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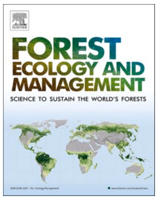

Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: A qualitative review

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ABSTRACT

There is an increasing interest in implementing Continuous Cover Forestry (CCF) as a tool to mitigate negative effects of the traditional rotation forestry system on biodiversity. However, the effects of CCF on forest growth and yield and on biodiversity is still poorly known. In this qualitative review, we compare biodiversity and long-term yield between the selection system, which is a type of CCF practiced in full-storied forests, and the traditional rotation forestry system. We specifically focus on forests dominated by *Picea abies*, which is a tree species of high economic relevance. Our literature search resulted in 17 publications on stand growth and yield and 21 publications on biodiversity. A majority of simulation studies found a higher long-term yield in the rotation forestry system, but it is challenging to conclude which system is the most productive. The magnitude of the difference in yield between systems, and how it varies across different environmental conditions, remains to be determined. For biodiversity, comparisons of species assemblage and individual species were only made to certain phases of the rotation cycle (recent clearcuts and middle-aged stands). Nevertheless, two aspects can be highlighted: i) the species assemblage in clearcuts differ substantially from stands managed with the selection system. Some of these effects may however be short lasting as examplified by studies on beetle assamblages showing that middle-aged rotation forestry stands become more similar to stands managed with the selection system, ii) the selection system maintains a similar species assemblage as the uncut control during the first years after cutting. In conclusion, management with the selection system may come with a loss in long-term stand yield, but much of the species assemblage is maintained after logging. We recommend future studies to specifically focus on long-term effects on biodiversity – in particular on species of conservation concern. There is also a need to establish a long-term research infrastructure to further develop the field.

1. Introduction

Forests cover almost one third of the total global land area, where boreal and temperate forests constitute 27 % and 16 % of the forested land, respectively (FAO, 2020). In northern Europe, where these forest types are dominating, there is currently an ongoing debate about expanding the use of continuous cover forestry (CCF). In fact, the European Union presented a new forest strategy stating that clearcutting should be avoided and alternative management methods such as CCF should be promoted (European comission, 2021).

In Fennoscandia, a large part of the forests in the north were managed either through high-grading (cutting all trees above a certain diameter) or selective cutting (focusing on specific dimensions, species or quality) at the end of the 19th century and early 20th century (Lie et al., 2012; Lundmark et al., 2013; Östlund and Roturier, 2011). In the mid 20th century, the rotation forestry system gained an increased interest and was gradually implemented in Sweden until being the dominant silvicultural system. It was seen as a more reliable and productive system that could meet the increasing demands of wood products (Lundmark et al., 2013).

The rotation forestry system is a cyclic system where each forest stand goes through distinct development phases, from regeneration to final felling. The system creates and maintains single-storied stands, where all trees are of similar height. In most parts of Fennoscandia, the regeneration is done by planting but natural regeneration using seed trees is also used. In both cases, the soil is usually scarified to promote

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survival and growth of seedlings. Almost all stands are thinned during their development, the common practice is thinning from below (removing small-diameter trees) but it is sometimes done from above (removing large-diameter trees). The final felling, ending the rotation cycle, is usually done as clearcutting, with or without leaving seed trees. Along with the implementation of the rotation forestry system, the average growing stock on productive forest land has increased from 96 to 141 m^3 ha^{-1} and the annual harvests from 51 to 92 million m^3 from the mid 1950's to 2018 in Sweden (Swedish national forest inventory). Kauppi et al. (2022) suggest that this was mainly due to improved management, but changes in the environment have most likely also played a role (Binkley and Högberg, 2016; Henttonen et al., 2017).

The rotation forestry system has transformed structurally complex forest stands, with large variation in tree size, high tree species diversity, large amount of dead wood, large and old trees, to less complex single-storied forest stands, with less variation in tree size, often dominated by a single tree species, little dead wood, and few large and old trees (Esseen et al., 1997; Linder and Östlund, 1998; Siitonen et al., 2000; Östlund et al., 1997). Old trees, forest continuity, and dead wood are some of the key elements important for many threatened species (Berg et al., 1994; Stenbacka et al., 2010) of which some require well-connected habitats of natural forests (Norden et al., 2013). In addition, clearcutting induces a rapid turnover in species communities (Hjältén et al., 2012; Jalonen and Vanha-Majamaa, 2001; Joelsson et al., 2017; Stenbacka et al., 2010), with negative effects on several rare and threatened species (Hjältén et al., 2012; Rudolphi et al., 2014) and with a slow recovery of species assemblages (Dynesius, 2015). Thus, forestry using clearcutting is considered a threat to many red-listed species (Hyvärinen et al., 2019; SLU Artdatabanken, 2020). To improve structural complexity and reduce the negative effects of clearcutting on forest dependent species, it is now common practice in forestry to protect forests with high conservation value from cutting, and to retain both living and dead trees on the harvested area (1–10 % of the harvested area in Fennoscandia; Gustafsson et al., 2012; Gustafsson et al., 2020; Johansson et al., 2013). However, a large proportion of the forest area is still unprotected and subjected to clearcutting, and this has negative effects on the local abundance of species with conservation concern (Rudolphi et al., 2014). Thus, additional management needs to be applied to mitigate negative effects of forestry on biodiversity.

The natural disturbance emulation theory is based on the concept that biodiversity can be maintained by recreating and maintaining biodiversity-related forest structures that is present under a natural disturbance regime (Stockdale et al., 2016). In northern Fennoscandia, the disturbance dynamics can be simplified into three types of stand dynamics (Angelstam and Kuuluvainen, 2004): even-aged dynamics driven by large stand-replacing disturbances, cohort dynamics driven by low- to medium stand-level disturbances and gap-phase dynamics driven by small scale disturbances at the group- or individual tree level. Stand-replacing disturbances caused by fire have been assumed to dominate the natural dynamics in the boreal forest (Berglund and Kuuluvainen, 2021; Kuuluvainen, 2009). However, recent studies suggest that more complex non-stand-replacing dynamics such as low-intensity fires, wind, fungi and insect outbreaks may have constituted a significant part of the natural dynamics, resulting in a mosaic of uneven-aged forests that differ in their structural composition (Berglund and Kuuluvainen, 2021; Kuuluvainen, 2009; Kuuluvainen and Aakala, 2011). If this holds true, the application of the rotation forestry system poorly mirrors today's understanding of the complex disturbance-succession cycle of a natural forest (Kuuluvainen, 2009). Thus, implementing management methods that more closely mimic the diversity of natural disturbance regimes may increase landscape heterogeneity, promote beta-diversity, and come with positive effects on aspects of biodiversity that are under threat in the current rotation forestry system.

The selection system is a type of continuous cover forestry that resembles the small-scale disturbances in gap-phase dynamics. This silvicultural system requires a full-storied stand, which means that trees of all sizes, from seedlings to large trees, are present in all parts of the stand at all times and that smaller tree sizes are more abundant than larger sizes (Fig. 1). Approximately 20–30 % of the standing volume is regularly or occasionally cut with single-tree selection (primarily focused on large trees), while still maintaining the full-storied stand structure. Trees are assumed to be naturally regenerated and successively grow into the stand from below. These stands are therefore dominated by tree species that are able to grow and survive in a dense stand, such as *Picea abies* (L.) Karst (Lundqvist, 2017).

Theory suggests that the more complex stand structure associated with selection system may promote biodiversity. The diversity-heterogeneity hypothesis predicts that spatially heterogeneous environments hold a higher diversity of species (Stein et al., 2014), where variation in vegetation height can be a predictor of stand-level species richness (e.g., for species of beetles, birds and fungi; Heidrich et al., 2020). In addition, the microclimate is likely to be relatively stable since the canopy cover and basal area, which affects the microclimate (Ehbrecht et al., 2017; Greiser et al., 2018), is only slightly reduced after cutting in the selection system. Thus, in comparison to rotation forestry, selection system has the potential to cause less harmful effects on several organism groups that have evolved in a more stable forest environment.

While the selection system could come with positive effects on biodiversity, it is necessary to also understand how long-term stand yield is affected by applying either the selection system or the rotation forestry system. Both because long-term yield is directly related to carbon uptake and may affect climate change mitigation, but also to understand how the systems differ in their potential to produce biomass for the forest industry.

In this review, we intend to map and critically assess studies that compare long-term yield and biodiversity between the selection system and the rotation forestry system in forests dominated by *P. abies*. A similar review has previously been published (Kuuluvainen et al., 2012), but given the highly relevant scope of the review, the new literature within the field, the specific focus on the selection system and our critical assessment of growth and yield studies, our study provides a valuable and updated examination of the published research on selection system. A meta-analysis on CCF and biodiversity also exists (Savilaakso et al., 2021), but only covers the combined effect of several methods associated with uneven-aged forest management (e.g., single-tree selection, shelterwood felling, strip felling and gap felling) on biodiversity whereas our review simultaneously examines the effect of single-tree selection on both biodiversity and forest growth an yield.

In this review, we ask the following questions: i) Is long-term yield highest in the selection system or the rotation forestry system? ii) How does biodiversity (in terms of species assemblage and individual species) differ between the selection system and the rotation forestry system? Following these questions, we also identify knowledge gaps and point out the direction of future studies.

2. Study selection

To find literature related to stand growth and biodiversity in the selection system and the rotation forestry system dominated by *P. abies*, we built a search string consisting of two components (search string described in supplementary materials). The first component contained 82 synonyms and semi-synonyms to continuous cover forestry that was extracted from relevant literature (Kuuluvainen et al., 2012; O'Hara, 2014; Pommerening and Murphy, 2004; Puettmann et al., 2015) complemented with 7 additional terms. As some of the synonyms were broad terms (e.g., excellent forestry, ecosystem management) or not associated with the type of forestry reviewed in this study (e.g., green tree retention, group selection), we excluded these and ended up with 56 synonyms that were included in the search string. To delimit our search to forests dominated by *P. abies*, we added a second component with synonyms to *P. abies*. The search string was used in four databases (Web of Science Core Collection, BIOSIS Citation index, Scopus, CABI: CAB

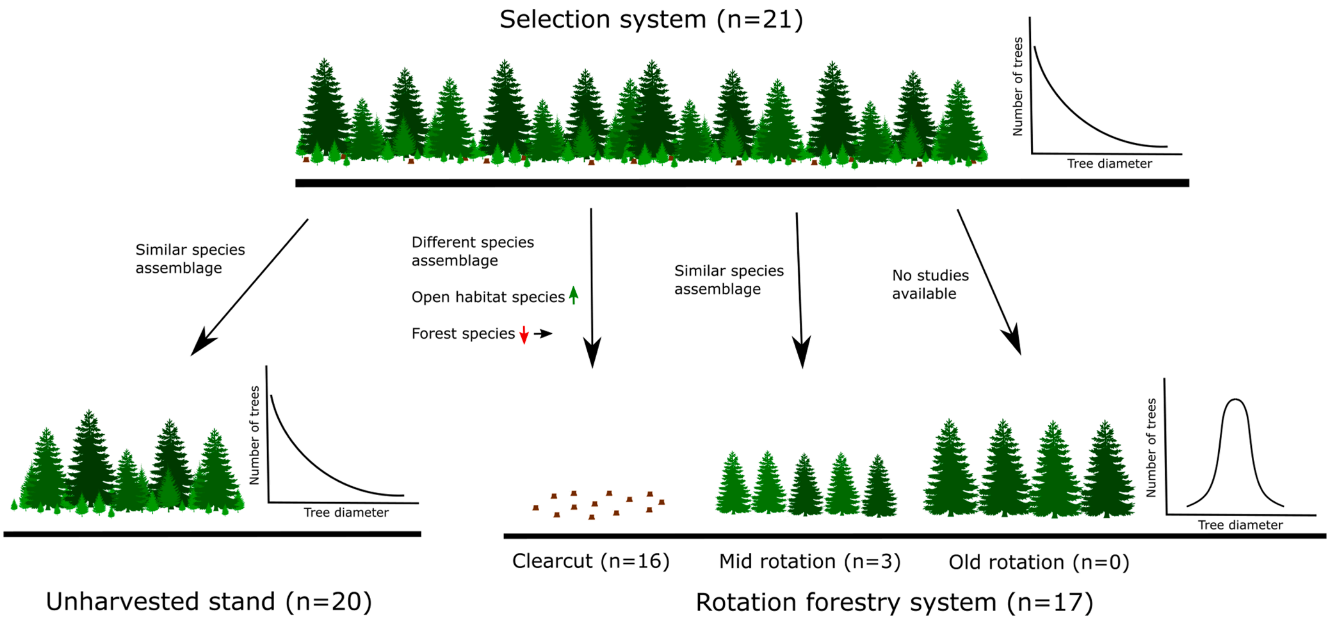

Fig. 1. A schematic overview of differences in biodiversity, stand structure and development over time between *Picea abies* forest managed with the selection system or the rotation forestry system. The difference in stand structure between the two silvicultural systems is displayed with both an illustration and a figure on diameter distribution. Note that several of the reviewed publications on biodiversity lacked a full-storied stand structure and were instead in transition to becoming multi- or full-storied. Number of biodiversity comparisons between stands subjected to thinning from above or single-tree selection with uncut/pre-cut stands or different phases of the rotation forestry system are shown in brackets. The reviewed publications suggest that much of the biodiversity is preserved after single-tree selection. In relation to the rotation forestry system, biodiversity in a stand managed with single-tree selection differs substantially from a clearcut, while being more similar to a mid-rotation forest (at least for beetles). Notably, no publication has compared biodiversity between an old rotation forest and a stand managed with the selection system.

Abstracts® and Global Health®) on the 23rd of May in 2022. To find additional publications on biodiversity, we also included 690 publications from the first sorting of a recent meta-analysis that covers the combined effect of uneven-aged forest management on biodiversity (i.e., publications kept after reading only the title and abstract; see Supplementary file 4 in Savilaakso et al., 2021). We also included publications that were not found in the search string (e.g., Ekholm et al. (2022) which had only been accepted and not published at the search date) and followed relevant citations in the retrieved literature. We only included scientific peer reviewed publications written in English (see Fig. 2 for workflow).

For stand growth and yield, we included field and simulation studies comparing the growth and yield (volume or basal area) between the selection system and the rotation forestry system (excluding studies using other response variables, e.g., Forrester (2019)). Thus, transformation forests (going from single- to full storied stands) and studies only comparing the economical differences between the silvicultural systems were excluded. Neither did we include forests on peatlands. We also excluded one comparative study (Gobakken et al., 2008) due to insufficient information on how growth was calculated (see supplementary materials for eligibility criteria).

To include as many studies on biodiversity as possible, we included studies where cuttings were done with the purpose to maintain or develop an irregular tree size structure (defined in Section 2.1).

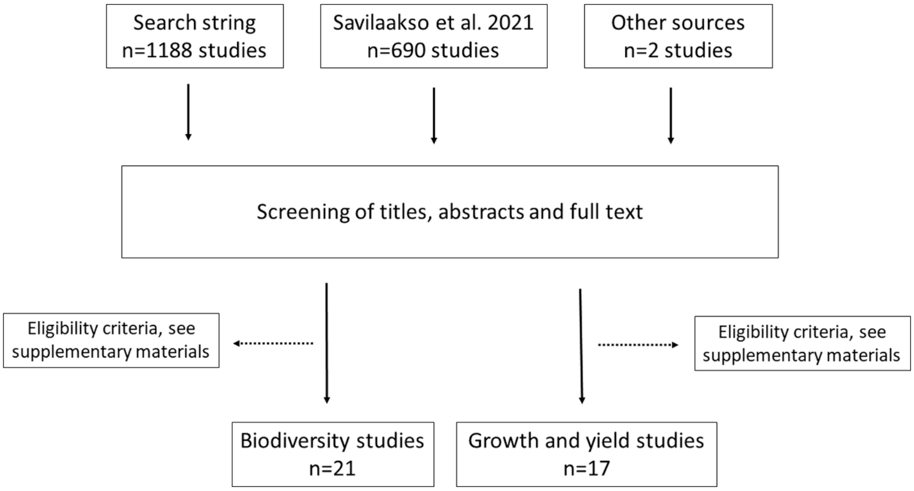

Fig. 2. A schematic overview of the workflow in this review. Publications were obtained from a search string, the meta-analysis of Savilaakso et al. (2021) and other sources (e.g., by following citations within a publication). All these publications were then screened by the main authors and by someone from the author group using the eligibility criteria described in the supplementary materials. In total, we ended up with 21 publications on biodiversity and 17 on stand growth.

Therefore the initial structure could be a single- or multi-storied stand in transition to become a full-storied stand (Table 3; some studies were excluded due to insufficient information on forest structure before or after cutting (e.g., Goßner et al., 2006; Hedenås and Ericson, 2003)). As comparators, we included publications comparing these stands to forests managed with the rotation forestry system, uncut control forests, natural, or near-natural forests. Studies on streamside buffer strips and studies focusing on pest species, such as *Heterobasidion parviporum* and *Armillaria spp*, were excluded as well (see supplementary materials for the full eligibility criteria).

In total, we found 1188 scientific publications in our search string. The list of publications was divided into the two categories "growth/yield" and "biodiversity". Each list was checked twice in order to assure that no study was missed - first by the main author (AE) and then by someone within the author group that had competence within one of the two categories. For each publication, we first scanned the title/abstract for relevance and then continued with reading the full text. Neither abstract nor full text could be accessed for eight publications; therefore these had to be excluded. In the end, we found 17 to be relevant for stand growth and yield, and 21 for biodiversity (Fig. 2). All studies originated from Fennoscandia, despite that this review had no geographical limitations. Including mixed species stands or stands dominated by other tree species than *P. abies* would likely have increased the geographical scope of the study. But this would also add an extra level of complexity, as species identity and species mixture would also need to be considered when calculating stand growth and yield.

2.1. *Terminology*

In several publications, selection system and single-tree selection is often described with terms such as CCF or uneven-aged management. In our review, we consistently use the term "selection system" for the silvicultural system and "single-tree selection" for individual treatments (as defined in the introduction) when this type of silvicultural system has been adopted, even if another term may have been used in the original publication. Thus, it must be stated in the publication that the stand structure is full-storied or that the diameter distribution follows an inverted j-shape as illustrated in Fig. 1, unless the height or diameter distribution is displayed in a figure. If the stand is multi-storied, we instead use the term "thinning from above" for individual treatments.

In some studies (mainly biodiversity studies) the stand structure before and after cutting was poorly described. The presence of more than one tree layer in a stand is often indicated by describing the stand structure as "uneven-aged". In these cases, we use the term "irregular forests" to indicate that the stand has an unknown number of tree layers and describe each treatment as "thinning from above".

In stands managed with the rotation forestry system, we assume that thinnings are aimed at removing the smallest trees in the stand. Therefore, we use the term "thinning from below" for a treatment in the rotation forestry system.

3. Results - Long-term yield in selection system and rotation forestry system

We identified 17 publications that compare stand growth and yield between the selection system and the rotation forestry system. To understand and critically assess growth and yield studies, we start this section by reviewing long- and short-term field studies (n = 2 and n = 8, respectively; Table 1). Hereafter, we use the term mean annual increment (MAI) for yield over a full rotation cycle and current annual increment (CAI) for growth over a subset of the rotation cycle. In the end of this section, we summarize the results of all simulation studies (n = 7; Table 2). For a background on the frameworks used in the simulation studies and the most common growth models applied in the simulation studies, see supplementary materials.

Table 1
A list of field studies comparing growth and yield between single-storied stands managed with rotation forestry system and full-storied stands managed with selection system. From left, each column refers to: the authors of the publication, the country in which the study was conducted, if the study covered a short part of the rotation cycle (short-term) or the full rotation cycle (from planting to final cutting; long-term), the treatments, stand structure and the type of study. Treatments are described in Section 2.1 Terminology.

Publication	Country	Short- or long-term study	Treatments or silvicultural system	Stand structure	Type of study
Lähde et al. (1999)	Finland	Short-term	Single tree selection Thinning from below	Full-storied or Irregular	Experiment
Lähde et al. (2001)	Finland	Short-term	Single tree selection Thinning from below Dimension cutting	Full-storied	Experiment
Lähde et al. (2002)	Finland	Short-term	Single tree selection Thinning from below	Full-storied	Experiment
Lähde et al. (2010)	Finland	Short-term	Single tree selection Thinning from below Dimension cutting No treatment	Full-storied	Experiment
Zenner (2016)	Finland	Short-term	Single tree selection Thinning from below	Full-storied	Experiment
Lundqvist et al. (2007)	Sweden	Short-term	Single-tree selection Thinning from below No treatment	Full-storied	Experiment
Lähde et al. (1994)	Finland	Short-term	Full-storied stands Even-aged stands	Full-storied	Survey
Hynynen et al. (2019)	Finland	Short-term	Thinning from above/Single-tree selection Thinning from below	Full-storied or irregular	Experiment
Nilsen and Strand (2013)	Norway	Long-term	Selection system Rotation forestry system	Full-storied[1]	Experiment
Lundqvist et al. (2013)	Sweden	Long-term	Selection system Rotation forestry system	Full-storied	Experiment

[1] The stand was irrelgular multi-storied during a short part of the study period.

3.1. *Yield in long-term field studies*

Nilsen and Strand (2013) compared yield between a stand managed with selection system against two plots managed with the rotation forestry system (subjected to either light or medium thinning intensities). The MAI over 81 years was 11 m^3 ha^{-1} a^{-1} in the stand subjected to light thinning, whereas it was 10 m^3 ha^{-1} a^{-1} in both the selection system and the medium thinned stand.

Similarly, Lundqvist et al. (2013) compared MAI of volume between a *P. abies* stand managed with the selection system and two stands that were clearcut and regenerated using seed trees of *Pinus sylvestris* L. or

Table 2

A list of simulation studies comparing long-term yield between the rotation forestry system (RF) and the selection system (SeS). From left, each column refers to: The authors of the publication, the modelling framework for the growth model (transition matrix model - TMM, single-tree model or a process-based model), and the respective models used to assess mortality, growth and ingrowth. The final two columns denote the system with the highest long-term yield and the stand structure. If it was possible to extract relative production of SeS in relation to RF from the study, this is presented in a parenthesis (visualized in Fig. 5). Note that Parkatti et al. (2019) is represented by two rows as they use two different growth models within the same publication.

Publication	Model framework	Model			Long-term annual growth (SeS/RF)	**Stand structure**
		Growth	Mortality	Ingrowth/Regeneration		
Tahvonen et al. (2010)	TMM[1]	Tahvonen et al. (2010)	Tahvonen et al. (2010)	Tahvonen et al. (2010)	RF [2]	Full-storied
Tahvonen (2011)	Single-tree model	Pukkala et al. (2009)	Pukkala et al. (2009)	Pukkala et al. (2009)	RF (67–77 %)	Full-storied
Rämö and Tahvonen (2014)	TMM[1]	Bollandsås et al. (2008)	Bollandsås et al. (2008)	Bollandsås et al. (2008)	SeS [3]	Full-storied
Tahvonen and Rämö (2016)	TMM[1]	Bollandsås et al. (2008)	Bollandsås et al. (2008)	Bollandsås et al. (2008), slightly modified	RF (78–90 %)	Full-storied [4]
Parkatti et al. (2019)	TMM[1]	Bollandsås et al. (2008)	Bollandsås et al. (2008)	Bollandsås et al. (2008)	RF (81–84 %)	Full-storied [4]
Parkatti et al. (2019)	TMM[1]	Pukkala et al. (2013)	Pukkala et al. (2013)	Pukkala et al. (2013)	RF (88–96 %)	Full-storied [4]
Kellomäki et al. (2019)	Process-based	–	–	–	RF (98–100 %)	Full-storied
Kellomäki et al. (2021)	Process-based	–	–	–	Stemwood = SeS (124 %–131 %), Timber and pulp = SeS (109–113 %)	Unknown

[1] Transition matrix model.

[2] Under conditions with unrestricted thinnings (not restricted to the four smallest size classes) and a minimum of 1450 seedlings.

[3] No artificial regeneration.

[4] Stand structure not visualized for all simulations.

planting of *P. sylvestris*. Planting led to a stand dominated by *P. sylvestris,* whereas the stand with seed trees had a volume of ~ 60 % of *P. abies*. Planting and seed trees resulted in a MAI of about 5 and 4 m^3 ha^{-1} a^{-1}, respectively, while MAI of the selection system was about 3 m^3 ha^{-1} a^{-1}. Selection system had a low CAI in the beginning of the study period, which was explained as an effect of heavy cutting that left a small growing stock. However, a larger growing stock at the end of the study period resulted in CAI of about 4.5 m^3 ha^{-1} a^{-1}, placing it in between the MAI of the planting and seed tree treatments. If the selection system treatment stabilizes at this level, it would indicate only a minor reduction of long-term yield compared to the rotation forestry system.

3.2. *Growth in short-term field studies*

Several field studies have been conducted at Vessari and Honka in central Finland, but also at other locations in Finland (Lähde et al., 1992). In Vessari and Honka, studies found both a near-significant higher CAI (2 m^3 ha^{-1} a^{-1}) after single-tree selection (Lähde et al., 1999) and no difference in growth (Lähde et al., 2001). Basal area growth has been followed over a longer time period (second and third cut). For the later of the two measurement periods (2003–2008), the ten most heavily cut single-tree selection stands had a higher absolute basal area growth than the ten stands best representing the prevailing practice of thinning from below, despite that the latter stands had a larger basal area (Lähde et al., 2010). Zenner (2016) further investigated basal area growth of trees with a dbh (diameter 1.3 m above ground) $\geq$ 10 cm and found growth to depend on stocking levels; single-tree selection resulted in a higher growth at a small basal area, whereas growth was higher after thinning from below when the basal area was large. However, the author found no evidence that either of the systems was more productive.

Apart from the stands established in Vessari and Honka, other studies in Finland and Sweden have reported a higher CAI in volume after single tree selection and thinning from above than after thinning from below (Lundqvist et al., 2007; Lähde et al., 1999; Lähde et al., 2002), but also with no difference (Lähde et al., 2001). Lähde et al. (2002) found the difference to be most pronounced at small standing volumes and was reduced at larger volumes. Data from the NFI in the south-western Finland found a higher relative growth rate in full-storied stands, but growth did not differ when comparing stands of similar volumes (Lähde et al., 1994).

Hynynen et al. (2019), which used a slightly more model-based approach, found that the rotation forestry system consistently resulted in a higher CAI. Following the guidelines of practical forestry in Finland, their results suggests that basal area growth is 25–30 % smaller after single-tree selection and thinning from above in comparison to mid- or late-rotation forests managed with thinning from below.

3.3. *Long-term yield in simulation studies*

Tahvonen et al. (2010) created a transition matrix model (TMM) based on the experiments in Vessari and Honka in central Finland. They found that long-term yield was maximised with a three-year cutting cycle. The pre-cut basal area was 12–15 m^2 ha^{-1} and generated a long-term MAI of 5.8–6.7 m^3 ha^{-1} a^{-1} depending on ingrowth. In comparison, the rotation forestry system was more productive than the selection system provided the initial number of trees exceeded 1450 trees per hectare 24 years after regeneration.

Later, Tahvonen (2011) modelled yield over several thermal zones (defined by accumulation of degree-days) of *Myrtillus* type forests. For the selection system, a cutting interval of five years maximized long-term MAI at 4.3–5.1 m^3 ha^{-1} a^{-1}, compared to 5.6–7.6 m^3 ha^{-1} a^{-1} for the rotation forestry system.

Rämö and Tahvonen (2014) found that cutting intervals longer than five years lowered the long-term yield, which implied that the selection system was the most productive system. However, this was under the condition that only natural regeneration was occurring also in the rotation forestry system. Since artificial planting is commonly used in the rotation forestry system, this type of comparison poorly represents the actual differences in long-term yield.

Later, Tahvonen and Rämö (2016) used a TMM that allowed flexible timing of harvests and both artificial and natural regeneration in clearcuts. They found rotation forestry to produce the highest long-term annual yield across three site productivities (Site index (SI), H40 = 11, 15, 17; Rotation: 4.8–9.0, Selection: 4.3–7.0 m^3 ha^{-1} a^{-1}).

Parkatti et al. (2019) compared the growth models of Bollandsås

Table 3

A summary of the 21 publications examining how biodiversity is influenced by thinning from above/single-tree selection. From left, each column refers to: the publication, the experiment area (see also Fig. 3), the studied taxonomic group, the comparative treatment, number of replicates in the experiment, the stand structure before and after cutting, the cutting intensity of single-tree selection or thinning from above and the study design (before-after-control-impact (BACI), control-impact (CI) or before-after (BA)).

Publication(s)	Experiment	Taxonomic group(s)	Comparator	Replicates	Stand structure before/after harvest	Harvest intensity	Study design
Jokela et al. (2019)	DISTDYN	Arthropods (Coleoptera)	Uncut stand, Clearcut	3	Even-aged/Irregular [1]	33–54 % volume removal	BACI
Pasanen et al. (2019)	DISTDYN	Polypores	Uncut stand, Clearcut	3	Even-aged/Irregular [1]	No info	BACI
Siira-Pietikäinen et al. (2001) Siira-Pietikäinen et al. (2003) Siira-Pietikäinen and Haimi (2009)	MONTA	Several arthropod groups, Bacteria, Fungi, Annelida	Uncut stand, Clearcut	4	Even-aged/Irregular [2]	30 % of the standing volume	BACI
Jalonen and Vanha-Majamaa (2001)Vanha-Majamaa et al. (2017)	MONTA	Lichens, Vascular plants, Bryophytes	Uncut stand or Pre-cut stand, Clearcut	8	Even-aged/Irregular [2]	30 % of the standing volume	BACI and BA
Koivula (2002)	MONTA	Arthropods (Coleoptera, Formicidae)	Uncut stand, Clearcut	8	Even-aged/Irregular [2]	10.9–33.7 % of trees	BACI
Matveinen-Huju and Koivula (2008)	MONTA	Arthropods (Aranae)	Uncut stand, Clearcut	4	Even-aged/Irregular [2]	10.9–33.7 % of trees	BACI
Atlegrim and Sjöberg (1996a)	Vilhelmina	Arthropods (Hymenoptera, Lepidoptera)	Uncut stand, Clearcut	3	Irregular/Irregular [3]	30 % of the trees; 45–50 % of the tree volume	CI
Atlegrim et al. (1997)	Vilhelmina	Arthropods (Coleoptera)	Uncut stand, Clearcut	3	Irregular/Irregular [3]	30 % of the trees; 45–50 % of the tree volume	CI
Atlegrim and Sjöberg (1996b)	Vilhelmina	Vascular plants (*Vaccinium myrtillus*)	Uncut stand, Clearcut	3	Irregular/Irregular [3]	30 % of the trees; 45–50 % of the tree volume	CI
Atlegrim and Sjöberg (1995)	Vilhelmina	Several groups of Arthropods	Uncut stand, Clearcut	3	Irregular/Irregular [3]	30 % of the trees; 45–50 % of the tree volume	CI
Atlegrim and Sjöberg (2004)	Vilhelmina	Characters important for biodiversity	Uncut stand, Virgin forest, Clearcut	3	Irregular/Irregular [3]	30 % of the trees; 45–50 % of the tree volume	CI
Joelsson et al. (2018a)	Västernorrland	Arthropods (Coleoptera)	Uncut stand, Thinned stand, Old growth stand, Clearcut	5–9	Irregular/Irregular	30 % of the standing volume	CI
Joelsson et al. (2017)	Västernorrland	Arthropods (Coleoptera)	Uncut stand, Thinned stand, Clearcut	5–9	Irregular/Irregular	30 % of the standing volume	CI
Hjältén et al. (2017)	Västernorrland	Arthropods (Coleoptera)	Uncut stand, Old growth stand	8–9	Irregular/Irregular	30 % of the standing volume	CI
Versluijs et al. (2020)	Västernorrland	Birds	Thinned stand	14	Irregular/Irregular	30 % of the standing volume	CI
Storaunet et al. (2014)	Saksumdalen	Lichen	Uncut stand	7 and 3	Irregular/Irregular [4]	41–53 % of growing stock	BACI
Kim et al. (2021)	Mid-Sweden	Fungi	Uncut stand, Clearcut	4	Full-storied/Full-storied	30 % of the basal area	CI
Ekholm et al. (2022)	Mid-Sweden	Wood-inhabiting fungi, Vascular plants, Bryophytes	Uncut stand	8–9	Full- and Multistoried/Full- and Multistoried	On average 34 % of the volume	BACI

[1] According to Koivula et al. (2014) the project aims “at providing structural variation similar to that found in unmanaged forests in Fennoscandia”.

[2] According to Jalonen and Vanha-Majamaa (2001) selection cutting was done by “cutting trees from age and size classes required to maintain or create an uneven-aged stand structure” and According to Koivula (2002) the forest “were cut with the aim of developing an uneven age structure of trees”.

[3] According to Atlegrim and Sjöberg (1996a) “cutting was distributed over all age classes”.

[4] According to stand reconstructions presented in Storaunet et al. (2008), the stands were irregular prior to cutting, but also after cutting according to personal communication with the main author.

et al. (2008) and Pukkala et al. (2013). The selection system resulted in about 80–96 % of the long-term yield of the rotation forestry system across different site productivities. In the selection system, Bollandsås et al. (2008) generally resulted in a higher steady state basal area than Pukkala et al. (2013), which was mainly attributed to differences in the ingrowth functions used in the two studies.

We found two publications that used a process-based model. These were primarily focused on carbon dynamics, but also studied long-term yield. First, Kellomäki et al. (2019) estimated MAI over a period of 300 years (225–525 years after start of simulation). MAI was found to be marginally higher in the rotation forestry system than the selection system over three levels of minimum basal area (Rotation: 5.47–6.47 m^3 ha^{-1} a^{-1}, Selection: 5.45–6.34 m^3 ha^{-1} a^{-1}). Notably, the selection system was highly influenced by number of seed crops: a reduction of 25–75 % in seed crop resulted in a 44–74 % decrease in volume yield over the full simulation period. Later, Kellomäki et al. (2021) simulated stand development over 1000 years starting from a clearcut. Over two time periods, 101–400 years and 401–1000 years after the start of the simulation, the long-term MAI was consistently higher within irregular stands subjected to thinning from above (8.3–8.9 m^3 ha^{-1} a^{-1}) than in stands managed with the rotation forestry system (6.7–6.8 m^3 ha^{-1} a^{-1}).

4. Results - biodiversity in selection system and rotation forestry system

4.1. Experimental studies

We identified 21 publications that followed either a before-after-control-impact (BACI), control-impact (CI) or before-after (BA) design. Several publications lacked detailed information on stand structure before and after cutting. For these publications, we therefore refer to the stand structure as “irregular” and call each treatment “thinning from above”, while we refer to a treatment in the rotation forestry system as “thinning from below”. Ten publications include studies conducted in forests with an irregular stand structure, one in full-storied stands, one in full- or multi-storied stands (multi = more than one tree-layer but not enough to be classified as full-storied) and the remaining nine publications examine stands that were even-aged but logged to develop an irregular structure (Table 3). In all of these publications, comparisons of biodiversity were done to either pre-cut or uncut control stands (n = 20), clearcuts (n = 16) or stands thinned from below (n = 3) (Fig. 1). Many of the reviewed publications utilized the same experimental plots. To display the diversity of study designs and how they overlap, we describe the study design and main results from six experiments below in separate sections (MONTA and DISTDYN are official names, while Vilhelmina, Uneven, Mid-Sweden, and Saksumdalen are unofficial names (Fig. 3; Table 3)).

4.2. *Monta*

The MONTA experiment consisted of eight study sites, located in two clusters in the eastern and western part of southern Finland. The experiment targeted soil-dwelling invertebrates (enchytraeids, collembolans, coleopterans), other arthropods, understorey vegetation, and microbes. Prior to cutting, the experimental forests were about 100 years old with a standing volume of approximately 310 m^3/ha^{-1}. The aim of the cutting was to “maintain or create an uneven-aged stand structure” (Jalonen and Vanha-Majamaa, 2001). Apart from thinning from above, the experiment also included an uncut control stand and a clearcut treatment.

Studies from this experiment found no or small effects of thinning from above on soil decomposers, the assemblage of microbes, soil-dwelling invertebrates (Enchytraeids, Collembola, Coleoptera), Aranae and other Coleopterans, in relation to the uncut control stand (Koivula, 2002; Matveinen-Huju and Koivula, 2008; Siira-Pietikäinen and Haimi, 2009; Siira-Pietikäinen et al., 2003; Siira-Pietikäinen et al., 2001). Three years after cutting two species of staphylinids (*Othius myrmecobius* and *Sipalia circellaris*) tended to be more common in stands subjected to thinning from above than in the control stands. For the understory vegetation, thinning from above had an immediate impact by reducing the bryophyte cover. The number of bryophytes species were also reduced in relation to the pre-thinning levels, but not in relation to the control (Jalonen and Vanha-Majamaa, 2001). Ten years after thinning from above, the understory vegetation had only partly recovered to the pre-thinning state: vegetation such as mosses, liverworts, dwarf shrubs and *V. myrtillus* had not yet fully recovered to pre-harvest abundance.

In contrast to thinning from above, clearcutting resulted in marked changes in the understory vegetation (Vanha-Majamaa et al., 2017) and the response of other taxonomic groups varied. For instance, numbers of soil herbivores were reduced, while open-habitat spiders and carabids were favoured by clearcutting.

4.3. *Vilhelmina*

Near lake Bielite (Vilhelmina, northern Sweden), insect herbivores, carabids, *V. myrtillus* (Atlegrim and Sjöberg, 1995, 1996a, 1996b; Atlegrim et al., 1997) but also stand complexity (abundance of dead wood, Betula spp and trees with berries; Atlegrim and Sjöberg, 2004) were studied in forests subjected to thinning from above and clearcutting. Three forests with a history of diameter limit harvests had randomly been assigned to one of the following 20 ha treatments: no treatment, clearcut (removing all trees) and thinning from above. The study focusing on stand complexity had an extra control consisting of a virgin forest (i.e., none or a small impact of forestry).

In relation to the untreated control stand, there was no evidence that thinning from above had any effect on species abundance, assemblage of arthropods (e.g., herbivorous larvae feeding on *V. myrtillus*, spiders and carabids) or herbivory on *V. myrtillus*. However, thinning from above resulted in a reduced and patchy distribution of *V. myrtillus*. Clearcutting on the other hand reduced the abundance of herbivorous larvae, which

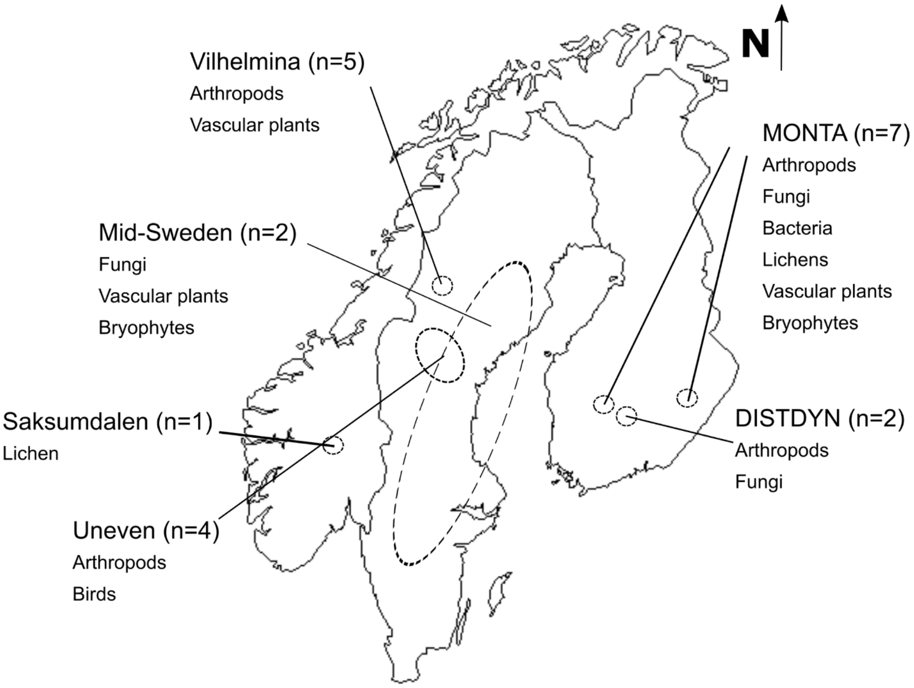

Fig. 3. The geographical location of the biodiversity studies in this review. The name and location of each experimental site together with the organism groups that was surveyed are shown in the map (see Table 3 for details). The brackets represents the number of publications produced from each experimental site. Map is derived from package *rworldmap* (South, 2011).

was attributed as either a direct effect of microclimate, or indirectly through changes in resource quality. For carabids, forest species were unaffected while one open-habitat species had a higher abundance in the stand subjected to clearcutting. In terms of structural complexity, thinning from above resulted in stands with a lower number of dead standing trees in comparison to the uncut control and the virgin forests. Clearcuts had a lower number of old logs than the stand subjected to thinning from above and the virgin forest. The number of new logs was higher in the virgin forest than in the clearcut, but did not differ between the other treatments.

4.4. *Distdyn*

The DISTDYN project aimed at capturing the long-term, landscape-level response of biota to nature-oriented forest management. This project involves two Finnish landscapes: Isojärvi and Ruunaa. The Isojärvi area is dominated by *P. abies* and has previously been managed with the rotation forestry system. In the winter of 2009/2010, the area was cut with a special focus on promoting structural variation and retaining live and dead trees (see more in Koivula et al. (2014)). So far, two publications have examined the short-term response of polypores and beetles to thinning from above and clearcutting. The stands were approximately 80 years old at the time of the treatments.

The number of beetle species increased after thinning from above but were again at similar levels to the control stand after two years. Similarly, the beetle assemblage was more different between the control stand and the stand subjected to thinning from above the first year after treatment than after the second. Both thinning from above and control stands preserved a similar proportion of species, although two species (*Dinaraea linearis* and *Epuraea terminalis*) tended to be more associated with uncut control stands (the species were however caught in low numbers) (Jokela et al., 2019). Clearcutting preserved a similar number of species as the uncut control and thinning from above, but the community composition was different in the clearcut stands. For polypores, the formation and quality of new dead wood seemed to be more important than the overall forest management intensity for explaining polypore richness. However, the polypore assemblage on cut logs and high stumps had a tendency to differ among treatments, where thinning from above was most similar to the control stands (Pasanen et al., 2019).

4.5. *Uneven*

In forests with an irregular structure located in central Sweden, the response of beetles to thinning from above was studied in relation to uncut control stands and old-growth stands. In addition, two parts of the rotation cycle was used as comparators: recent clearcuts and 50–60 year old even-aged stands generated after clearcutting (Hjältén et al., 2017; Joelsson et al., 2017). In Joelsson et al. (2018a), differences among treatments was studied using two different trapping methods (bolts and window traps). Thinning from above in irregular stands and thinning from below in even-aged stands was conducted 2–15 years prior to the study.

In general, there were only minor differences in beetle abundance and richness among treatments. In contrast, the assemblage differed substantially between stands subjected to clearcutting and the thinning treatments, but not between thinning treatments. In terms of functional groups, cambivore assemblage differed between thinning from above and the uncut controls, with a tendency for a similar difference within obligate saproxylics and fungivores. No difference in assemblage of functional groups was found between thinning treatments. The difference between cambivores was mainly attributed to the higher abundance of two species associated with semi-open habitat (*Crypturgus hispidulus* and *Crypturgus cinereus*) after thinning from above. Also, *Phloeotribus spinulosus* was thought to be disfavoured by more open stands as it was less common in stands subjected to thinning from above then in the control stand (Hjältén et al., 2017; Joelsson et al., 2017). There was also a tendency for differences in assemblage of saproxylic beetles associated with decayed wood between thinning treatments (Joelsson et al., 2018a) and higher abundances of certain old-growth forest species after thinning from above compared to thinning from below (Joelsson et al., 2017).

In partly overlapping sites, Versluijs et al. (2020) compared the assemblage of boreal birds between irregular stands subjected to thinning from above and 40–60 year old even-aged stands that had been thinned from below (cutting done 3–28 years prior to the study). They found that species richness, abundance of ground nesting species and succession generalists were higher in stands thinned from below. These stands also hosted a higher number of long-distance migratory species and a higher abundance of ground feeders. In terms of individual species, *Parus major, Anthus trivialis,* and *Ficedula hypoleuca* were all more common in stands that were thinned from below. This was opposite to the authors' prediction that the more complex irregular forests would have a higher species richness and abundance of birds than the even-aged stands.

4.6. *Mid-Sweden*

In mid Sweden, Ekholm et al. (2022) studied the short-term response of wood-inhabiting fungi, vascular plants and bryophytes. Full-storied and multi-storied stands were treated with single-tree selection or thinning from above. The treatments included a fertilized and an unfertilized part. They found that the species assemblage was relatively intact the first few years after cutting. The plant coverage tended to increase, whereas the bryophyte cover tended to decrease in relation to the control stand. This effect was most pronounced in the fertilized treatment, where the moss species *Hylocomium splendens* decreased and the grass *Avenella flexuosa* increased in coverage.

In a subset of the sites used in Ekholm et al. (2022), Kim et al. (2021) studied the response of the soil fungal community to single-tree selection, but this study also included a clearcut treatment. They found that single-tree selection maintained similar soil chemical properties, while clearcutting differed more in soil chemistry. The effects on soil chemistry was reflected in the soil fungal community: the diversity and species richness of fruiting bodies and soil fungi, but also the composition of fruiting bodies was similar between uncut control stands and those subjected to single-tree selection. Although the soil fungi communities derived from DNA metabarcoding differed between the treatments and the control, single-tree selection generally maintained the soil fungal community rather well.

4.7. *Saksumdalen*

In Saksumdalen (Norway), Storaunet et al. (2014) performed an experiment in irregular forest stands with varying intensity of past cutting (Storaunet et al., 2008) to assess the response of the epiphytic lichen *Usnea longissima* to cutting. Logging spared trees containing *U. longissima*, resulting in a standing volume between 100 and 170 m^3 ha^{-1}. Occasionally group and strip cutting were performed where *U. longissima* was lacking. For trees with *U. longissima*, the number of thalli was highest in trees that had a low to medium basal area around the trees. They suggested that about 50 % of the growing stock could be cut in their study area, under the condition that no lichen bearing trees are removed and the humidity remains at a relatively high level.

5. Discussion

This literature review focus on long-term yield and biodiversity in *P. abies* forests managed with either the selection system, a well-defined type of CCF requiring a full-storied stand structure (Lundqvist, 2017), or the currently dominating rotation forestry system. A majority of the simulation studies found that the rotation forestry system is the most productive silvicultural system and the two long-term field studies support this but they suffer from poor experimental design – which makes it challenging to conclude which system is the most productive. In terms of biodiversity, comparisons between the selection system and the rotation forestry system were only made with some phases of the rotation forestry system (clearcut and mid-rotation stands). These incomplete comparisons limit our understanding on which regime creates an environment with the highest biodiversity (i.e., alpha-diversity), but also how biodiversity differ between the two management regimes (i.e., beta-diversity) and to what extent these two management methods can be combined to increase landscape-level diversity (i.e., gamma diversity). However, in relation to uncut control stands, single-tree selection maintained a similar assemblage of species the first few years after cutting, indicating limited effects on species associated with older forests. Below, we start the discussion by evaluating the current knowledge of first growth and yield and then biodiversity. We end by identifying knowledge gaps and outline the most critical fields for future research.

5.1. *Long-term yield in the selection system*

The two long term field studies showed a higher yield in the rotation forestry system but are inconclusive due to poor experimental design (Lundqvist et al., 2013; Nilsen and Strand, 2013). They are unreplicated and the rotation forestry stand in Lundqvist et al. (2013) contain a high number of *P. sylvestris*.

In the short-term field studies, the study by Hynynen et al. (2019), who compared growth over a large part of the rotation cycle (but not the full cycle), also found a superior stand growth in the rotation forestry system. Growth in terms of volume and basal area tended to be similar or higher after single-tree selection than thinning from below in the young stands followed in the Honka and Vessari field study (Lähde et al., 2010; Lähde et al., 1999; Lähde et al., 2001) and in old stands from Finland and Sweden (Lundqvist et al., 2007; Lähde et al., 1999; Lähde et al., 2001; Lähde et al., 2002). Given that the CAI varies substantially over time in the rotation forestry system, but is relatively stable in selection system (Fig. 4), it is difficult to draw conclusions about long-term differences in MAI between the two silvicultural systems from field studies that only compares CAI. Thus, these studies are comparing two kinds of thinning, from below or above, rather than two silvicultural systems.

In the simulation studies, four out of seven publications found lower yield in the selection system than in the rotation forestry system, one study found that yield was comparable and two studies found that the selection system was more productive than the rotation forestry system (Table 2; Fig. 5). In studies where it was possible to calculate a relative yield between the systems, the yield of the selection system ranged 67–131 % of that of the rotation system. The explanation to this quite large variation may partly come from the use of different modelling frameworks and the assumptions within them: Rämö and Tahvonen (2014) made a comparison under the condition that only natural regeneration was allowed in the rotation forestry system, which is not realistic as artificial regeneration is essential and by far the most common regeneration practise within the rotation forestry system. Notably, the two process-based models predicted a comparable (Kellomäki et al., 2019) or higher yield (Kellomaki et al., 2021) in the selection system, which was contrary to the TMM that generally predicted a higher yield for the rotation forestry system. It is possible that this discrepancy is related to the modelling framework, but this is not further examined in this review.

In summary, the number of studies and their quality is evidently limited. The long-term field studies are inconclusive due to poor experimental design, whereas a majority of the simulation studies found the rotation forestry system to be more productive. Despite the new literature in the field, it is not possible to determine which silvicultural system is associated with the highest long-term yield (Kuuluvainen et al., 2012). However, simulation studies is likely to play a key role in comparing these silviculture systems. Therefore, it is necessary to understand how simulations compare to experimental data, which we examine below.

5.2. *Field versus simulation studies*

To compare if annual growth differ between growth derived from simulation studies and a larger data set of field studies, we extracted and plotted data on growth and standing volume from the permanent field- and simulation studies obtained in this review (when this was possible to obtain; Fig. 6A; table S1). The reason for only including permanent field studies is that they deviate the least from the “true” growth (further explained in supplementary materials; Lundqvist, 2004). To gain a larger set of field studies, we also included permanent field studies from a review on the selection system by Lundqvist (2017) (Fig. 6B). The overall pattern is that volume growth (CAI) is consistently higher in simulation than field studies (Fig. 6). The reason for this cannot be

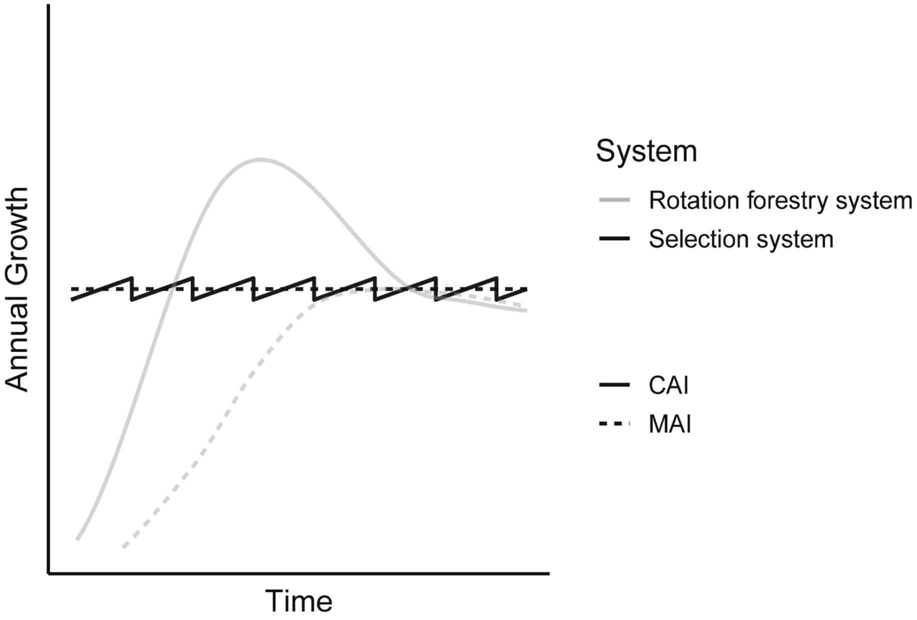

Fig. 4. A schematic overview of the development of mean (MAI; dotted line) and current (CAI; solid line) annual volume increment in selection system (black line) and rotation forestry system (grey line; no thinning in the rotation scenario). For the rotation forestry system, MAI is the yield divided by the no. of years elapsed since the start of the rotation. In the figure, the two systems are assumed to give the same long-term yield. Note that CAI varies substantially over time in the rotation forestry system, while being relatively stable in the selection system. Therefore, short-term comparisons of CAI between the two silvicultural systems, over a period of, e.g., 10 years, could give contrasting results if the comparison is made early or late in the rotation cycle.

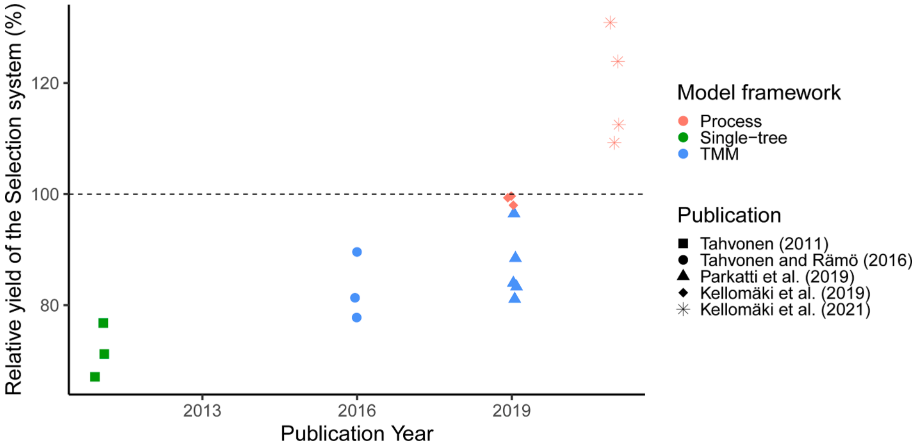

Fig. 5. The relative difference in long-term yield between the rotation forestry system and the selection system in simulation studies (where this information was possible to obtain, see Table 2). Each publication is presented with a separate symbol and each model framework by separate colors.

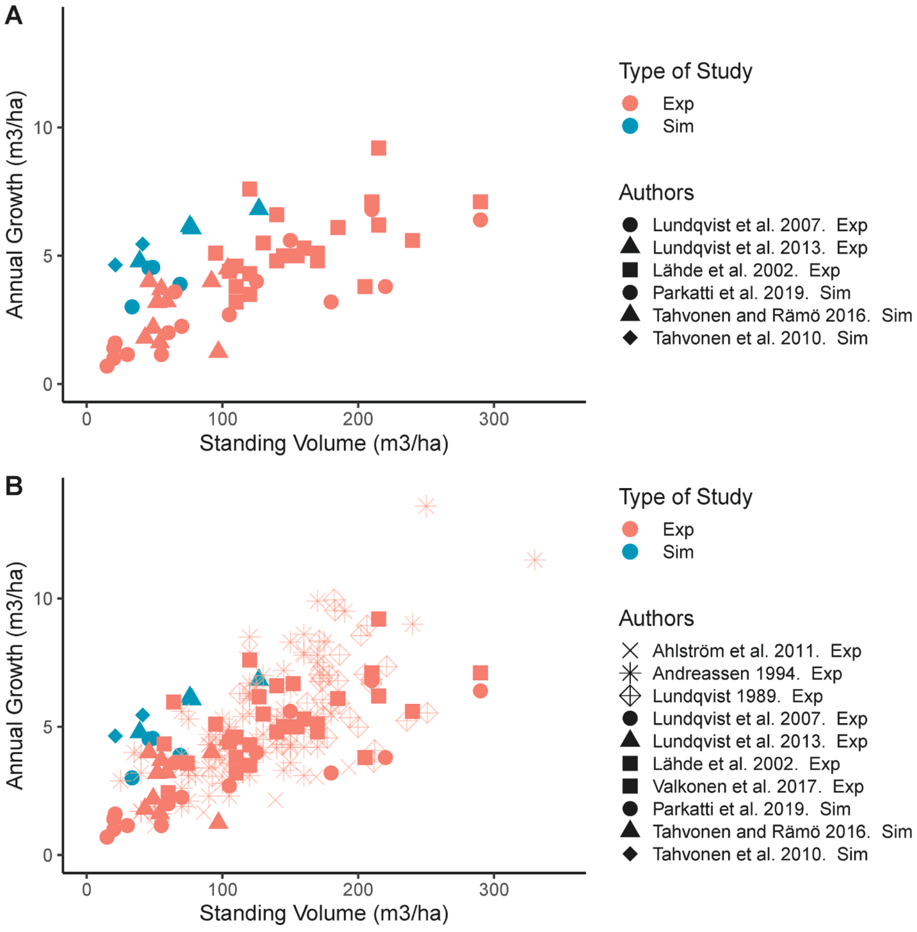

Fig. 6. A) The relationship between current annual volume growth (CAI, m^3 ha^{-1} a^{-1}) and standing volume (m^3 ha^{-1}) from experimental (Exp, red) and simulation (Sim, blue) studies on the selection system included in this review. In B) additional field studies are included from a review on selection system by Lundqvist (2017). Transparent points represent publications that are not scientifically peer reviewed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined in this review, but below we present a number of plausible explanations as to what could cause this pattern.

First, as the dominant management regime in Fennoscandia is the rotation forestry system, a substantial part of forest stands in this region are single-storied. Therefore, it may be challenging to find full-storied stands that can be used to develop growth models. For instance, the NFI-based models by Bollandsås et al. (2008) likely represent a wide range of growing conditions, but it is not clear to what extent these capture growing conditions in full-storied forests managed with selection system. In addition, the growth models by Pukkala et al. (2009) and Pukkala et al. (2013) utilize data from the field study in Vessari and Honka. These stands were managed with shelter-wood felling, a practice within the rotation forestry system, as late as in the 1940's and only has a short history of management according to the selection system, and should be seen as being under transformation (see appendix for a more detailed description of these stands).

Secondly, ingrowth is critical to maintain long-term production within the selection system, but relatively little is known about this process. In most simulation studies, the bottom of the smallest dbh size class is 4–5 cm, i.e., representing trees that are 4–5 m in height, and it takes a long time for small spruces to reach this size in full-storied stands. Eerikäinen et al. (2014) showed that it could take between 35 and 100 years for a seedling to reach 1.3 m height in a full-storied stand. Based on diameter increment in such stands it would take another few decades to reach 4–5 m height. This uncertainty is also reflected in different growth models: Rämö and Tahvonen (2014) reported a substantial difference in ingrowth between Bollandsås et al. (2008) and Pukkala et al. (2009), where the latter study has more than twice as high ingrowth at a stand basal area around 10 m^2/ha. Similarly, Pukkala et al. (2013) had about twice as high ingrowth compared to Bollandsås et al. (2008) over a large range of stand basal area (Parkatti et al., 2019). In fact, when the latter two growth models were compared against each other, they differed by up to 0.8 m^3 ha^{-1} a^{-1} in growth which was attributed to the difference in ingrowth functions (Parkatti et al., 2019). Thus, the predicted long-term yield is sensitive to the type of growth models used. The dynamics of ingrowth in full-storied stands need further attention in order to produce more accurate models.

Thirdly, several of the simulation studies use transition matrix models, which has the potential to bias growth (Picard and Liang, 2014; Zuidema et al., 2010). In matrix models, trees are distributed into discrete size classes, and the transition probabilities make it possible for a small fraction of the trees to unrealistically move several size classes in a few time steps. This may result in an unrealistically fast growth as tree basal area and volume is a function of dbh^2 and dbh^3, respectively.

Based on the reviewed studies, it is challenging to conclude which of the two systems is the most productive. In particular, it is necessary to bridge the potential gap between field and simulation studies to make valid growth and yield assessments. We suggest that a starting point would be to collect more data on growth, ingrowth and mortality from full-storied stands and continue to develop modelling frameworks.

5.3. Comparison of biodiversity between the silvicultural systems

The rotation forestry system consists of distinct development phases, such as the pre-commercial thinning phase, the commercial thinning phase and the final felling phase. To compare patterns in biodiversity in the selection system and the rotation forestry system, it is necessary to consider all phases over time or over a landscape. The studies that we review fail to create a complete comparison between the silviculture systems since no study compared selection system to all phases in the rotation forestry system. We only found studies comparing thinning from above to recent clearcut stands ($n = 16$ publications) and/or to a mid-rotation forest ($n = 3$ publications); no studies compared thinning from above to the final felling phase. One explanation to the skewed representation of late rotation forestry phases in the reviewed studies could be a lack of forests that have been subjected to clearfelling that now are mature to be harvested. In addition, many organism groups are poorly represented (e.g., birds, lichens and molluscs where we found no or only a few studies), whereas other taxonomic groups such as arthropods are more well-represented in the material (Table 3). Thus, based on the reviewed studies it is not possible to, in full, compare all aspects of biodiversity between the systems. In the following sections, we instead focus on the comparisons that can be made (between the selection system and early/mid-phase of the rotation forestry system and how biodiversity is influenced by single-tree selection) and then discuss to what extent these systems may complement each other.

5.4. Comparing biodiversity between the selection system and early/mid phases of the rotation forestry system

The reviewed publications suggest that species assemblage differs substantially between recent clearcuts and stands managed with the selection system. A rapid turnover in species assemblage after clearcutting is well-documented also in other studies (e.g., Jalonen and Vanha-Majamaa, 2001; Joelsson et al., 2018a; Jokela et al., 2019), with immediate effects such as a reduction in bryophyte cover (Jalonen and Vanha-Majamaa, 2001) and negative effects on the survival of rare and red-listed species (Rudolphi et al., 2014). Thus, at this phase the two systems differ substantially from each other (i.e., high beta-diversity). To what extent these assemblages can recover after clearcutting and approach a similar state as stands managed with the selection system is not known, but studies on bryophytes indicate a slow recovery after clearcutting (Dynesius, 2015). Previous work has shown that even salvage logging can influence the recovery of a forest (Leverkus et al., 2021). However, studies on beetle assemblage suggest a rapid recovery as mid-rotation forests were similar to those managed with thinning from above (Joelsson et al., 2018a; Joelsson et al., 2017). But the recovery was not complete: species abundant in the uncut control stands tended to successively decline in abundance in the irregular stands subjected to thinning from above, even-aged stands thinned from below, and recently clearcut stands (Joelsson et al., 2017). This result is consistent with a meta-analysis on uneven-aged forest management (including certain types of shelterwood felling, gap felling and selective logging) that found forest dependent species to be more favoured by uneven-aged than even-aged management (Savilaakso et al., 2021). If the selection system holds more late-successional species than the rotation forestry systems, this may further increase difference in biodiversity (higher beta-diversity). Therefore, we continue by discussing the taxonomic–specific responses to single-tree selection for the species groups studied in the reviewed literature (Table 3).

5.5. Biodiversity in stands managed with the selection system

Among invertebrates (mostly insects), the reviewed publications suggest that single-tree selection maintain much of the original species assemblage (i.e., that found in uncut control stands). Other studies focusing on selective cutting or variable retention harvest found a similar or slightly different species assemblage after cutting (Goßner et al., 2006; Huber and Baumgarten, 2005; Légaré et al., 2011; Wu et al., 2020). A short-term increase in beetle richness and two cambivore species after thinning from above (Hjältén et al., 2017; Jokela et al., 2019) suggest that harvesting residues associated with single-tree selection or thinning in the rotation forestry system may result in a pulse of phloem and cambium feeders.

Although only appearing in a small portion of the reviewed publications, we see that bryophyte cover was reduced and vascular plants were only slightly affected by thinning from above. Retention studies from North America show a similar pattern: high levels of retention (75 % of basal area) resulted in a decrease of bryophyte cover and especially liverwort cover (Bartels et al., 2018), while vascular plants maintained a similar assemblage as the control stand (Craig and Macdonald, 2009; Macdonald and Fenniak, 2007). Since bryophyte assemblages are sensitive to the microclimate (Hylander et al., 2005; Táborská et al., 2020), it is possible that the combination of changes in microclimate and cutting-induced damage to the ground has a negative effect on the cover of bryophytes. For promoting richness of epiphytic lichens and bryophytes, retaining several tree species of different size is preferable (Kaufmann et al., 2021).

Forest management has an impact on the plant community (Boch et al., 2013), where gaps may have a positive effects on vascular plants (Hurskainen et al., 2017; Kirchner et al., 2009). The minor effect on vascular plants found here may be explained by the relatively low cover of vascular plants in stands with large volume or stem density (Hedwall et al., 2013). As single-tree selection only removes a small part of the canopy, which may be closed quickly by expanding tree crowns, this may not be enough for species to respond to the change in environment (cf. del Alba et al., 2021).

Of the single publication on lichens included in this review, Storaunet et al. (2014) found that the number of *U. longissima* thalli is favoured by relatively open stands, which is consistent with a retrospective analysis from the same study area (Storaunet et al., 2008). However, the response of lichens to cutting is highly variable: Hedenås and Ericson

(2003) found that three out of five late successional lichen species were negatively affected by a removal of 50 % of the standing volume. In hardwood stands, *Lobaria pulmonaria* and *Lobaria quercizans* was up to five times more common and more fertile in uncut control stands than stands subjected to thinning from above (Edman et al., 2008). In contrast, Coxson et al. (2003) found no difference in lichen loading for three groups of lichens (*Alectoria* spp., *Bryoria* spp. and foliose lichens) between coniferous stands that was thinned from above and uncut control stands. Similarly, Rolstad et al. (2001) found no relationship between the historically harvested volume and abundance of several species of lichens in *P. abies* forests. Thus, the effect of single-tree selection on lichens is likely to vary among species.

The soil fungi assemblage is sensitive to soil properties and tree species composition (Goldmann et al., 2015; Kim et al., 2021), while wood-inhabiting fungi is highly dependent on dead wood quantity and quality (e.g., decay stage, size and tree species; Junninen and Komonen, 2011). Purahong et al. (2014) found no difference in community structure of wood-inhabiting fungi in beech forest when comparing two types of forest management and an unmanaged forest. Similarly, Pasanen et al. (2019) found that the number of polypore species was best explained by dead wood variables, but also that community assemblage on cut logs and high stumps was influenced by basal area of the living trees. The extent to which single-tree selection influence soil properties and dead wood composition is therefore likely to be reflected in the fungi assemblage.

In terms of bird assemblage, Versluijs et al. (2020) found that thinning from above did not maintain higher species richness or abundances of birds than stands thinned from below. Forest management generally have an effect on the bird communities (Czeszczewik et al., 2015; Klein et al., 2022; Virkkala, 1987), however it remains to be studied how birds respond to the selection system. In particular, it is relevant to assess their response on the landscape-level. For instance, by testing how a landscape-level increase in forests managed with selection system influence habitat quality and the dispersal ability of forest associated species such as the *Perisoreus infaustus* (Pukkala et al., 2012).

In summary, the general pattern in the reviewed publications is that single-tree selection maintains a similar species assemblage as the uncut stands. Species assemblages are influenced by the microclimate (Joelsson et al., 2018b; Seibold et al., 2016; Táborská et al., 2020) and microclimate is in turn affected by canopy cover, basal area and stand structural complexity (Ehbrecht et al., 2017; Greiser et al., 2018). Since single-tree selection maintains a high degree of canopy cover and basal area, much of the pre-cutting assemblage may therefore be conserved. Evidently, single-tree selection will not benefit all forest dependent species, as demonstrated above, but it may benefit some disturbance-sensitive species that are disfavoured by the rotation forestry system. However, the reviewed studies only cover short-term effects on biodiversity. Furthermore, the forest stands used in the reviewed studies at best have a limited history of being managed with the selection system. This limits the validity of conclusions regarding the long-term effects of the selection system on biodiversity.

Apart from the stand-level, increasing the fraction of stands managed with the selection system may be beneficial for late-successional species on the landscape-level as well. In a landscape managed with the rotation forestry system, the extinction and colonization is expected to be frequent as the old forests managed with the rotation forestry system becomes clearcut. Managing a part of the landscape with the selection system may favor late-successional species by increasing the amount of habitat, and making it stable in time.

While there is evidence that beta-diversity is high between the selection system and early phases of the rotation forestry system, a similar difference between old rotation forests can only be hypothesized (i.e., by stands managed with the selection system holding more late-successional species). Similar to Kuuluvainen et al. (2012), we argue for experiments covering larger temporal and spatial scales, but we also emphasize the need for studies on how species disfavored by the rotation forestry system (i.e., red-listed and late-successional species) respond to the selection system. If some of these species are favored, then the selection system could be a valuable tool to increase landscape-level biodiversity (i.e., gamma diversity).

5.6. The way forward – Future studies on selection system

Based on the reviewed publications, it is apparent that both biodiversity and yield in the selection system require more studies. Nevertheless, we see two ways forward: The first is to establish a research infrastructure that could provide short-term data to be used in model simulations, but also long-term experimental data. In the case of Sweden, *P. abies* forests with a full-storied structure are mainly present in the sub-alpine areas of north-western Sweden, with small areas scattered across other parts of the country. Identifying these areas and setting up a research infrastructure that covers a wide spectrum of environmental conditions is necessary to, e.g., examine how site productivity influence the difference in yield between the two silvicultural systems, understand how to transform two- or multi-storied *P. abies* stands into full-storied stands. Simulations are likely to be the best tool for fast predictions of yield in different silvicultural systems, and data from a well-designed infrastructure could be used already after a few years to improve simulations and hopefully reduce/explain the gap in growth between experimental and simulation studies (Fig. 6). From a biodiversity perspective, a research infrastructure would give an opportunity to study long-term effects on various aspects of biodiversity – with a particular need to focus on species of conservation concern that suffer from the rotation forestry system. Similarly, several taxonomic groups are severely under-represented in the reviewed literature and hence in need of more attention. Finally, it is also necessary to assess the landscape-level effects of the selection system on biodiversity (see, e.g., Schall et al., 2018).

As a second way forward, we see great value in conducting meta-analyses. However, the current material is insufficient for this, mainly because of the low number of studies, but also due to methodological differences between studies. For instance, the diversity of simulation frameworks (e.g., transition matrix models and process-based models) questions to what extent the framework influence the differences in yield between the silvicultural systems. Secondly, several simulation studies are based on the same empirical data, which does not make them independent. This also applies to studies on biodiversity, as all originate from one of six experimental locations. In order to synthesize studies on both yield and biodiversity in a future meta-analysis, more detailed description of silvicultural stand variables are required also in studies on biodiversity. In many cases, we were not able to determine if the study fell under the definition of the selection system or not. Describing the stand structure by presenting the diameter or height distribution before and after treatment, the tree species composition, standing volume, site productivity, how the cutting was done and possibly information on the silvicultural history would make it easier to put the results into a silvicultural context.

5.7. Management implications

The rotation forestry is considered the most prominent threat to many forest-demanding species. While the selection system maintains assemblages associated with late-successional forests, the rotation forestry system can be argued to promote species requiring open habitats, such as those dependent on sun-exposed dead wood. However, currently there is no deficiency in open habitats in the managed forest landscape. Importantly, not all species will be able to maintain a viable population in the production landscape, and setting aside protected areas and using management aimed at mimicking natural disturbance (e.g., fire) should still be considered. This is because biodiversity responses to clear-felling and natural large scale disturbances are significantly different (Heikkala et al., 2016; Kuuluvainen, 2009).

A requirement for managing forests with the selection system is that the stand has a full-storied stand structure (Lundqvist, 2017). While it is relatively easy to switch from the selection system to the rotation forestry system (i.e., by clearcutting a full-storied stand), switching the other way around is associated with a high production loss over a long time period (Drössler et al., 2014). Managing forests toward multi-storied or even full-storied structure requires long-term commitment and could potentially lead to both biodiversity benefits and increased functionality in, e.g., riparian buffers (Hasselquist et al., 2021). In the meantime, managing the remaining full-storied stands with selection system instead of the rotation forestry system can be useful, but preferably with cautious monitoring until we know more about how this silvicultural system influences biodiversity, timber production, economy and other ecosystem services.

CRediT authorship contribution statement

Adam Ekholm: Conceptualization, Methodology, Visualization, Writing – original draft. **Lars Lundqvist:** Conceptualization, Methodology, Writing – review & editing. **E. Petter Axelsson:** Conceptualization, Methodology, Writing – review & editing. **Gustaf Egnell:** Conceptualization, Methodology, Writing – review & editing. **Joakim Hjältén:** . **Tomas Lundmark:** Conceptualization, Methodology, Writing – review & editing. **Jörgen Sjögren:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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