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Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia

Matti Koivula[1] and Ilkka Vanha-Majamaa[2*] ⓘD

Abstract

Intensive forest management has been applied in most Fennoscandian forests for a period of almost one felling rotation. This paradigm has produced even-aged and even-structured forests of different successional stages that cover about 90% of forest land. At the same time, wildfires have been nearly eliminated in most of the Fennoscandian nature. Consequently, hundreds of species are red-listed because of forest management. To support these species, forest management requires improvements. Variable retention forestry and habitat restoration have been suggested to mitigate negative effects of forest management on biodiversity, and these have been practiced to some extent during the past few decades. Here, we review experimental results on the effects of variable retention and two restoration measures (prescribed burning and artificial addition of coarse woody debris) on different species groups in Fennoscandia. Our key findings are as follows: (i) Many species respond positively to felling within a few years, apparently due to released and often ephemeral resources, such as fresh residue and stumps. Species associated with shady conditions are negatively impacted, but any retention supports many of these, and their species composition remains almost unaffected with 50–70% retention of the initial tree volume. (ii) These effects remain detectable for at least 10–30 years or, according to some studies, nearly 100 years, e.g., in polypore fungi. (iii) Initial effects of prescribed burning on most species groups (apart from pyrophiles) are negative, but within 10–15 years post-fire sites begin to support many rare and threatened deadwood-dependent species. Epiphytic lichens, however, remain negatively affected. (iv) Artificial addition of deadwood (mostly high stumps) supports a wide spectrum of deadwood-dependent species, but the species composition differs from that of naturally died trees. (v) Moisture and micro-habitat variation are crucial for forest species at harvested sites, at least in forests dominated by Norway spruce. We conclude that felling method as such is of little importance for threatened forest species, although retention mitigates many negative effects. These species require microclimatic continuity, and maintenance and active increase of legacies, such as deadwood of different qualities (species, downed/standing, snag/log/stump, decay stage), very old trees, and tree species mixtures.

Keywords: Beetle, Forest management, Invertebrate, Polypore, Resilience, Resistance, Restoration, Saproxylic, Soil fauna, Understory vegetation

* Correspondence: ilkka.vanha-majamaa@luke.fi
[2]Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FI-00790 Helsinki, Finland
Full list of author information is available at the end of the article

Background

Intensive forest management, usually based on clear felling with site preparation and subsequent planting or seeding, followed by a few thinning operations during the rotation cycle, has been practiced in most of Fennoscandia (Finland, Norway, and Sweden) since the 1950s. Consequently, more than 90% of productive forest land in Finland and Sweden is structurally simplified, even-aged and even-structured (Gustafsson et al. 2010). Moreover, in Finland, less than 3% of forest land area is protected or otherwise not available for wood production, whereas the remaining 97% is available for wood production (Korhonen et al. 2016). Such large-scale implementation of intensive forest management has both short- and long-term effects on biodiversity.

Since the implementation of variable retention forestry (VRF) in the 1980s, it has become a common practice in many parts of the world, with usually rather modest retention, but occasionally the levels may be 30–40% (Beese et al. 2019; Scott et al. 2019). In Russia, for example, felling operations have been accompanied by such high levels of retention already since the early twentieth century (Shorohova et al. 2019). Effects of VRF on biodiversity have been studied in several experiments, first in North America (e.g., Beese et al. 2019), but later on also in Fennoscandia (Kuuluvainen and Grenfell 2012; Koivula et al. 2014). Although conventional clear felling is increasingly often replaced with alternative felling methods in Fennoscandia, it is still the prevailing regeneration felling method, usually combined with up to 3% of retention (proportion of the volume of living trees), i.e., about ten retention trees per ha (Kuuluvainen et al. 2019). It is notable that Fedrowitz et al. (2014) consider such low-level retention (< 2%) as clear felling and not VRF.

According to Fennoscandian red lists, based on IUCN criteria, nearly one-third of threatened species live in forests (Kålås et al. 2010; ArtDataBanken 2015; Hyvärinen et al. 2019). Hence, actions carried out especially in commercial forests are important for maintaining forest biodiversity in Fennoscandia.

Unlike most of the boreal region, forest fires have not been a major disturbance in recent decades in Fennoscandia. In Finland, for example, the annual burned area has declined steeply during the past hundred years, mainly because of effective fire detection and suppression, and forest management (Lindberg et al. 2020). The latter includes dense forest road network, small forest stands, thinning operations, and intentional removal of dead or damaged and deciduous trees. Therefore, introduction of prescribed burning has been recommended as a conservation and management measure (e.g., Kotiaho et al. 2015; Kontula and Raunio 2018; Äijälä et al. 2019; Hyvärinen et al. 2019). Research on ecological effects of prescribed burning has been carried out for several decades, whereas burning combined with VRF is a more recent topic. An overall review of the effects of prescribed burning has thus far been missing.

Prescribed burning increases habitat for pyrophilous species, but it also creates a rich pulse of dead wood, a crucial resource for thousands of species in Fennoscandia (e.g., Esseen et al. 1997; Siitonen 2001). Current management guidelines also commonly recommend to retain and actively create dead wood in harvesting operations (Anonymous 2019a). However, according to the national forest inventories in Finland, the average amount of dead wood has not increased since the 1990s; on the contrary, this number has declined rather steeply in northern Finland, from about 9.5 to the current 7 m^3 ha^{-1} (Anonymous 2016). This pattern is important as the maintenance of biodiversity depends on this resource: hundreds of Fennoscandian species are threatened because of the shortage of dead wood (Kålås et al. 2010; ArtDataBanken 2015; Hyvärinen et al. 2019).

In this paper, we review the main findings of experiments assessing the ecological impacts of VRF and restoration operations (here, prescribed burning and manipulation of coarse woody debris, CWD) on different species groups. With experiments, we refer to felling or restoration operations that were done in a replicated manner to isolate particular mechanisms that potentially affect biodiversity, thus excluding ad hoc comparisons of, e.g., differently treated stands. We focus on Fennoscandia but exclude its Russian part, as this has been discussed in Gustafsson et al. (2020). However, as we are aware of relevant papers from the Baltic countries (notably Estonia), we expand the geographic focus accordingly. Thus, unless specified otherwise, below we refer to Estonia, Finland, Norway, and Sweden as Fennoscandia for brevity.

Experiments allow powerful assessments of biological impacts for at least three reasons: species community composition before operations is often known, which increases the reliability of results; operations are done similarly at multiple locations, providing a quantification of site-to-site variation of impact; and unharvested reference (or control) forests are included in the same site type and area as the treatments. Despite these strengths, however, compilations of experimental results have thus far been missing.

History of VRF and restoration experiments in Fennoscandia

Due to rising concerns about losing old-growth forest species, retention of a few trees in clear felled stands started to become part of Fennoscandian forest management in the 1980s, with retention of aspen trees

(*Populus tremula*). Growing interest in harvesting methods other than clear felling resulted in the first VRF experiments with biological sampling, NaturKultur and Härjedalen, in 1989 in Sweden to study selection felling. Variants of selection felling have since been assessed in several experiments (Table 1).

In the 1990s, several forest management experiments were established both in Finland and in Sweden, such as MONTA, RETREE, Snöberget, and Medelpad-Ångermanland (Table 1). Many of these had been established to compare different forest management options and their biodiversity effects. Meanwhile, also restoration became a popular research topic. The first biodiversity-oriented trials on prescribed burning, combined with a significant amount of retention, were established in 1989 in the Patvinsuo national park, eastern Finland, in 1990 in Haraldstjärn, Älvdalen, central Sweden, and in 1992 in the Evo area, southern Finland (Wikars 1995; Penttilä and Kotiranta 1996; Penttilä et al. 2013). However, these trials had only 1–2 site replicates and no intentional, untreated reference sites. Therefore, experiments such as FIRE, EVO, and Future Forest were established in the early 2000s to study the combined effects of VRF and prescribed burning in both Scots pine-dominated and Norway spruce-dominated forests. In FIRE, retention level varied, whereas in EVO constant dispersed retention was combined with manipulated amount of downed deadwood, and Future Forest assessed gap felling accompanied with so-called high stumps (1–5 m tall artificial snags), cut using a harvester or a chain saw. High stumps have been studied also in, for example, the Fagerön and Spruce CWD (Sweden), MONTA (Finland), and Hedmark (Norway) experiments (Table 1).

The scope of research has recently been expanded from stand to landscape level. The DISTDYN experiment was established in Finland in 2009, followed by the Effaråsen experiment in Sweden in 2012. The idea in DISTDYN is to treat forested landscapes (not just stands) with varying felling methods and levels of retention (10% or 50% in felled patches, including living and intentionally killed trees). Effaråsen applies 3%, 10%, 30%, 50%, and 100% retention, also including living and intentionally killed trees, and prescribed burning (Table 1).

In the following, the main findings of Fennoscandian experiments are discussed for both short- and long-term effects. In the current forest management, the prevailing practice in Finland is to retain about ten trees per hectare, usually in groups, in clear cuts as required by the Programme for the Endorsement of Forest Certification (pefc.org). We refer to this as "standard retention" below. Moreover, with "short term" we refer to the first three post-harvest years (the usual funding period of academic sources), whereas with "long term" we refer to

longer follow-ups. The oldest Fennoscandian VRF experiments are from late-1980s or mid-1990s, which defines the upper limit for experimentally assessed post-harvest processes. We summarize results for different species groups, beginning with short- and long-term responses to retention, and ending with prescribed burning, manipulations of CWD, and possible other important aspects, particularly soil moisture and site preparation. Finally, we discuss these results together with chronosequence studies and ad hoc comparisons on felling and restoration, to define recommendations for a better maintenance of biodiversity in managed forests.

Publication search, and included experiments

We first sought experiments using the Northern European Database of Long-Term Forest Experiments (noltfox.metla.fi, Karlsson 2008). We then continued this search, and expanded it to experiment-based publications, by using Web of Science and Scopus (30 September 2019). We used the following search-term thread: forest* AND (Finland OR Sweden OR Norway OR Estonia OR Latvia OR Lithuania) AND (logg* OR fell* OR harvest* OR cut* OR select* OR thinn* OR gap OR deadwood OR dead wood OR fire OR burn* OR restor* OR stump*) AND (plant* OR moss* OR lichen* OR polypor* OR fung* OR beetle* OR insect* OR diversit*). After pruning the initial set of papers down to relevant ones, we complemented the search by using first and senior author names and reference lists of the detected papers (Additional file 1: Table S1).

Below, we review the results of Fennoscandian forest management experiments containing biological sampling (Table 1, Fig. 1). All experiments compare VRF or restoration approaches to unharvested reference forests ("control") and often also clear felling without retention. The most commonly assessed methods are retention of up to about 50 m^3 ha^{-1}, usually in a few groups of trees, and selection felling (Fig. 2). The latter can aim at an uneven age structure of trees, selective removal of the largest trees, or ordinary commercial thinning (Table 1). The RETREE and Medelpad-Ångermanland projects assessed retention patches of about 0.01–0.60 ha in size, while patches have been smaller in the other experiments. Gap felling has thus far been studied in four experiments; the gaps are usually smaller than 0.2 ha, except in DISTDYN with gaps 0.1–0.3 ha, the largest (diameter 50–60 m) being sometimes referred to as patch (or partial clear-cut) felling.

Deadwood can be artificially added in many ways to increase CWD for saproxylic (deadwood dependent) organisms; most often artificial CWD substrates are high stumps (Fig. 2). Since the mid-1990s, high stumps have become common elements of Fennoscandian forest management experiments. Other ways to increase deadwood—apart from burning trees—are less common: in

Table 1 Replicated retention and restoration experiments in Fennoscandia. Note that abbreviations or names may not be official. Numbers after each abbreviation indicate source for information (see footnote). Establ = year of establishing the experiment; Durat = realized or planned duration (Long-term = more than 10 years); Type = dominant tree species (Mixed = deciduous and coniferous); the subsequent six columns explain applied treatments as follows: Rete = retention trees in clear felled sites; Gap = gap felling (diameter up to about 50 m); Select = selection felling; CWD = coarse dead wood manipulation (usually high stumps); Fire = prescribed burning applied; Other = possible other variables included in the experimental design. The bottom-part columns show studied taxa or other assessed aspects: Veget = understory vegetation (vascular plants, forest floor mosses and lichens); Epiph = epiphytic and epixylic lichens and bryophytes (epix = epixylic species distinguished); Polyp = polypore fungi; Ground = ground-dwelling beetles and spiders; Saprox = saproxylic and other actively-flying beetles; Other = other taxa; CWD = coarse woody debris inventoried; Timber = timber production assessed; Social = aesthetic or recreational values assessed; and Econ. = economic viability of the applied operations assessed. * = to our knowledge, results not yet published in peer-reviewed English-language journals

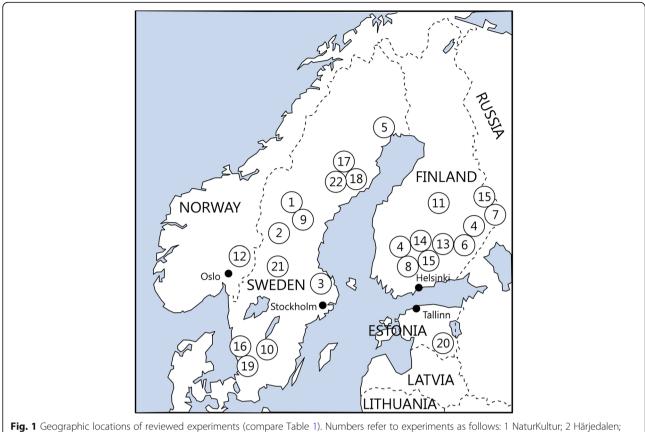General information about experiments

Abbreviation	Experiment name	Country	Establ	Durat	Type	Rete	Gap	Select	CWD	Fire	Other
NaturKultur 1	NaturKultur (2050–2061)	Sweden	1989	Long-term	Mixed			X			Planting
Häljedalen 2	Conventional clear-cutting and variable thinning	Sweden	1989	Long-term	Pine, Spruce			X			
Fagerön 3	High-stump experiment	Sweden	1994	5 years	Mixed			X	X		
MONTA 4	Biodiversity in the regeneration of managed forests	Finland	1995	Long-term	Spruce	X	X	X	X		
Snöberget 5	Selection cutting experiment	Sweden	1997	5 years	Spruce			X			
RETREE 6	Effect of the size of retention tree groups on biodiversity in forest regeneration	Finland	1998	Long-term	Spruce	X					Moisture
FIRE 7	Boreal forest fire experiment	Finland	2000	Long-term	Pine	X				X	
Medelpad-Ångermanland 8	Retention tree group size and biodiversity	Sweden	2000	Unknown	Mixed	X					
EVO 9	Rehabilitating boreal forest structure and species composition	Finland	2001	Long-term	Spruce	X		X	X	X	Moisture
Oak forest 10	Partial cutting in mixed oak forests	Sweden	2001	Long-term	Oak, mixed			X			
Deadwood 11	Deadwood addition follow-up	Finland	2002	Long-term	Pine, spruce				X		Felling, girdling
Hedmark 12	High-stump experiment	Norway	2004	2 years	Mixed						Edge distance
PuroMONTA 13	Importance of valuable boreal brook habitats in conserving species richness	Finland	2004	Long-term	Spruce	X		X	X		Brook sides
UPM experiment 14	Effects of logging, mounding, and removal of logging residues and stumps	Finland	2005	3 years	Spruce	X			X		
DISTDYN 15	Forest management inspired by natural disturbance dynamics	Finland	2009	Long-term	Pine, spruce	X	X	X	X		

Table 1 Replicated retention and restoration experiments in Fennoscandia. Note that abbreviations or names may not be official. Numbers after each abbreviation indicate source for information (see footnote). Establ = year of establishing the experiment; Durat = realized or planned duration (Long-term = more than 10 years); Type = dominant tree species (Mixed = deciduous and coniferous); the subsequent six columns explain applied treatments as follows: Rete = retention trees in clear felled sites; Gap = gap felling (diameter up to about 50 m); Select = selection felling; CWD = coarse dead wood manipulation (usually high stumps); Fire = prescribed burning applied; Other = possible other variables included in the experimental design. The bottom-part columns show studied taxa or other assessed aspects: Veget = understory vegetation (vascular plants, forest floor mosses and lichens); Epiph = epiphytic and epixylic lichens and bryophytes (epix = epixylic species distinguished); Polyp = polypore fungi; Ground = ground-dwelling beetles and spiders; Saprox = saproxylic and other actively-flying beetles; Other = other taxa; CWD = coarse woody debris inventoried; Timber = timber production assessed; Social = aesthetic or recreational values assessed; and Econ. = economic viability of the applied operations assessed. * = to our knowledge, results not yet published in peer-reviewed English-language journals *(Continued)*

Abbreviation	Experiment name	Country	Establ	Durat	Type	Rete	Gap	Select	CWD	Fire	Other
Eriksköp 16	Target diameter cutting	Sweden	2009	Long-term	Pine, spruce			X			
Future Forest 17	Restoration strategies for the future	Sweden	2010	Long-term	Pine, spruce		X			X	
Spruce CWD 18	Addition of spruce CWD	Sweden	2011	Unknown	Spruce				X		
Rogberga 19	Target diameter cutting	Sweden	2012	Long-term	Mixed		X	X			
Shelterwood 20	Shelterwood cutting experiment	Estonia	2012	Long-term	Pine			X			Shelterwood
Effaråsen 21	Economic and ecological impact of partial cutting, CWD creation and prescribed burning in boreal pine forest	Sweden	2012	Long-term	Pine	X			X	X	
UNEVEN 22	The efficiency of uneven-aged forestry as a conservation tool	Sweden	2013	Long-term	Spruce			X			

Sampled species groups and other aspects

Abbreviation	Veget	Epiph	Polyp	Ground	Saprox	Other	CWD	Timber	Social	Econ.
NaturKultur	X*							X	X*	X*
Härjedalen	X									
Fagerön					X					
MONTA	X	Xepix	X*	X	X	Ants*, snails*, soil fauna, decomposers, small mammals*	X	X		X
Snöberget		X								
RETREE	X	Xepix	X	X		Snails*	X	X*		
FIRE	X	X	X	X	X	Flat bugs, flies, pollinators, bats, mycorrhiza	X			
Medelpad-Ångermanland		Xepix								
EVO	X	Xepix	X	X	X	Ants	X	X		
Oak forest	X	X	X	X	X	Fungus gnats	X	X		
Deadwood		X								
Hedmark					X					

Table 1 Replicated retention and restoration experiments in Fennoscandia. Note that abbreviations or names may not be official. Numbers after each abbreviation indicate source for information (see footnote). Establ = year of establishing the experiment; Durat = realized or planned duration (Long-term = more than 10 years); Type = dominant tree species (Mixed = deciduous and coniferous); the subsequent six columns explain applied treatments as follows: Rete = retention trees in clear felled sites; Gap = gap felling (diameter up to about 50 m); Select = selection felling; CWD = coarse dead wood manipulation (usually high stumps); Fire = prescribed burning applied; Other = possible other variables included in the experimental design. The bottom-part columns show studied taxa or other assessed aspects: Veget = understory vegetation (vascular plants, forest floor mosses and lichens); Epiph = epiphytic and epixylic lichens and bryophytes (epix = epixylic species distinguished); Polyp = polypore fungi; Ground = ground-dwelling beetles and spiders; Saprox = saproxylic and other actively-flying beetles; Other = other taxa; CWD = coarse woody debris inventoried; Timber = timber production assessed; Social = aesthetic or recreational values assessed; and Econ. = economic viability of the applied operations assessed. * = to our knowledge, results not yet published in peer-reviewed English-language journals *(Continued)*

Abbreviation	Veget	Epiph	Polyp	Ground	Saprox	Other	CWD	Timber	Social	Econ.
PuroMONTA	X	X	X		X		X			
UPM experiment	X	Xepix					X			
DISTDYN	X		X		X	Ants*, birds*	X	X*	X	X*
Eriksköp	X*			X				X		
Future Forest	X	X	X		X	Flat bugs	X			
Spruce CWD										
Rogberga	X*							X*		
Shelterwood	X	X								
Effaråsen	X	X	X		X	Mycorrhiza*	X	X		X
UNEVEN	X	X			X		X			

1 Djupström and Weslien 2019; 2 Hagner 1992; 3 Lindhe and Lindelöw 2004; 4 Kaila 1998; 5 Hedenås and Ericson 2003; 6 Matveinen-Huju et al. 2006, Vanha-Majamaa and Hautala. 2010; 7 Hyvärinen et al. 2005; Kouki 2019; 8 Perhans et al. 2009; 9 Toivanen et al. 2004, Lilja et al. 2005, Vanha-Majamaa et al. 2007; 10 Götmark 2007; 11 Pasanen 2017; 12 Fossestol and Sverdrup-Thygeson 2009; 13 Toivanen et al. 2004, Selonen and Kotiaho 2013; 14 Rabinowitsch-Jokinen and Vanha-Majamaa 2010; 15 Koivula et al. 2014; 16 Drössler 2016; 17 Hägglund et al. 2015; 18 Olsson et al. 2011; 19 Drössler 2016; 20 Tullus et al. 2019; 21 Djupström and Weslien 2019; 22 Joelsson et al. 2017
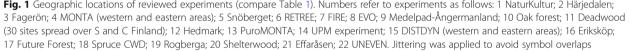
Fig. 1 Geographic locations of reviewed experiments (compare Table 1). Numbers refer to experiments as follows: 1 NaturKultur; 2 Härjedalen; 3 Fagerön; 4 MONTA (western and eastern areas); 5 Snöberget; 6 RETREE; 7 FIRE; 8 EVO; 9 Medelpad-Ångermanland; 10 Oak forest; 11 Deadwood (30 sites spread over S and C Finland); 12 Hedmark; 13 PuroMONTA; 14 UPM experiment; 15 DISTDYN (western and eastern areas); 16 Eriksköp; 17 Future Forest; 18 Spruce CWD; 19 Rogberga; 20 Shelterwood; 21 Effaråsen; 22 UNEVEN. Jittering was applied to avoid symbol overlaps

Fig. 2 Examples of practical retention and restoration. Top-left: retention tree group and high stumps in a clear-cut, first post-harvest summer (MONTA experiment, Finland, June 1996). Top-right: gap felling combined with high stumps, third post-harvest winter (Future Forest experiment, Sweden, March 2013). Bottom-left: selectively-felled mixed uneven-aged forest, third post-harvest summer (DISTDYN experiment, Finland, June 2012). Bottom-right: combined prescribed burning and intentionally killed, pushed-down trees at and around a paludified patch, seventh post-harvest summer (EVO experiment, Finland, May 2009). Photos © Matti Koivula

the EVO experiment, CWD was created by felling 5, 30, or 60 m^3 ha^{-1} of trees, and another 50 m^3 ha^{-1} of standing trees was retained in a dispersed manner (Fig. 2). In the Deadwood addition follow-up in Finland, CWD was created by felling or girdling (Table 1).

Prescribed burning was first applied in a replicated manner in the FIRE experiment, followed by EVO and Future Forest. RETREE and EVO study sites, on the other hand, were established at and around paludified patches that are fairly common in spruce forests (Fig. 2). The idea in such placing was to assess possible interactions between within-site variation and felling (and burning in EVO), and whether such patches could act as "life boats" for species occupying shady or wet forests.

The studied species groups vary according to the experiment due to resource limitations, and a large part of the collected material still remains unanalyzed or unpublished (Table 1). Nearly all experiments with biological sampling have assessed understory vegetation (at least vascular plants). Invertebrates have thus far been sampled in 12 experiments; beetles have been sampled most frequently using flight-intercept window traps or pitfall traps, but also spiders, flat bugs (Heteroptera: Aradidae), soil invertebrates, and land snails have been sampled in some experiments. Data on lichens, mosses, liverworts (both forest-floor and epixylic species) and polypore fungi have also been commonly collected, whereas vertebrates have been studied rarely because their home ranges usually exceed the study scale, i.e., the stand. Exceptions are small mammals (voles, shrews) sampled in MONTA, and birds sampled in DISTDYN where the design consists of multiple landscapes of about 200–300 ha, so bird counts potentially produce sufficiently large and diverse data for analysis. Data on living and dead trees have been commonly collected, and assessments of the economic profitability of felling methods have been conducted in several experiments. Social dimension (public attitude to forest management) has thus far been assessed in NaturKultur and DISTDYN (Table 1).

Ecological findings in VRF and restoration experiments

Below we present main findings from the experiments (Table 1) for different species groups. We distinguish short- and long-term effects of VRF, prescribed burning, manipulation of deadwood, and possible other factors that were found to be important. An at-glance summary of these results can be found in Table 2.

Understory vegetation
Short-term responses to retention
Increasing harvesting intensity causes increasingly drastic alterations in the species composition of understory vegetation. In mesic Norway spruce stands, resistance is higher in herbs than in other species groups, and late-successional bryophytes are particularly sensitive to harvesting (Jalonen and Vanha-Majamaa 2001; Götmark et al. 2005). Selection felling and gap felling change understory vegetation less than conventional clear felling or 7% retention felling (Jalonen and Vanha-Majamaa 2001). Uniform shelterwood felling accompanied by site preparation in Estonian Scots pine forests increased the species richness of vascular plants and bryophytes, largely through an increase in the number of pioneer species (Tullus et al. 2019).

Long-term responses to retention
The standard retention does not maintain species that require late-successional forest conditions, as even several times higher number of retention trees (about 50 trees per ha in a few groups) in spruce and pine forests does not support, e.g., mosses, liverworts, or lichens (Hämäläinen et al. 2016; Vanha-Majamaa et al. 2017). The general response to harvesting depends on the level of retention, possible other retention measures, and species in question (Bergstedt and Milberg 2001; Johnson et al. 2014; Vanha-Majamaa et al. 2017). Retention of 7% (23 m^3 ha^{-1}, in three groups) results in almost similar vegetation composition as clear felling in Norway spruce forests (Vanha-Majamaa et al. 2017). Corroborating results have been found in Scots pine-dominated stands for considerably higher retention (50 m^3 ha^{-1}) (Johnson et al. 2014). Selection felling (67% retained) and gap felling (50% retained) have rather similar long-term effects on understory vegetation, but resilience within these treatments is higher than in 7% retention (Vanha-Majamaa et al. 2017). In Estonia, shelterwood felling had a small effect on bryophytes in Scots pine dominated stands but was destructive for bryophytes of conservation concern in mesic Norway spruce stands (Tullus et al. 2018). Moreover, in Scots pine forests, Rodriguez and Kouki (2015) showed that, 13 years after felling, blueberry (*Vaccinium myrtillus*) cover, flowering, and berry production were still lower than in unharvested forest, irrespective of retention level (10 or 50 m^3 ha^{-1}), whereas the resilience of lingonberry (*Vaccinium vitis-idaea*) was higher (but see Granath et al. 2018). Riparian brook-side forests, studied in the PuroMONTA experiment in central Finland, are important for many rare and red-listed forest species (Selonen et al. 2011; Selonen and Kotiaho 2013; Selonen 2014; Oldén et al. 2019a). This experiment showed that if clear felling is applied in adjacent forests, unharvested buffer zones surrounding brooks must be at least 35–45 m wide to support the initial riparian plant and moss communities. Selection felling within these buffers affects indicator mosses negatively, apparently due to increasing light

Table 2 Summary of experimental results on different species groups. Short- (up to 3 years post harvest) and long-term effects (> 3 years) are separated by a slash line. + = positive, − = negative and ± = not detectable or ambiguous effect, and na = not assessed. Retention = effect of standard or higher retention; Fire = effect of prescribed burning; CWD = effect of artificial large-sized dead wood; Paludified = effect of moist micro-sites within forest; Site prep = effect of site preparation (usually disc trenching or mounding); Interactions = two of the previous variables have been observed to interact; Other aspects = other important determinants of species-group abundance or species richness. 1 = experimental data contain several red-listed or highly specialized species

Ecological group	Retention	Fire	CWD	Paludified	Site prep	Interactions	Other aspects
Understory vegetation							
Late successional	+/+	−/−	na/na	+/+	−/na		
Pioneer	−/−	+/+	na/na	na/na	+/na		
Mosses and lichens	+/+	−/na	na/na	+/+	−/−		
Epiphytic and epixylic bryophytes and lichens							
Epiphytic 1	+/+	−/−	na/na	+/na	−/na		Long–term effect of fire may be positive
Epixylic 1	+/+	−/na	na/na	na/na	−/−		
Fungi							
Polypores 1	±/+	−/+	+/+	na/na	na/na	Rete x Fire	Downed CWD better than high stumps
Macrofungi	na/na	na/+	na/na	na/na	na/na		
Ground-dwelling arthropods							
Ground beetles, shade-requiring	+/+	−/−	na/+	na/±	−/na		Microsite variation larger than felling effect
Ground beetles, open-habitat	−/−	+/+	na/−	na/−	+/na		Microsite variation larger than felling-effect
Ground beetles, shade generalists	−/−	−/+	na/±	na/−	±/na		
Ground beetles, mire species	+/+	na/−	na/±	+/+	na/na		
Spiders, forest web builders	+/na	na/na	na/na	na/na	na/na		
Spiders, hunting spiders	−/na	na/na	na/na	na/na	na/na		
Harvestmen (Opilionidae)	+/na	na/na	na/na	na/na	na/na		
Saproxylic and other actively-flying beetles							
Early-stage xylophages 1	+/±	+/±	+/±	na/na	na/na	Fire x CWD	CWD quality important; if CWD is abundant, felling is of minor importance
Late-stage xylophages 1	±/+	±/±	±/+	na/na	na/na	Fire x CWD	CWD quality important; if CWD is abundant, felling is of minor importance
Mycetophages 1	+/+	−/−	+/+	na/na	na/na	Fire x CWD	CWD quality important; if CWD is abundant, felling is of minor importance
Non-saproxylic	−/−	+/+	±/±	na/na	na/na		
Other groups							
Flat bugs 1	+/+	+/+	na/+	na/na	na/na		
Red wood ants (Formica)	±/na	na/−	na/±	na/na	na/na		
Millipedes and centipedes	+/+	na/na	na/na	na/na	na/na		
Springtails and soil mites	+/+	na/na	na/na	na/na	na/na		

Table 2 Summary of experimental results on different species groups. Short- (up to 3 years post harvest) and long-term effects (> 3 years) are separated by a slash line. + = positive, – = negative and ± = not detectable or ambiguous effect, and na = not assessed. Retention = effect of standard or higher retention; Fire = effect of prescribed burning; CWD = effect of artificial large-sized dead wood; Paludified = effect of moist micro-sites within forest; Site prep = effect of site preparation (usually disc trenching or mounding); Interactions = two of the previous variables have been observed to interact; Other aspects = other important determinants of species-group abundance or species richness. 1 = experimental data contain several red-listed or highly specialized species *(Continued)*

Ecological group	Retention	Fire	CWD	Paludified	Site prep	Interactions	Other aspects
Soil decomposers	+/+	na/na	na/na	na/na	–/–		
Pollinator insects	na/–	na/+	na/±	na/na	na/na		
Tachinid flies	na/–	na/±	na/±	na/na	na/na		
Fungus gnats	+/na	na/na	+/na	na/na	na/na		
Eastern pygmy shrew	+/na	na/na	na/na	na/na	na/na		
Wood lemming	+/na	na/na	na/na	na/na	na/na		
Northern bat	na/+	na/na	na/na	na/na	na/na		

(canopy openness) and alterations in temperature and moisture (Oldén et al. 2019b).

Prescribed burning

Most short-term effects of burning, combined with VRF, on vegetation are negative even after a low-severity fire, but half of the understory species reappear within 2–3 years, and the number of early-successional species increases (Table 2, Vanha-Majamaa et al. 2007). Apart from time since fire, also forest type and climate zone are important predictors of the effects of burning on herbaceous plant richness (Eales et al. 2018). Burning combined with VRF may increase structural and microclimatic heterogeneity and promote preservation of biological legacies, such as CWD and remnant vegetation (Heikkala et al. 2014; Johnson et al. 2014). For instance, lingonberry benefits from increasing retention level at burned sites (Rodriguez and Kouki 2015; Granath et al. 2018).

Manipulation of dead wood

No results reported.

Other aspects

Site preparation at felled sites strongly impacts understory plants (Table 2). This impact generally takes place at within-stand level, thus impacting the spatial variation in abundance of plant species in the short term. The resilience of understory vegetation against site preparation is higher in gap-felled (about 0.16 ha gaps) than in 2 ha clear-felled stands with 7% aggregated retention, apparently due to microclimatic differences and edge effects (Vanha-Majamaa et al. 2017).

Epiphytic and epixylic species
Short-term responses to retention

Even if any retention supports some of the studied epixylic species (Table 2), higher than standard retention may not suffice for all of them. Perhans et al. (2009), Hautala (2008), and Hautala et al. (2011) studied retention patches of 0.01–0.60 ha in different forest types in Sweden and Finland. These authors found that such patches were too small for some lichens and bryophytes, particularly liverworts, which suggest microclimatic changes and edge effects in the interiors of even the largest of these patches. Harvesting-caused change in the total number of epixylic species depends on retention-patch size (Hautala et al. 2011), suggesting that larger patches maintain epixylic diversity better than smaller patches. Cover declines inside these patches are particularly striking for mosses, but the relative decrease may be highest for liverworts (Hautala et al. 2011). In Swedish temperate mixed oak forests, selection felling to release space for oak trees resulted in an increase in epixylic lichen but not in bryophyte richness (Paltto

et al. 2008). These authors also found that red-listed species may be affected by selection felling only little, supporting Perhans et al. (2009) who found retention to mitigate declines of, or even increase, red-listed and indicator lichens.

Long-term responses to retention

Higher than standard retention, including group retention, may not suffice for all closed-canopy species. Hämäläinen et al. (2014) studied lichens in pine forests 11 years after felling and witnessed a negative effect of increasing felling intensity on micro-lichen richness. On the other hand, selection felling with 50% removal of trees did not markedly increase the mortality of aspen cyanolichens but it reduced their growth in northern Swedish spruce-dominated forests (Hedenås and Ericson 2003). In Swedish mixed oak forests, epixylic lichens and bryophytes benefited from selection felling aiming at releasing space for oak trees as compared to untreated reference forests (Nordén et al. 2012). Moreover, this operation also supported species of conservation concern, increased the colonization rate, and decreased the loss rate (Nordén et al. 2012). In Finnish spruce forests 10 years post-harvest, considerably more bryophyte species were lost after selection felling with 67% retention than after gap felling with 50% retention (Vanha-Majamaa et al. 2017). This finding suggests that aggregated retention supports bryophytes better than dispersed retention.

Prescribed burning

First-order effects of fire are negative to most epixylic and epiphytic species (Table 2). Effects of fire on these species can be short term (Rudolphi et al. 2011) but sometimes also long lasting. For example, epiphytic lichens in pine forests remained at lower level 11–12 years post fire (Hämäläinen et al. 2014; Hämäläinen 2016). Fire not only kills these species directly but also changes the quality of substrates and microclimatic conditions.

Manipulation of dead wood

No results reported.

Other aspects

Site preparation affects epixylic mosses and lichens negatively (Hautala et al. 2011; Rabinowitsch-Jokinen et al. 2012; see also Tullus et al. 2018, 2019). The effects of site preparation on substrates of these species (large-sized CWD) depend on the site-preparation method and/or its intensity, but may cause up to 70% loss in the CWD volume (Hautala et al. 2011). Highly decayed CWD is particularly vulnerable to site preparation, which affects epixylic species richness and cover negatively (Hautala et al. 2011). Continuous site preparation methods,

such as disc trenching, are more harmful for CWD (and thus epixylic species) than non-continuous methods, such as mounding (Rabinowitsch-Jokinen and Vanha-Majamaa 2010; Rabinowitsch-Jokinen et al. 2012).

Fungi
Short-term effects of retention
Polypores tend to decline in harvested areas, but the new substrates created in harvesting—stumps and logging residue—support some species (Table 2; Suominen et al. 2018, 2019). In VRF, tree deaths due to senescence, wind, or other factors may be expected to provide continuity of large-sized snags and logs that many polypores and other saproxylic species utilize (Junninen et al. 2008; Berglund et al. 2011). Even small numbers of retention trees, and stumps and logging residue (Berglund et al. 2011), are important for polypores (and for other saproxylic taxa; de Jong and Dahlberg 2017). Different groups of fungi respond in different ways: in southern Swedish mixed oak forests, selection felling to release space for oak trees benefited ascomycete fungi but caused declines of basidiomycete fungi (Nordén et al. 2008). Moreover, in Finnish brook-side forests, perennial, annual, or red-listed polypores did not show detectable short-term responses to selection felling inside 15-m buffer zones between brook and clear cut (Timonen 2011).

Long-term responses to retention
High retention is more beneficial for pine-forest polypores than low retention (50 vs. 10 m^3 ha^{-1}; Suominen et al. 2015, Table 2). Rare and red-listed polypores require long time to colonize substrate trees that die gradually due to wind impact, and indeed these species benefit from retention in the long term (Suominen 2018; Suominen et al. 2018, 2019); however, such effect was not detected by Pasanen et al. (2019).

Prescribed burning
The immediate effect of fire may be a general decline in species occurrences (Table 2), but most polypores and other macrofungi recover within a few years. Berglund et al. (2011) found no significant effects of different levels of downed-and-burned CWD on species composition or richness of polypores a few years after burning, but some species were positively affected. In the long term, many rare and red-listed polypores (Junninen et al. 2008; Suominen et al. 2018) and saprotrophic Basidiomycota and Ascomycota fungi (Salo et al. 2019) benefit from burning (Table 2). Higher retention at burned sites provides greater benefits at least in Scots pine-dominated stands (Suominen et al. 2015), but the effect also depends on whether deadwood consists of stumps, slash, or whole trees (Suominen et al. 2019).

Manipulation of dead wood
High stumps and other intentionally killed trees support a wide spectrum of saproxylic species (Table 2; Olsson et al. 2011; Pasanen 2017), but compared to naturally died CWD, they host lower species richness (Pasanen et al. 2014, 2019) and their species compositions are different (Pasanen et al. 2018). Lindhe et al. (2004) showed, 9 years after CWD addition, that downed logs maintained higher species richness than high stumps, and that larger diameter of CWD had a positive effect on polypore richness.

Other aspects
No results reported.

Ground-dwelling arthropods
Short-term effects of retention
Macro-arthropod (mostly spiders and beetles) richness and abundance increase after logging, but even standard retention mitigates some assemblage changes (Koivula 2002a; Pietikäinen et al. 2003; Table 2). Selection felling removing up to 25–30% of trees, or 30–50% of tree volume, does not affect these groups much (Koivula 2002b; Matveinen-Huju and Koivula 2008). Gap felling (50% retention with three 0.16-ha clearings per ha) retains the initial spider and ground beetle (Carabidae) faunas considerably better than standard retention, particularly in unharvested parts of these stands (Koivula 2002a; Koivula and Niemelä 2003; Matveinen-Huju et al. 2006, 2009; Martikainen et al. 2006a). Generally, following harvesting, species associated with closed canopies decline, whereas canopy generalists and open-habitat species increase rapidly (Niemelä et al. 2007). Aggregated retention (0.01–0.60 ha patches) also supports at least some of the ground beetle and spider species specialized on living under closed canopies and/or forest mires (Martikainen et al. 2006a; Matveinen-Huju and Koivula 2008). However, even in the largest of these patches, interior parts are apparently affected by adjacent clear-felled environments through various edge effects (Matveinen-Huju et al. 2006, 2009; Matveinen-Huju 2007).

Long-term effects of retention
Ten years after logging, 0.01–0.03 ha retention tree groups host lower densities of predatory spiders and open-habitat ground beetles than adjacent clear cuts, suggesting smaller assemblage change (Siira-Pietikäinen and Haimi 2009; Koivula et al. 2019; Table 2). Thus, even such small groups impact the spatial distribution and/or abundance of arthropods for a long time. Gap felling mitigates changes in the arthropod assemblages so that they may be little affected in unharvested fractions, whereas in gaps, alterations can be considerably larger and open-habitat species thrive (Koivula et al. 2019).

Prescribed burning

Harvested and subsequently burned sites support higher ground beetle richness than either untreated or harvested-only sites in the short (Martikainen et al. 2006a) and in the long term (Toivanen et al. 2014) (Table 2). Interestingly, paludified patches within felled and burned sites host many mire specialist species, such as the ground beetle *Platynus mannerheimii*, at least 7 years after treatments (Toivanen et al. 2014). Similarly, in the short term, ground beetles tend to aggregate to retention patches of harvested-and-burned sites (Martikainen et al. 2006a). These studies exemplify the importance of structural heterogeneity of forests for the overall biodiversity and disturbance resistance.

Manipulation of dead wood

In the EVO experiment, 7 years after felling operations, higher down-wood retention affected ground beetle richness negatively, whereas closed-canopy species benefited, perhaps due to increasing shelter against direct sunlight or changes in other microclimatic factors (Toivanen et al. 2014) (Table 2).

Other aspects

Site preparation affects ground beetles so that closed-canopy specialists avoid, and open-habitat species prefer, strips of visible mineral soil in clearings (Table 2; Pihlaja et al. 2006). However, in a new analysis of data from Koivula (2002a), Koivula (2012) did not detect strong effects of site preparation. The impact on within-stand spatial distribution of individuals may nevertheless be larger than logging-caused effect (Koivula and Niemelä 2003). Similarly, Koivula (2001, 2002a) for the short and Toivanen et al. (2014) for the long term showed that moisture variation within stands may be a more important ground beetle assemblage determinant than felling or prescribed burning.

Saproxylic and other actively flying beetles
Short-term effects of retention

The benefits of standard retention on saproxylic beetles are small (Heikkala et al. 2016a), but it supports some of these species, provided that CWD substrates are sufficiently abundant (Jokela et al. 2019) (Table 2). Saproxylic beetle abundance and richness increase rapidly after felling, but numbers return close to the background level within a few years in both pine and spruce forests (Hyvärinen et al. 2006; Toivanen 2007; Heikkala et al. 2016a, 2016b). These changes may be minor after selection felling (Joelsson et al. 2018a), but species composition may vary considerably within stands, as felling trails host different composition from the less open, selectively felled fractions (Joelsson et al. 2018b). Selection felling in spruce forests, aiming at an uneven age

structure of trees, maintains the saproxylic beetle assemblage well, whereas ordinary commercial thinning causes large deviations (Hjältén et al. 2017a; Joelsson et al. 2017). In these operations, the amount of post-harvest CWD is important (Joelsson 2017). Gap felling, with gaps 20 m in diameter, benefits cambium consumers, particularly bark beetles (Scolytidae: Scolytinae), but has minor effects on the overall composition of the beetle assemblage (Hjältén et al. 2017b; Kärvemo et al. 2017). Specifically, xylophages of fresh CWD benefit from felling, apparently due to the rich pulse of slash and stumps, whereas some other species groups may decline, such as mycetophages (Heikkala et al. 2016b; Jokela et al. 2019; Table 2). If CWD is plentiful, retention level as such has often minor effects on saproxylic beetles unless there is no retention at all (Hyvärinen et al. 2005, 2009; Toivanen 2007; Toivanen and Kotiaho 2010; Heikkala et al. 2016b; Table 2). On the other hand, increasing size of felled gaps impacts non-saproxylic spruce-forest beetles positively (Jokela et al. 2019). Finally, in southern Swedish mixed-oak forests, selection felling to release space for oak trees increased the richness of herbivorous and saproxylic beetles by about 35% (Franc and Götmark 2008).

Long-term responses to retention

Heikkala et al. (2016a) showed that the overall species richness of saproxylic pine-forest beetles peaks within a few years from felling and then declines rapidly to the pre-treatment level, but late-stage xylophages remain abundant for at least 10 years (Table 2). Retention level per se has minor effects on saproxylic beetles (Toivanen and Kotiaho 2007a; Heikkala et al. 2016a). High level of retention, however, may protect pine saplings from pine weevil (*Hylobius* spp.) attacks, perhaps through providing alternative food sources for these beetles (Pitkänen et al. 2005, 2008). Selection felling aimed at releasing space for oak trees in southern Swedish mixed forests continues to support saproxylic beetles for at least 10 years post-harvest, whereas herbivorous beetles may not show a response any longer (Gran and Götmark 2019).

Prescribed burning

Fire rapidly changes the species composition (Hyvärinen 2006; Heikkala 2016; Hägglund and Hjältén 2018) and functional diversity of saproxylic beetles (Heikkala et al. 2016b), and increases their species richness, especially if combined with retention (Toivanen and Kotiaho 2007a; Hjältén et al. 2017b; Table 2). These effects may remain detectable for at least 10 years (Heikkala et al. 2016a). Fire also supports open-habitat associated species (Heikkala et al. 2016b) and many red-listed and rare saproxylic species (Hyvärinen et al. 2006; Toivanen and Kotiaho 2007b), an effect that may become more pronounced with increasing amount of deadwood (Komonen et al. 2014).

On the other hand, burning affects some bark beetles negatively (Toivanen and Kotiaho 2010), so prescribed burning may also decrease risks for economic damage (though see, e.g., Kärvemo et al. 2017).

Manipulation of dead wood

Artificial addition of CWD in harvesting operations (high stumps, girdled trees, pushed-down logs, etc.) positively affects cambium consumers and wood borers, including rare and red-listed species (Toivanen 2007; Toivanen and Kotiaho 2010; Table 2). The functioning of such CWD, however, depends on how trees are killed, and tree species (Hägglund and Hjältén 2018). Such operations might be thought to increase risks of bark beetle outbreaks, but sampling at pine and spruce retention-felling sites suggests that these risks are small (Martikainen et al. 2006b; Toivanen et al. 2009). Felled and standing pieces of artificial CWD host partly different beetle assemblages so that cambium consumers, fungivores and red-listed species may be more common in the latter (Gibb et al. 2006; Johansson et al. 2006; Hjältén et al. 2010; Andersson et al. 2015). Furthermore, high stumps of different decay stages and tree species host different beetle assemblages (Lindhe and Lindelöw 2004). Moreover, in a Norwegian high-stump experiment, high stumps at clear-cut edges hosted different beetle assemblages from high stumps located at central parts of clear cuts (Fossestol and Sverdrup-Thygeson 2009), probably because of microclimatic factors, sun exposure and edge effects.

Other aspects

The species of a dying or dead retention tree appears important for saproxylic species in general, as each tree species hosts a distinctive set of specialists (Toivanen 2007; Toivanen and Kotiaho 2010).

Other taxa
Short-term effects of retention

Johansson et al. (2010) and Hägglund et al. (2015) detected an overall increase of flat bugs (Heteroptera: Aradidae) following gap harvesting in Swedish spruce forests. Heikkala et al. (2017) found that retention in pine-forest clear cuts supports these species (Table 2). Also the decomposer community is impacted by felling method. Siira-Pietikäinen et al. (2001) and Siira-Pietikäinen (2002) found that the community structure, as indicated by phospholipid fatty-acid pattern, changed in the first year, followed by declines in microbial biomass and respiration in the second, and an increase of Enchytraeidae worms in the third year in clear cuts. However, selection felling had no detectable impact on the decomposer community. In the MONTA experiment, short-term effects of felling on common small mammals broadly followed species habitat requirements. Thus, the field vole (*Microtus agrestis*) benefited, whereas the

bank vole (*Myodes glareolus*) suffered, from felling; interestingly, the Eurasian pygmy shrew (*Sorex minutus*) seemed to benefit from small retention patches left in clear cuts (Heikki Henttonen, pers. comm.). The latter seems to benefit from forest edge habitats (Henttonen et al. 1998). The wood lemming (*Myopus schisticolor*), a specialist of old mossy spruce forests, was scarce in most years. In the first post-harvest summer, however, it was remarkably abundant in reference stands but remained scarce in up to 0.03-ha retention patches of clear-felled stands (Heikki Henttonen, pers. comm.).

Long-term responses of retention

Siira-Pietikäinen and Haimi (2009) showed in Norway spruce forests that enchytraeid worms remain at elevated levels in clear cuts and gap felled stands for at least 10 years. In the same study, macro-arthropods declined in these two treatments but not in selection felling, particularly herbivores, microbivores, and some detritivores. The decomposer community remained affected for the entire 10-year follow-up, and up to 0.03-ha retention tree groups appeared similar to the surrounding clear-felled parts of the same stands (Siira-Pietikäinen and Haimi 2009; Table 2). In pine forests of the FIRE experiment, felling impacted the pollinator community strongly, whereas the retention level (10 or 50 m^3 ha^{-1}) had only a minor effect (Rodriguez and Kouki 2017; Table 2). Bees (Apidae) and hoverflies (Syrphidae) in particular were more abundant in felled than in unharvested forests; the latter hosted a subset of the assemblage found in felled sites. The general felling-caused increase was associated with the amount of deadwood (perhaps reflecting structural heterogeneity and consequent nesting sites), blueberry and lingonberry flower abundance (foraging), and exposed mineral soil (important particularly for solitary bees) (Rodriguez and Kouki 2015). Moreover, tachinid flies (Diptera: Tachinidae) that parasitize herbivorous insects had higher richness due to felling, which was associated with the functional diversity of plants (Rodriguez Olmo 2018). Retention trees as such are important too: Thorn et al. (2018) found, 15 years after felling, that Northern bats (*Eptesicus nilssonii*) roost under the loose bark of standing dead trees in clear-felled pine forests.

Prescribed burning

In the short term, flat bugs benefit from burning, indicated by the elevated richness and abundance of rare and red-listed species (Johansson et al. 2010; Hägglund et al. 2015; Hägglund 2016; Heikkala et al. 2017; Table 2). However, retention level in burned pine stands (10 or 50 m^3 ha^{-1}) was not important for flat bugs (Heikkala et al. 2017). Mound-building ants (*Formica rufa* group, red wood ants), on the other hand, were negatively

affected by burning and decreasing level of retention in the EVO experiment, whereby lower retention had apparently contributed to a more intense soil-surface fire, thus damaging ant mounds (Toivanen et al. 2014; Table 2). In the long term, pollinator insects benefit from fire, possibly through fire-caused increase in structural heterogeneity (Rodriguez and Kouki 2015, 2017). Moreover, in an exclosure experiment, den Herder et al. (2009) showed that burning decreased the browsing-caused mortality of deciduous trees, possibly because burned forests are relatively open, providing little shelter for moose, deer, and hare.

Manipulation of dead wood
No results reported.

Other aspects
Økland et al. (2008) found, in mixed oak forests in southern Sweden, that logging residue from selection felling of other than oak trees supported wood-associated fungus gnats (Mycetophilidae).

Wrap-up of biodiversity responses to VRF and restoration
The studied experiments, reviewed above, demonstrated that responses to felling and restoration operations vary greatly, depending on species or taxonomic group, and that many if not most effects are detectable for more than 10 years. From management and conservation points of view, however, not all responses are equally (or ecologically) important. This is because most species thrive in present-day managed forests, whereas red-listed and other highly specialized species do not, so the latter should determine management and conservation actions. Below, we do not discuss the above findings species group by species group, but at a general level: short- and long-term responses of forest biodiversity to VRF, prescribed burning, manipulation of dead wood, and other findings. We end this paper with suggestions to modify forest management and point out knowledge gaps for future research.

Short-term responses of forest biodiversity to VRF
Many species respond positively to felling operations, apparently due to released resources (light, minerals, competition-free sites) and certain ephemeral resources, particularly fresh CWD (residue and stumps); moreover, many rare or red-listed species benefit from the latter. The standard retention, ten trees per ha, is insufficient to maintain biodiversity at the stand level, as even several times higher amount of retention does not mitigate the effects of harvesting particularly on specialist species (Perhans et al. 2009; Hautala et al. 2011; Johnson et al. 2014; Vanha-Majamaa et al. 2017). In Fennoscandia, the

prevailing retention method is aggregated retention. Retention patches should be preferably at least 1 ha in size, as retention patches of up to 0.6 ha, or nearly 50-m-wide riparian buffer zones against clear cuts, were shown to be too small to maintain the initial core-habitat species composition, largely due to microclimatic changes associated with edge effects (Chen et al. 1993; Heliölä et al. 2001; Oldén et al. 2019b). These findings are in accordance with North American research (e.g., Nelson and Halpern 2005).

Another important aspect in VRF is tree-species composition. In practical management, the decision on which tree species to retain is often based on susceptibility to wind or other mortality factors, and timber value: retention trees are often aspen or other low-economic value species. Hämäläinen et al. (2016) found in harvested Scots pine-dominated forests that smaller, aggregates of, and pine or birch, trees were less prone to mortality than larger, dispersed, and spruce, respectively. Decisions concerning retention patch size and composition are also ecologically important: epiphytic lichens growing on deciduous trees may benefit, whereas lichens growing on spruce may decline, following felling (Ranlund et al. 2018). Spruce forests are generally shadier than other forests, and lichens are adapted accordingly, thus being more sensitive to changes in light conditions (Esseen and Renhorn 1998; Rheault et al. 2003).

Long-term responses of forest biodiversity to VRF
Community compositions of most groups of forest species reflect felling treatments for at least 10 years. However, any retention mitigates some community changes, and with about 50% dispersed retention, most shade-associated species thrive in managed stands. In other words, community alterations become more pronounced the more intense the felling method. Also, the long-term resilience after felling varies among taxonomic groups. Among understory plants, herbs are rather resilient, whereas mosses, liverworts, and dwarf shrubs require tens of years to recover (Reinikainen et al. 2000; Hedwall et al. 2013; Tonteri et al. 2016; Vanha-Majamaa et al. 2017). Timber harvesting generally has minor effects on frequent ectomycorrhizal fungi in a 30–50 years perspective (Varenius et al. 2016), whereas polypores in forests that had been selectively felled hundred years earlier still reflected an initial 10–80% felling-intensity gradient (Bader et al. 1995). This finding suggests that the overall biodiversity does not fully recover until the structures and microclimate return to near-pristine conditions. The size, species, and quality of retained trees are important in this respect (Kuuluvainen et al. 2019).

Retention reduces negative long-term biodiversity impacts. We show above that increasing retention supports red-listed polypores, a finding similar to a

Northern Finnish chronosequence of selectively felled forests (Sippola et al. 2004). Even single retained aspen trees support some epiphytic bryophytes and lichens (Hazell and Gustafsson 1999) and rare and red-listed beetles (Martikainen 2000). Sometimes conservation requires thinking the other way around: examples include selective felling to release space for oak trees in southern Swedish mixed forests (see above), and intermediate-intensity felling that supported the lichen *Usnea longissima* in Norway (Storaunet et al. 2008, 2014) and some old-growth lichen species in Estonia (Lõhmus et al. 2012).

As we show above, aggregated retention may be better than dispersed retention at least for bryophytes. Similarly, the diversity of epiphytic and epixylic indicator lichens was maintained better in retention patches than on solitary trees in Northern Finnish spruce forests (Ylisirniö and Hallikainen 2018). The relative benefits of dispersed and aggregated retention in North European conditions would clearly warrant more research (e.g., Lencinas et al. 2008; Lee et al. 2017).

Short- and long-term impacts of prescribed burning

Short-term effects of prescribed burning are negative on most species groups, except for pyrophilous species. In the long term, burning benefits open-habitat associated and saproxylic species, including red-listed ones. Epiphytic lichens show negative long-term responses 10–15 years post fire (Table 2), but an Estonian study suggests that the trend may turn positive a few years later (Lõhmus et al. 2018). Accordingly, prescribed burning combined with retention higher than 50 m^3 ha^{-1} may have positive long-term effects on the species composition, occurrence, and abundance of rare and threatened polypores (Penttilä and Kotiranta 1996; Penttilä et al. 2013).

As we show above, understory plants, polypores, and ground-dwelling arthropods face smaller changes the higher the retention at burned sites. Retention at fire sites improves conditions for saproxylic species, but it also supports pyrophilous species (Wikars 1995) and common shade-associated species (see above). Open-habitat associated species, on the other hand, do better the lower the retention at fire sites (see above); similarly, a Norwegian study at a post-fire stand reported high abundance of open-habitat associated ground beetles, such as *Pterostichus adstrictus* (Gongalsky et al. 2006).

Prescribed burning impacts also micro-sites and substrates for species. In spruce-dominated forests, burning may affect within-site moisture variability, as the water-table level rises following fire, thus potentially increasing topography-related paludification in depressions. On the other hand, fire may destroy up to 40% of the pre-treatment CWD, particularly CWD of advanced decay (Eriksson et al. 2013), and thereby only partly contribute to the CWD continuity. Moreover, fire increases the surface area of charred wood (> 50%) and reduces vegetation cover on these pieces of wood by 60–98% (Eriksson et al. 2013). The new CWD created by prescribed burning is also determined by the level of retention and stand age (Sidoroff et al. 2007).

Artificial deadwood and retention trees benefit saproxylic species, but with preconditions

The amount and quality of CWD are important richness determinants of saproxylic species (e.g., Similä et al. 2003; Santaniello 2017; Santaniello et al. 2017a; Jokela et al. 2018). Artificial CWD, mostly as high stumps, supports saproxylic organisms; however, these CWD also host partly different communities from CWD of natural origin. The quality of artificial CWD is important for many threatened specialists. Felled or standing pieces of artificial CWD host partly different beetle assemblages so that cambium consumers, fungivores, and red-listed species may be more common in standing CWD (Sverdrup-Thygeson and Ims 2002; Lindhe et al. 2004; Gibb et al. 2006; Hjältén et al. 2010; Andersson et al. 2015). Furthermore, high stumps of different decay stages and tree species host different beetle assemblages (Lindhe and Lindelöw 2004; Lindbladh et al. 2007; Jonsell and Hansson 2011; Stokland et al. 2012; Jonsell et al. 2019; Sandström et al. 2019), indicating biodiversity benefits of a continuous supply of CWD. Moreover, decomposer fungi determine the beetle assemblage in high stumps (Jonsell et al. 2005; Abrahamsson et al. 2008). Hence diversities of different taxonomic groups seem to be tied together, and an impact to one group may have cascading effects on the whole ecosystem.

Increasing retention results in higher amount and more diverse quality of CWD (Santaniello et al. 2016, 2017b), and retention tree groups also add structural variation to managed forests (Kruys et al. 2013). The location (site type) and size (level of retention) of retention tree groups are important determinants of the much-needed continuity of large-sized CWD for saproxylic species. In spruce forests, retention tree groups should preferably be placed in paludified patches with initially more CWD of different stages of decay as compared to upland patches (e.g., 16 vs. 2 m^3 ha^{-1}; Vanha-Majamaa and Jalonen 2001) to "lifeboat" species over the regeneration phase. This way, much if not most of the initial CWD might be retained (Hautala et al. 2004). Another motive is to mimic natural disturbances, as in natural conditions these sites burn less often than upland sites (Wallenius et al. 2004). However, susceptibility to uprooting is higher in paludified than in upland sites: during the first few post-harvest years in spruce forests, uprooting percentages in these biotopes were 48 and 15, respectively (Hautala and Vanha-Majamaa 2006; Hautala

et al. 2011). Moreover, Heikkala et al. (2014) found that retention of 10 m³ ha⁻¹ apparently did not contribute much to the continuity of CWD as trees died rather quickly, whereas in 50 m³ ha⁻¹ trees died over a longer time and thus functioned considerably better in this respect. Site type and retention level thus largely determine the future formation of CWD: formation can be faster in paludified than in upland sites, whereas the continuity may be better in the latter and with increasing retention level.

The ecological importance of paludified patches, site preparation and logging residue

Paludified patches in spruce forests, particularly if left unharvested, are important for the population maintenance of many forest-species groups, such as epixylic and epiphytic vegetation and beetles occupying spruce mires. Earlier research suggests that these patches are crucial for some red-listed specialists, such as the beetle *Pytho kolwensis* (Siitonen and Saaristo 2000). In the Russian part of Fennoscandia, paludified patches have been retained for almost a hundred years (Shorohova et al. 2019). Regrettably, research on biodiversity effects of this practice is largely missing but even ad hoc sampling at these sites would provide insights into long-term effects of VRF.

According to the Finnish Forest Act, paludified patches and certain other woodland key biotopes may be managed cautiously with selection felling (www.finlex.fi). It is notable, however, that in most of the above-reviewed experiments, and in available data about their stand characteristics, these patches had often not been identified and located. Such lack of information may lead to unintentional felling of these sites; most harvesting is done in winter months, when the snow cover makes their identification challenging. Due to the ecological importance of paludified patches, it would be important to describe, map, and completely retain them when implementing harvesting operations.

It is notable that even though site preparation has been widely used since the 1960s, its effects have earlier seldom been separated from the effects of felling per se. Site preparation shapes the within-site spatial distribution of understory plants and beetles. Combined with felling, however, it also partly determines the retention and continuity of CWD at harvested sites (Haeussler et al. 2004). With dispersed retention, the disturbance on CWD may concern the whole harvesting area, whereas aggregated retention may preserve CWD at least in retained fractions. In clear cuts, nearly 10% of the pre-treatment volume of CWD is destroyed by harvesting machinery, and subsequent disc trenching may destroy an additional 70% (Hautala et al. 2004). Disc trenching may have destroyed 4–6 M m³ of CWD

during 1960–2000 in Finland alone (Hautala et al. 2004), which has probably greatly contributed to the loss of saproxylic organisms, such as epixylic species (Rabino-witsch-Jokinen et al. 2012). This method was the most common site preparation method in Finland until 2005, after which mounding has become more common (Anonymous 2014). However, even mounding may destroy over 30% of CWD, including 70% of CWD of advanced decay, especially if combined with stump harvesting (Rabinowitsch-Jokinen and Vanha-Majamaa 2010). These findings indicate that site preparation is particularly devastating for specialists of advanced-decay CWD—and may well locally break down the continuity of such deadwood. Hence CWD quality, not just amount, should be considered in assessments of forest management.

We show also that logging residue and stumps are useful resources for saproxylic species, particularly beetles (Jonsell and Schroeder 2014). However, residue and stumps are often targeted by energy-wood harvesting (Ranius et al. 2018). This practice impacts saproxylic beetles negatively through a loss of substrates (Victorsson and Jonsell 2014; Work et al. 2016; Ranlund and Victorsson 2018) and through functioning as ecological traps: piles of residue and stumps—with beetles in them—are eventually moved from forest to power plants (Hedin et al. 2008; Victorsson and Jonsell 2013). A modeling study suggests that the risk of extinction of these species may be small if only 10% of the total clear-cut area in a forested landscape is stump harvested, but the risk rises with increasing intensity of extraction (Persson and Egnell 2018). Harvesting of stumps and residuals also impacts, e.g., epiphytic and epixylic species through exposing mineral soil and destroying CWD; lichens are more severely impacted by slash removal than by stump removal (Hiron et al. 2017).

Future research needs

In many of the reviewed papers, results have been reported by species groups, which may produce estimations too general for conservation or management purposes about the effects of felling, burning or high stumps. Almost all such groups include species with positive, neutral, and negative responses to these factors. Most of the reviewed species (groups) thrive in managed forests, whereas a small fraction (specialized and red-listed species) does not. Considering the low percentage of Fennoscandian forests dominated by natural disturbances, processes, and structural features, conservation and management efforts should focus on supporting this fraction. Indeed, the member nations of the European Union (EU) have accepted the EU Biodiversity Strategy, which "aims to halt the loss of biodiversity and ecosystem services in the EU and help stop global biodiversity loss by 2020" (Anonymous 2019b).

Landscape structure may determine benefits of VRF, restoration, and other conservation measures (Hanski 2000; Hedenås and Ericson 2008), so that areas with generally more resources (habitat, substrates, etc.) would be better in this respect. Kouki et al. (2012) have shown that these benefits may also partly depend on regional land-use history. However, in a series of Swedish studies, nearby areas of high conservation value did not determine saproxylic beetle diversity of high stumps, whereas the timber volume and tree-species composition of surrounding forests did (Lindbladh and Abrahamsson 2008; Abrahamsson et al. 2009; Hallinger et al. 2018; Jonsell et al. 2019).

Forest practitioners are under increasing pressure to better account for a diverse set of values, including biodiversity, in management operations. This cannot be achieved without a solid basis on research. We identify the following knowledge gaps: (i) merits of aggregated and dispersed retention, and threshold sizes of felled gaps; (ii) modifications of site preparation, and their ecological effects; (iii) mechanisms behind species responses to forest management; (iv) impacts of forest management on inter-specific relationships; (v) species resilience and community-level responses at the landscape level; (vi) effects of VRF on ecosystem functioning and ecosystem services (carbon dynamics, nutrient cycling etc.); and (vii) meta-analysis of the effects of VRF and prescribed burning.

Conclusions

Retention levels may not reach, let alone exceed, 50% in the foreseeable future in countries whose economy largely relies on forest industry, such as Finland, Sweden, and Russia. However, some actions to support biodiversity do not increase harvesting costs considerably. These include retention of existing CWD, damaged trees, and tree species of minor economic value. Felling operations can be planned and implemented so as to maintain the CWD continuum and, in turn, saproxylic species. The success, however, depends on updating forester education and public awareness about the importance of biodiversity, ecosystem services, and aesthetic, recreational and other multiple-use values. As shown in our review, the amount and quality of legacies are more important than the VRF method per se for many red-listed species. By maintaining or even artificially increasing CWD and some large-sized trees in harvested sites, many if not most saproxylic species can be life-boated over the regeneration phase.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s13717-019-0209-1.

Additional file 1: Table S1. Papers from Fennoscandian retention and restoration experiments, sorted according to experiment acronym (compare Table 1) followed by first author and publication year.

Author details
[1]School of Forest Sciences, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland. [2]Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FI-00790 Helsinki, Finland.

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