adapted to the sunny conditions in the early phases of succession. Different species thrive in mature even-aged forests than in younger forests because availability of light and microclimate is different. More fungi and snails that mostly prefer shaded and moist habitats were found in the mature even-aged forests. Similarly, there were more species of fungi in natural forests compared to uneven-aged forests although the difference was only marginally significant (Fig. 15).

Magnitude of effects

Where forest management had significant or even marginally significant impact on species richness or abundance, the effect sizes were in most cases large. Usually, effect size of 0.2 is considered a small effect, d = 0.5 an intermediate effect and d = 0.8 a large effect [62]. A review of meta-analyses in ecology and evolution found

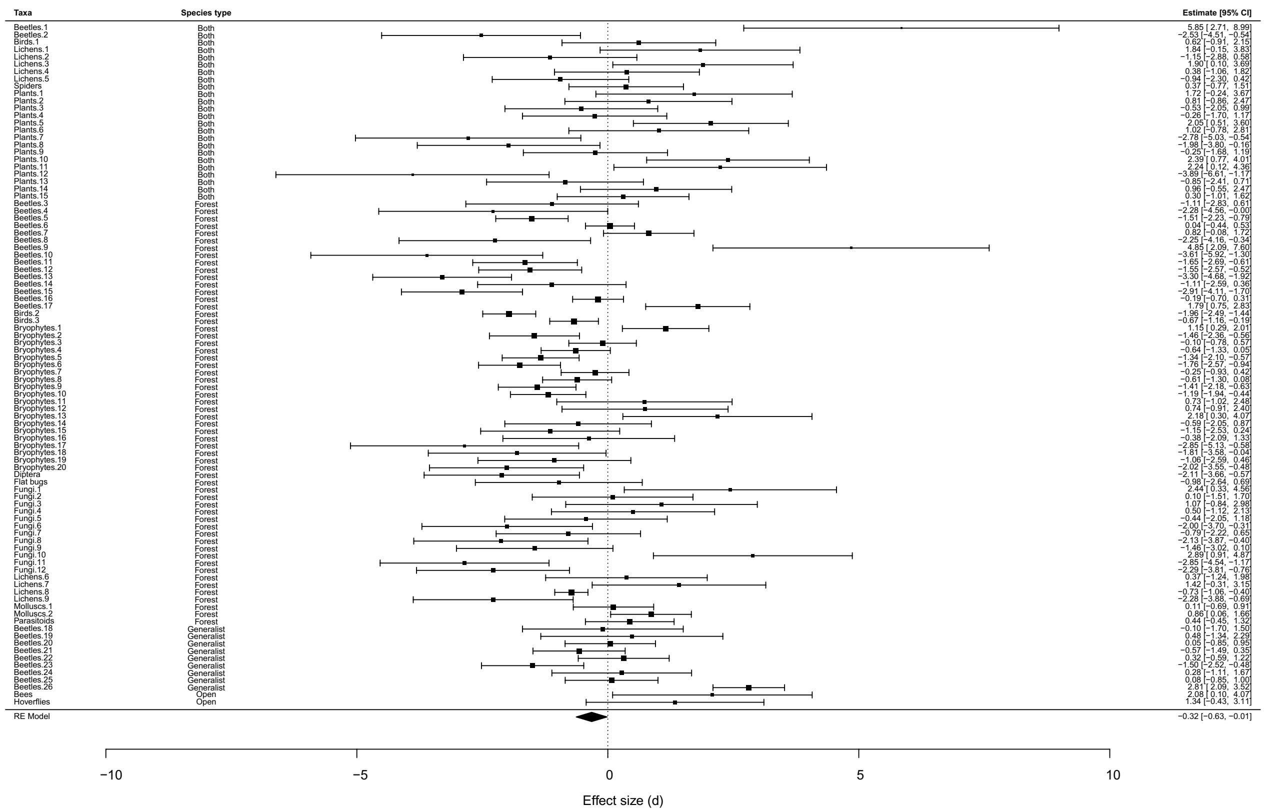

Fig. 16 Forest plot of effect sizes for species richness (mean standardized difference between even-aged forest and natural forest). Effect sizes on the right side of zero mean that even-aged forest is more diverse than natural forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond shows the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

that the mean value of d in ecological meta-analyses was 0.603 [63]. In our results, effect sizes were commonly above one, especially impacts on forest dependent and open habitat species. The smallest effect size for the differences in species richness and abundance when habitat specialism was considered was -0.796 for the comparison of abundance between young and mature even-aged forest. The large effect sizes indicate a strong response from the studied groups and mean that forest management approaches explain a considerable amount of variance at the level of habitat specialism. Responses in different directions (positive or negative) would reduce the mean effect size for the studied group (e.g. forest dependent species) as seen in the overall results where species with different habitat specialism were combined in same analyses and effect sizes were smaller but not necessarily small. They ranged from -0.32 (species richness of even-aged forest compared to natural forest) to 1.012 (species richness of uneven-aged forest compared to mature even-aged forest) for significant and marginally significant results. Considering that more than half of the studies come from experimental set up and most of the observational studies had aimed to minimise bias from environmental variation across study sites, we are confident that the large effects found in this review are representative of true effects in nature for the studied species groups.

Reasons for heterogeneity

Besides habitat specialism, effects of taxa and three forest attributes (deadwood, years since harvest, and intensity of harvesting in uneven-aged forest) were studied. Although many analyses were conducted on richness and abundance of different taxa, statistically significant results were obtained only for a few comparisons (Table 13). In addition to plants, snails and fungi discussed above, there were significant differences in abundance of spiders and flower visiting insects when uneven-aged forest was compared to mature even-aged forest (Fig. 13). Both these taxa were more abundant in uneven-aged forest than in mature even-aged forest benefiting from the openness created by selective harvest. The lack of effect of taxa

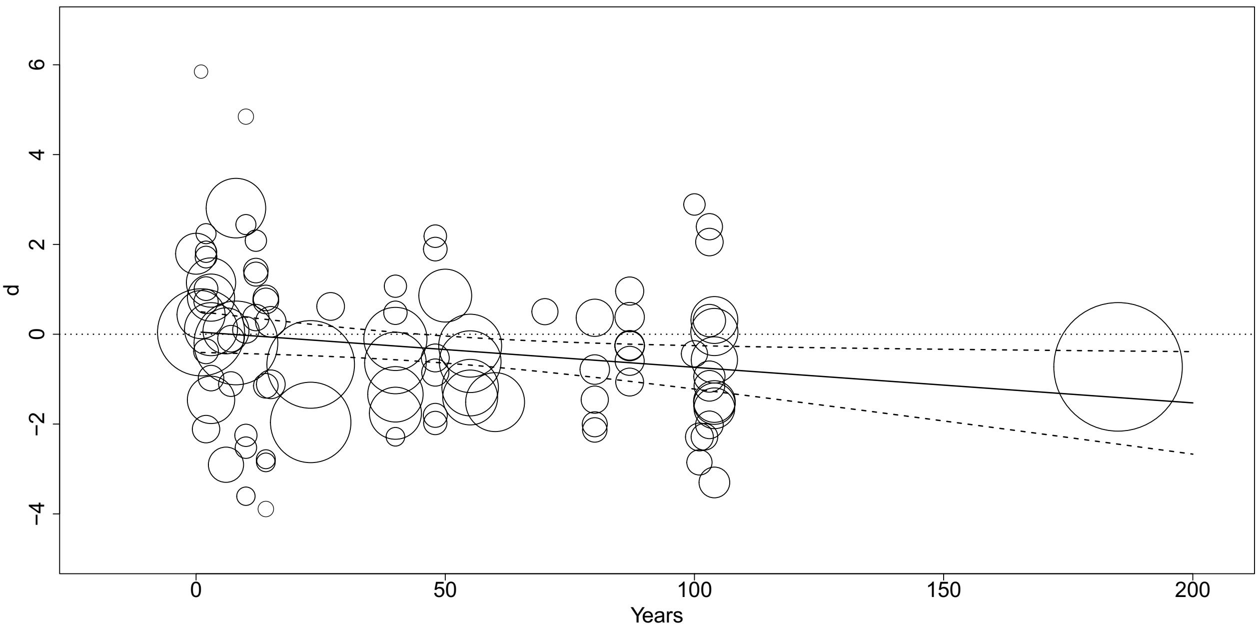

Fig. 17 Changes in species richness between even-aged and natural forest plotted against the years since even-aged forest was logged. Positive effect size means more species in even-aged forest than in natural forests. Circles show individual studies. Their radius is proportional to the inverse of the standard errors meaning that larger circles are for more precise studies. A solid line for predicted average species richness is added with 95% confidence intervals. When the 95% confidence intervals do not cross the dotted line, the effect is statistically significant

and lack of consistency in the effect has been noted in a previous review comparing uneven-aged and even-aged forests to each other [25]. The most likely reason for the lack of effect in this review is that studied taxa often had species with different habitat specialisms. Unfortunately, in our study there was not enough data for an analysis of the combined effect of taxa and habitat specialism.

Of the three forest attributes studied, deadwood, harvesting intensity and years since harvest, only years since harvest had significant influence on species richness and individual abundance. When comparing young and mature even-aged forests, species richness was higher in young even-aged forest during the first years after logging of the young even-aged forest (Fig. 21). This was explained by the increase of open-habitat species soon after logging. Similarly, the abundance of open habitat species was higher during the first years after harvesting of the uneven-aged forest compared to the mature unharvested even-aged forest. When comparing even-aged and natural forests, species richness became significantly higher in natural forests 50 years after harvesting of the even-aged forest. This was explained by the different habitat preferences of open habitat and forest dependent species. Young even-aged forests harbour more open habitat species. When the even-aged forest grows older, the number of open habitat species decreases, and the amount of forest dependent species becomes an important determinant for the overall species richness. Our results are similar to an earlier meta-analysis by Paillet et al. on the impacts of forest management on species richness in Europe [64], which found that 20 years after management was abandoned, unmanaged forests became more species rich. Until the 20-year cut-off, managed forests had higher species richness. We also found marginally significant impact of years since harvesting when uneven-aged forest was compared to mature even-aged forest. For other comparisons, years since harvesting did not significantly influence species richness or individual abundance. This is most likely the result of similar environmental conditions, e.g. between young even-aged forests and forests undergone retention cuts.

The amount of deadwood did not have significant impact on species richness and abundance, but the lack of data should be noted. Only 6 out of 14 comparisons had enough data to conduct analysis and even in those cases the number of studies that had recorded the amount of deadwood was small. We found only one case where the amount of deadwood was marginally significant to individual abundance, but the lack of evidence should not be mistaken for the absence of effect. A previous systematic review focused on the impact of deadwood on species richness and abundance concluded that increasing the amount of deadwood has positive effects on the abundance and richness of saproxylic insects and

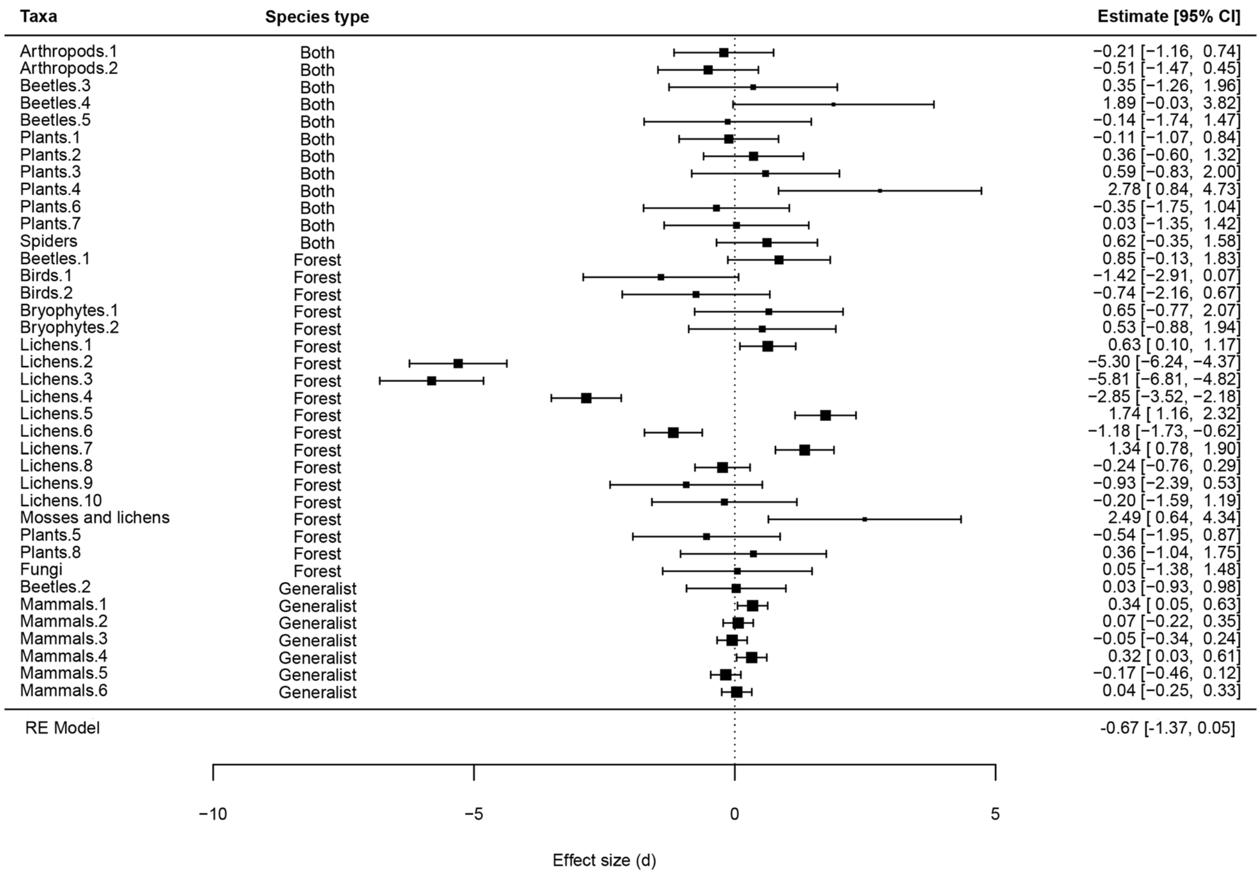

Fig. 18 Forest plot of effect sizes for individual abundance (mean standardized difference between uneven-aged and natural forest). Effect sizes to the right of zero mean uneven-aged forest has more individuals than natural forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The error bars represent 95% confidence intervals. Effect size below the bottom line on the right is the overall effect with 95% confidence intervals

fungi although there was heterogeneity in the responses [65].

Intensity of harvesting in uneven-aged forests had no impact on species richness or abundance. This corresponds with results of Paillet et al. [64] where species richness was not impacted by selective cuttings. It is likely that the impact of harvesting intensity is masked by habitat preferences as open habitat species benefit when more trees are removed whereas forest dependent species in general do not.

Knowledge gaps

Geographical scope

The review included articles from all the countries within the geographical scope, but substantially more studies were from Finland than from other countries. It is worth noting though that there were more studies concentrating on uneven-aged than even-aged forest management from Norway. The uneven distribution of studies was even more prominent among the studies included in the meta-analysis. In the case of even-aged management there were many more studies from Finland and Sweden than from the other countries. In the case of uneven-aged management, there were more studies from Finland than from the other countries altogether, and no studies from Russia were included in the meta-analysis. Hence, caution should be exercised when generalising the results of this review to the whole study area, and especially this should be noted in the case of uneven-aged forest management.

Influence of effect modifiers

Although overall, the number of studies in the meta-analysis (n = 68 (uneven-aged) and n = 143 (even-aged) for species richness and n = 130 (uneven-aged) and n = 206 (even-aged) for abundance) was large (less than 25 studies is common in ecology and evolution [66]), information at the comparator forest level is limited. As a result, the influence of effect modifiers could not be explored in detail. Hence, significant knowledge gaps remain about

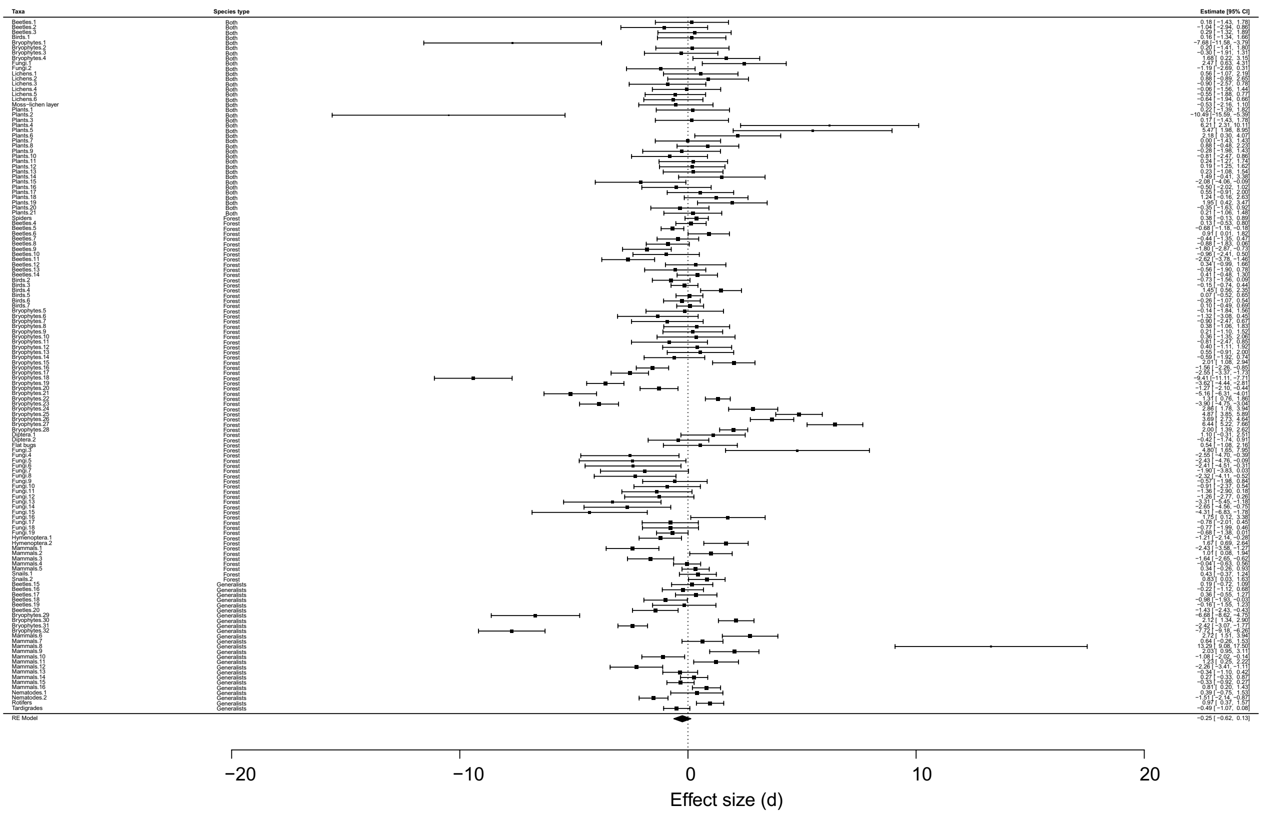

Fig. 19 Forest plot of effect sizes for individual abundance (mean standardized difference between even-aged and natural forest). Effect sizes to the right of zero mean even-aged forest has more individuals than natural forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond is the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

the impact of potential effect modifiers on species richness and abundance at differently managed sites. Of the analysed effect modifiers particularly the volume of deadwood was so rarely reported that hardly any conclusions could be made on its effect on outcomes. Similarly, knowledge remains limited on species specific responses to different management approaches as forest dependent species, generalists and open-habitat species were often studied together (not differentiating the species based on their habitat specialism).

Taxonomic groups

There are also knowledge gaps regarding taxonomic groups. The most studied taxonomic group was arthropods. The number of studied taxa was larger related to even-aged forest management, which is natural, since there were fewer studies concentrating on uneven-aged management. There were relatively more studies on lichens and arthropods within the uneven-aged management studies than within the even-aged management studies. Regardless of the management regime, there were relatively few studies on mammals, birds and soil animals. In the case of uneven-aged management, there were also relatively few studies on fungi and in the case of even-aged management on lichens. Hence, generalisation of the results of this review should be done carefully.

Landscape level

The biggest knowledge gap relates to landscape level studies. Although we had aimed to review impacts at both landscape and stand level, only stand level impacts could be summarised due to lack of studies.

Review limitations

Limitations of the review

During the search, the aim was to achieve comprehensiveness, both in the cases of the search string and the sources searched. However, the full search string could only be used in few databases, and when other sources were searched, simplified search strings had to be used. Despite our best efforts to be as comprehensive as possible, all sources with possibly relevant articles have most likely not been searched and maybe even identified. However, the number of sources searched in this review

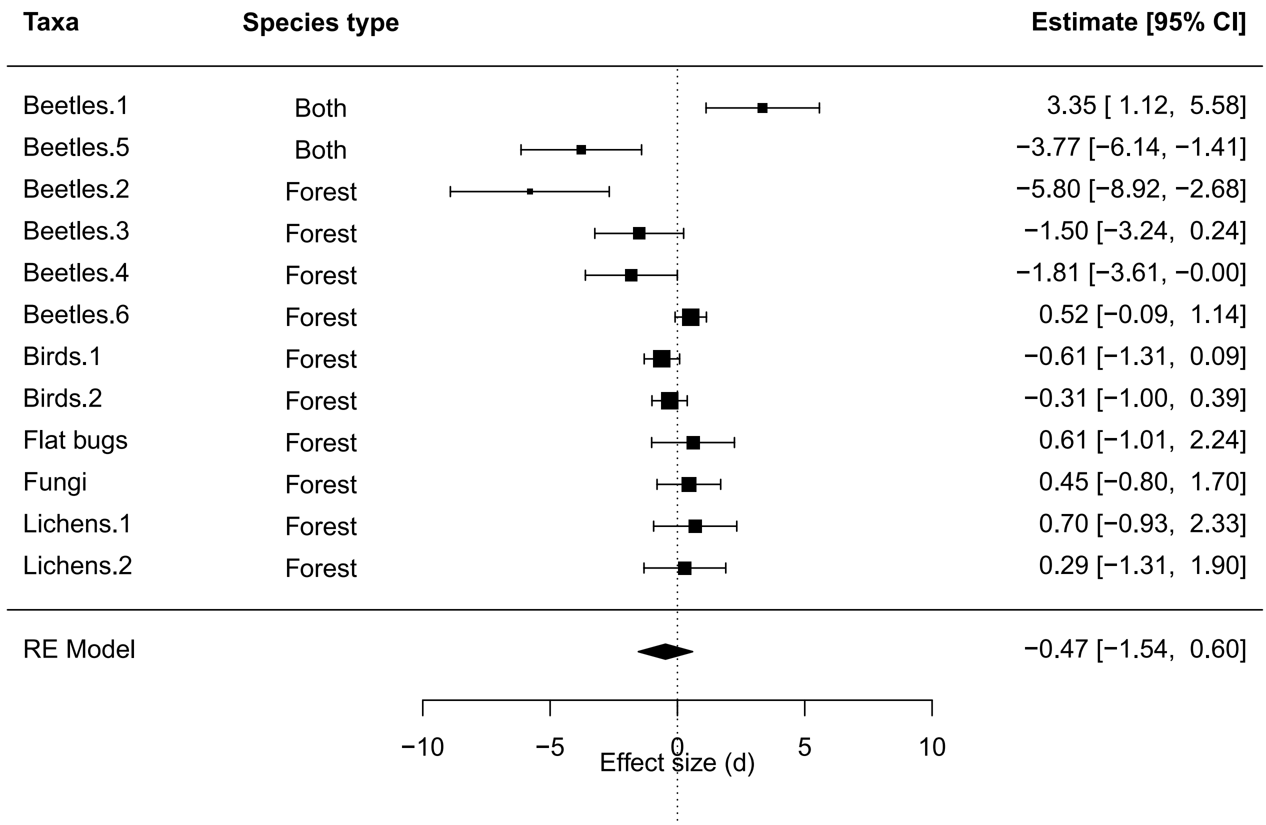

Fig. 20 Forest plot of effect sizes for species richness (mean standardized difference between young even-aged and retention forest). Effect sizes on the right side of zero mean that even-aged forest is more diverse than retention forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond shows the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

was large even in the scale of systematic reviews, and therefore, the risk of publication bias due to lack of comprehensiveness is small. The language-based scope of the review was comprehensive within the geographical area with one exception. Because none of the research group members understands Norwegian, studies published in Norwegian were left out from the review. Therefore, it is possible that relevant studies are missing.

Some rational selection had to be made when choosing between multiple potential exposures and/or comparators, and with study years, locations and study designs (BACI, BA or CI) to avoid extraction of duplicate or non-independent data. Although inclusion criteria were defined before the review was conducted, it is possible that the criteria influenced the results of this review. For example, if data were available from multiple years, we used data from the last year only. The effects of different forest management approaches may have been different, for example, had we used data from the first time of reporting, which was often within a year of harvesting meaning less recovery time for species and the ecosystem.

Our lack of deeper knowledge of Russian forestry resulted in exclusion of some of studies. Russian manner of reporting results of studies differs from the other included countries. Methods are often described very briefly and inadequately, and a reference to "standard methods" is a common description. As none of the authors is an expert on Russian forestry and the methods referenced as "standard", articles with these kinds of methodology had to be excluded as it was unclear what had been done. The problem with Russian studies was partially that forest management regimes in Russia are not fully comparable with management regimes in Finland, Sweden and Norway. In Russia there are different harvesting practices, many of which at some level combine even-aged and uneven-aged managements. This is one reason why so many Russian articles had to be excluded from this review.

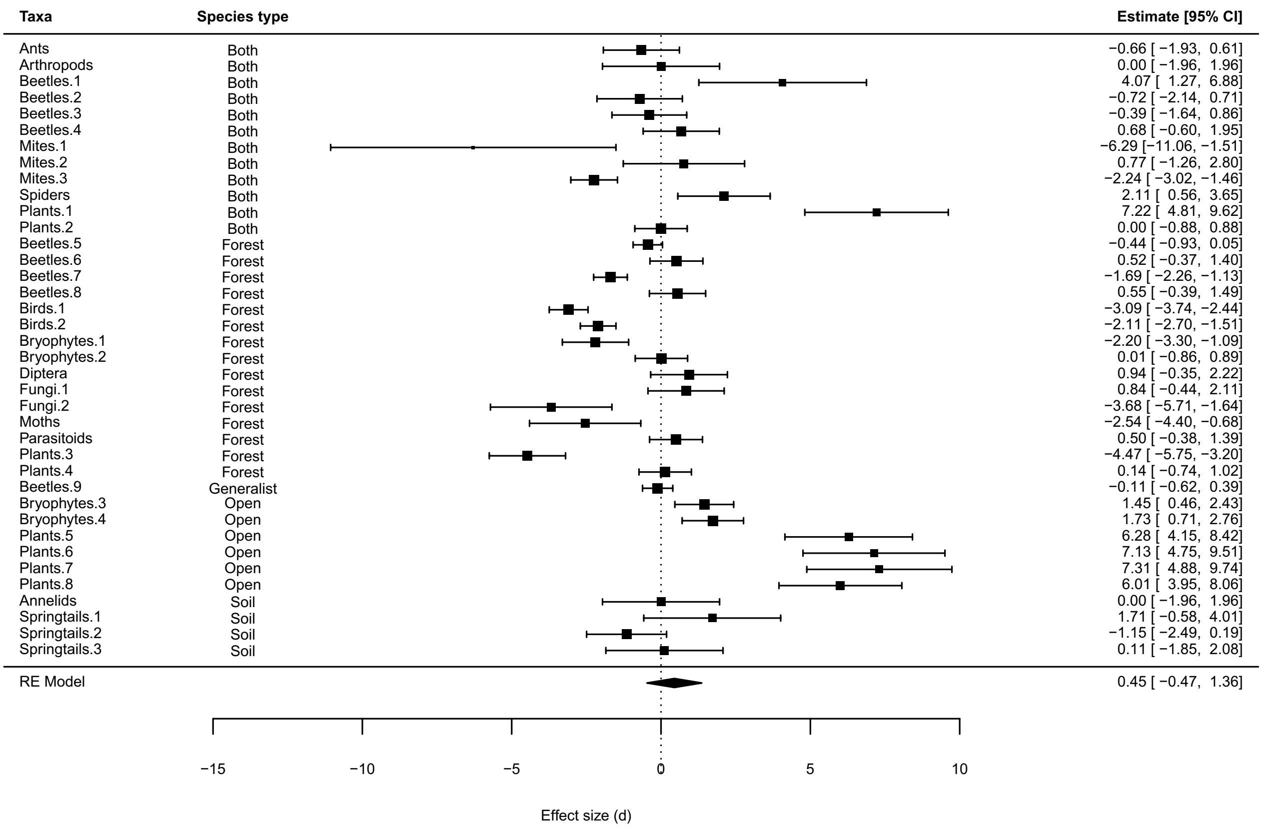

Fig. 21 Forest plot of effect sizes for species richness (mean standardized difference between young and mature even-aged forest). Effect sizes on the right side of zero mean that young even-aged forest is more diverse than mature even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond shows the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

Limitations for generalising the results

Even though there were relatively many studies concerning uneven-aged management in Finland, it should be noted that several of these studies were conducted in same areas. On one hand, studies conducted in same study areas are comparable with each other and they offer more comprehensive results than individual studies conducted in different locations. On the other hand, the large proportion of MONTA studies potentially reduces external validity of the results. However, it should be noted that no significant differences were found on species richness and abundance between MONTA studies and those from other areas. The large number of studies from one area also indicates that the research on uneven-aged forest management in Finland is not as broad and diverse as could be concluded by the number of articles and studies only. Follow-up studies producing time series data over several decades would be important for examining the long-term effects of different forest management regimes, but for example, many of the MONTA study plots have already been taken back to traditional forestry usage (Markus Strandström, Metsäteho Oy, personal communication 7.4.2020).

Although all exposures and comparators were defined when composing the eligibility criteria, it should be noted that there were differences within exposures and comparators between different studies. The uneven-aged forest management could be a single-tree selection or group selection method with varying volumes or numbers of trees removed. Even-aged forests were of different ages and some of them were clearcuts with and some without retention trees. Internal variation existed also within comparators. For example, natural forest comparator could be of any age and in retention harvest the amount and distribution of retention trees could differ. A recent meta-analysis on the impact of retention harvests on biodiversity concluded that more retained trees benefits forest species but their spatial arrangement had no impact [23].

Majority of the studies focused on forest dependent species as could be expected when the objective was to study the effects of forest management. There were

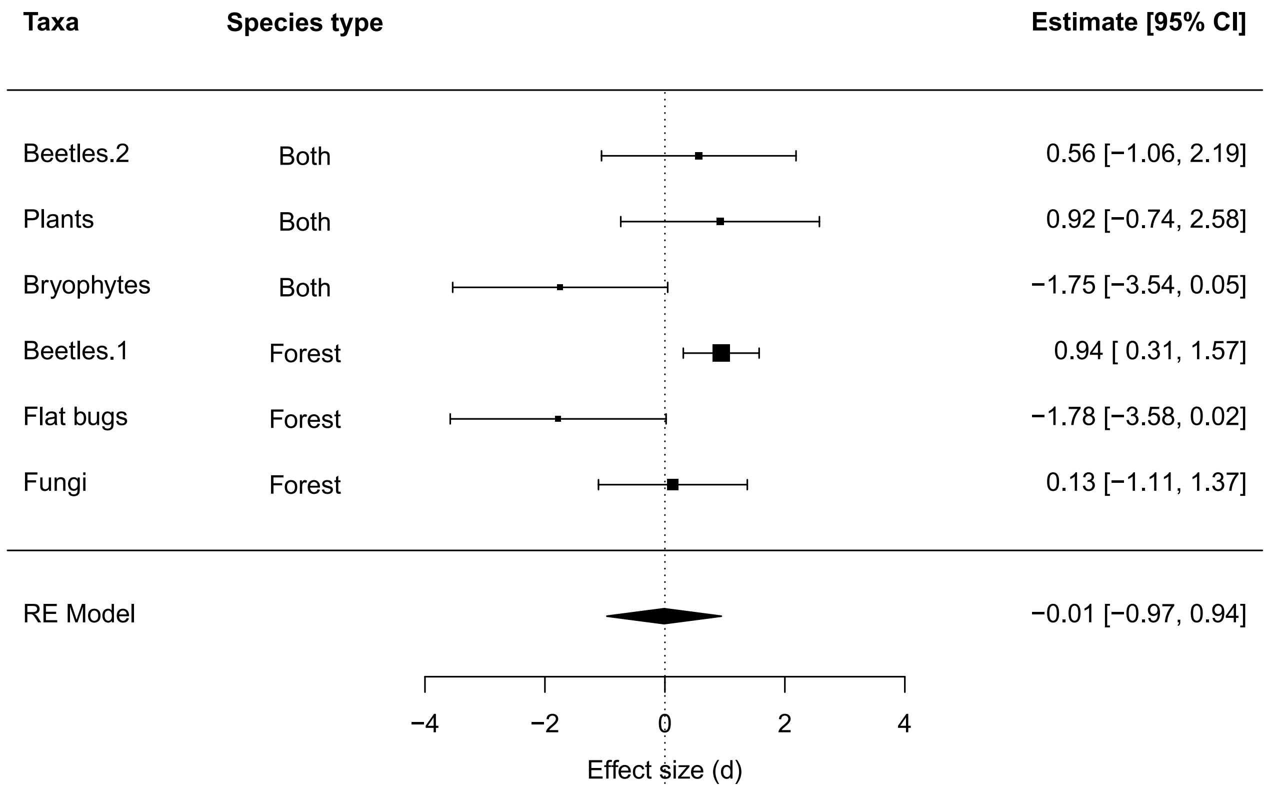

Fig. 22 Forest plot of effect sizes for individual abundance (mean standardized difference between young even-aged and retention forest). Effect sizes on the right side of zero mean that young even-aged forest is more diverse than retention forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond shows the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

relatively few studies on species that prefer open habitats with more light, and therefore the results concerning open-habitat species are not as reliable as results concerning forest dependent species. It should be noted also that the studies concentrating on non-terrestrial species in a forest (e.g. temporary ponds of melting water, forest streams) were excluded as the focus was on direct impacts rather than secondary. However, it is assumed that as forest management impacts the microclimate of the managed stands, and, thus, formation of ponds and environmental conditions of other waterbodies, there could be effects on non-terrestrial species as well.

Even though all the studies included in this review were field studies, sampling methods differed not only between different taxa but also within one. For example, beetles were collected with pitfall traps, flight interception traps and sweep nets. There were also few studies where sampling was conducted in a rather unusual way. For example, Kauserud et al. [67] sampled fungal spores from air. The methods were not fully comparable with other fungal studies either in the study of Heinonsalo and Sen [68], where they grew ectomycorrhizal fungi in laboratory after sampling it from the forest.

Review conclusions

Implications for policy/management

Here we present key results that can inform policy makers, forest managers and those providing advisory services for forest owners.

Firstly, habitat preference is the most important determinant of species' response to forest management at stand-level. Both forest dependent and open habitat species were included in the analyses. Thus, due this heterogeneity we found few significant differences in overall individual abundance and species richness. Similarly, in majority of cases it was impossible to conclude how different taxa respond to harvesting as there were both forest dependent and open habitat species within taxa. This is also the most likely reason why we did not find any impact of harvesting intensity (i.e. % of tree volume removed) of uneven-aged forest on species richness and abundance. Unfortunately, there was not enough data to

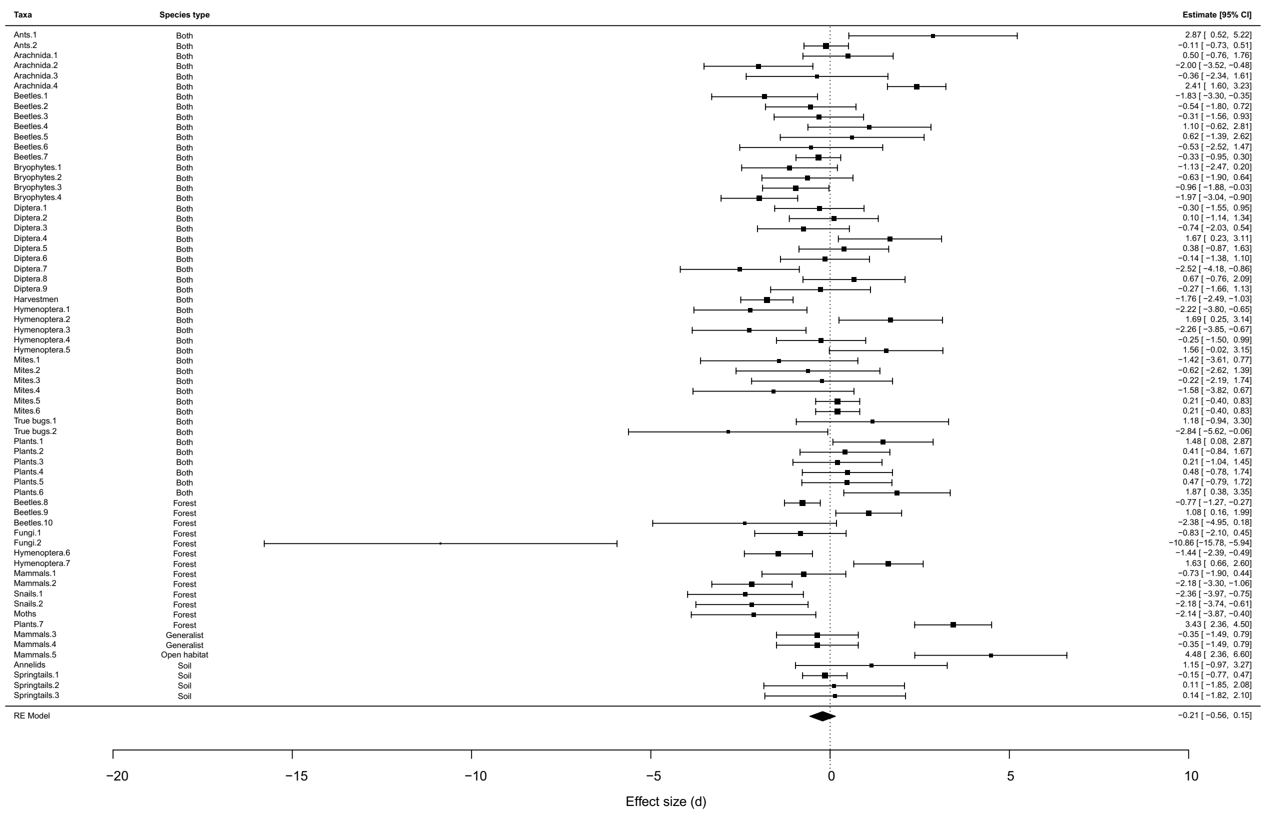

Fig. 23 Forest plot of effect sizes for individual abundance (mean standardized difference between young and mature even-aged forest). Effect sizes on the right side of zero mean that young even-aged forest is more diverse than mature even-aged forest. Different habitat specialisms of the taxa are given. The category 'both' includes both open habitat and forest dependent species. Numbers after the taxa denote different studies. The grand mean noted by a diamond shows the summary effect of all the individual effect sizes. The error bars represent 95% confidence intervals

test the impact of harvesting on forest dependent species. Therefore, we have to rely on the evidence of effect at the level of habitat preferences and hope that in the future more detailed analysis will be possible.

Secondly, the review shows that uneven-aged forest management is more favourable for forest dependent species than even-aged forest management (up to 80 years since harvesting) when the two management regimes are compared to each other or when both are compared to natural forests and the effect is strong (i.e. magnitude of effect size is large). However, there are variables whose influence could not be considered in this review. For example, type of harvesting (e.g. single tree versus group cutting) in uneven-aged forests can influence environmental conditions and subsequently species' response. Similarly, environmental conditions of different sites can vary, for example regarding soil type. Therefore, an overarching conclusion on when and where uneven-aged forest management is beneficial cannot be drawn. In light of our results and considering that even-aged forest management is the dominating silvicultural system in Fennoscandia and Russia, forest owners and managers need support and advice to enable an increase in the use of uneven-aged forest management.

Thirdly, young even-aged forest (< 80 years old) cannot support forest dependent species compared to comparator forest areas (uneven-aged, mature even-aged and natural forests). Over time, the impact of harvesting seems to lessen when uneven-aged and even-aged forest management are compared but even older production forests (> 80 years since harvest) have less forest dependent species than natural forests. This points to the importance of ensuring conservation of natural and near natural forests to safeguard forest dependent species in the future.

Given that a broader set of biodiversity aspects are to be protected within landscapes, i.e. both forest and open habitat specialists, best overall biodiversity impacts for a variety of species at landscape level can be achieved by ensuring that there is a mosaic of different habitats within landscapes. Thus, there should be both even-aged and uneven-aged production forests in various ages at landscape level with special attention given to natural and near natural forests. Approximately 50-50 ratio of uneven-aged and even-aged managed forests has been suggested in simulations [69], which would enable decision-making based on site characteristics and landowner's objectives.

There was lack of evidence about the impact of deadwood as it was not commonly reported and even when it was, there were only few studies in each data set. We found only one case (comparison between uneven-aged and young even-aged forest) where the amount of deadwood was marginally significant to individual abundance, but the lack of evidence should not be taken for a lack of effect. Previous systematic review solely focused on the impact of deadwood on species richness and abundance concluded that increasing the amount of deadwood has positive effects on the abundance and richness of saproxylic insects and fungi although there was heterogeneity in the responses [65].

Although the evidence-base is limited in terms of taxa and geographical scope, the results of this systematic review are rather uniform and in line with current understanding on the impact of disturbance from forest harvesting.

Implications for research

The gaps in geographical distribution of the articles and studies included in this review indicate that more research concerning the biodiversity effects of even-aged and uneven-aged forest management is needed. In the case of uneven-aged management the knowledge base is limited regarding whole of Fennoscandia and European Russia.

Among the major organism groups, birds, mammals and soil animals were subjects in only relatively few studies. Therefore, future research should focus on these groups, especially studies on the effects of uneven-aged forest management. During all research, it would be also meaningful to sort species by their habitat specialism to be able to examine the effects of different forest management regimes and within uneven-aged forest management, different harvesting types and levels on different groups, e.g. forest specialist species.

Most of the studies included in this review were observational studies and therefore determined as medium-risk studies. More carefully planned experimental studies that either control or broadly record effect modifiers would be needed to enhance the validity of the knowledge base. Especially maintaining and establishing long-term experimental studies is important.

In this systematic review, data on species assemblages was not extracted, but it was noticed that this could have been done. Considering assemblages would add value to the examination of the biodiversity effects and it would give more detailed information of the actual differences between species in differently managed forests.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13750-020-00215-7.

Additional file 1. ROSES form for systematic review reports.

Additional file 2. Search strategy and results. A list of all sources searched with information on search dates, languages, search strings/terms, search settings/restrictions, the number of hits received, and the number of articles included on each stage of the screening.

Additional file 3. Translations of the search string. Full search strings and simplified search strings for Google and Google Scholar in English, Swedish, Russian and Finnish.

Additional file 4. List of articles included by title/abstract. There are different sheets for articles included by full text, articles included by full text with independent data (articles in narrative synthesis), articles excluded by full text (with reasons for exclusion) and unretrievable articles.

Additional file 5. Metadata and validity assessment uneven-aged forest. File includes metadata of different studies, data on effect size modifiers and validity assessment.

Additional file 6. Metadata and validity assessment even-aged forest. File includes metadata of different studies, data on effect size modifiers and validity assessment.

Additional file 7. Results from sensitivity analyses without studies with imputed SDs.

Additional file 8. Results from the comparison of abundance between even-aged and natural forest when high risk studies are excluded from the analysis.

Additional file 9. Funnel plots with trim and fill-tests to detect publication bias.

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Authors' contributions

This review is written by SS, AJ, and MH. AU and TS built and tested the final search string. AU, TS, SS, MH and AJ conducted the searches. SS, AJ, and MH screened the articles. Data extraction and critical appraisal was conducted by AJ and MH. AJ conducted the narrative synthesis and SS the quantitative analysis. SS, AJ, and MH wrote the first version of the manuscript. MM and PP contributed to the subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Datasets related to this article are available as additional files apart from datasets used in meta-analysis. The datasets used in quantitative analyses are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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