Dissertationes forestales 266

Promoting biodiversity and ecosystem services in managed boreal forests through disturbance-mediated functional heterogeneity

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Academic dissertation

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ABSTRACT

The majority of global forest area is considered neither forest plantation nor formally protected. In these forests multiple-use prevails and forests have the potential to be managed sustainably while providing multiple ecosystem goods and services. However, in practice, management in these forest areas is usually intensive, often securing the provision of a single commodity: wood biomass. This management leads to forest simplification, disregarding forest multi-functionality, biodiversity conservation and ecosystem services provided by forest biodiversity.

In this thesis, I evaluate the effect of increasing forest functional heterogeneity on biodiversity and multiple ecosystem services in managed boreal forests. My research takes advantage from a large-scale, replicated ecological experiment initiated in Finland in 2000, where forest structure was manipulated following disturbance guided management, with several retention levels at harvesting in combination with prescribed fire in 24 study sites.

The results show that local scale heterogeneity mediated by fire and high retention improves lingonberry yield and performance in burnt harvested forests. Dead wood and post-fire soil structure from these forests are beneficial for bee abundance and diversity, through an increase in nesting resources. Early successional burned forests exhibit increased levels of parasitoid functional diversity driven by higher structural complexity of vegetation mediated by disturbance.

At a landscape scale, old-growth forests provide with abundant bilberry cover, spring flowering and berry yield, offering complementarity of flowering resources for pollinators nesting on post-harvest forests. Habitat diversity generated by old-growth forests, variable tree retention and fire intensity, promotes pollinator spatial and temporal turnover, especially in burned harvested forests, and large-scale parasitoid functional trait diversity.

In conclusion, emulation of forest disturbance at harvesting, together with the preservation of natural old-growth forests increase functional heterogeneity in managed boreal forests and hold promise for reconciling production forestry with sustainable forest management, provision of critical ecosystem services and biodiversity conservation.

Keywords: Biological legacies; retention forestry; prescribed fire; *Vaccinium* shrubs; pollination; natural biological control.

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LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following two papers and one manuscript, which are referred to in the text by Roman numerals **I–III**. Articles **I** and **II** are reproduced with the kind permission of publishers. Manuscript **III** is the author's version of the submitted manuscript.

I. Rodríguez, A., Kouki, J. (2015). Emulating natural disturbance in forest management enhances pollination services for dominant *Vaccinium* shrubs in boreal pine-dominated forests. Forest Ecology and Management 350: 1–12. http://doi.org/10.1016/j.foreco.2015.04.029

II. Rodríguez, A., Kouki, J. (2017). Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. Ecological Applications 27(2): 589–602.
http://doi.org/10.1002/eap.1468

III. Rodríguez, A., Pohjoismäki, J.L.O., Kouki, J. Diversity of forest management promotes parasitoid functional diversity in boreal forests. Manuscript.

Authors' contributions

AR is responsible for the compilation of this thesis.
JK designed, initiated and coordinated the field experiment in which this thesis is based since 1999.
AR, together with JK, conceived the idea and sampling design for all articles.
AR collected the data on vegetation for article **I**, and data on pollinators and parasitoids for articles **I**, **II** and **III**.
AR identified insect specimens for articles **I** and **II**. JLOP contributed significantly to the identification of specimens as well as their biological trait data for article **III**.
AR planned and executed data analyses for all articles.
AR wrote the first draft of the manuscript as leading author for all articles. All the authors contributed substantially and critically to manuscript drafts.

TABLE OF CONTENTS

TERMINOLOGY

β diversity: "The extent of change in community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments" (Whittaker 1960). In a multiplicative partitioning of diversity framework (Tuomisto 2010), β diversity is quantified as the ratio of γ diversity (total species diversity at the landscape or regional scale) and α diversity (average species diversity at the local scale), and it can be understood either as turnover or as variation in community composition (Anderson et al. 2011).

Biological legacies: "Organisms, organic materials, and organically-generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem" (Franklin et al. 2000). Human-caused disturbances (e.g. clear-cutting) differ markedly from natural disturbances (e.g. wildfires, wind, insect outbreaks), with much lower amount and degree of heterogeneity of biological legacies after anthropogenic disturbance (Kouki et al. 2001; Swanson et al. 2011).

Ecological disturbance: "A discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (Sousa, 1984). Note that this definition, although devised for natural disturbances, does not differentiate between natural or human-caused disturbances.

Ecosystem services: "The benefits people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as regulation of floods, drought, land degradation, and disease; supporting services such as soil formation and nutrient cycling; and cultural services such as recreational, spiritual, religious and other nonmaterial benefits" (Millennium Ecosystem Assessment 2003).

Functional composition: originally defined as "community aggregated trait values" (Garnier et al. 2004). Also known as functional identity: "The mean value of functional traits, weighted by abundance, across all species present in a given community" (Mouillot et al. 2013). Functional composition is mathematically defined as "community-weighted mean trait values" (CWMs), with

$$CWM = \sum_{i=1}^{S} p_i x_i$$

, where p_i is the relative abundance of species i (i = 1, 2, …, S), and x_i is the trait value for species i. As such, it summarize the shifts in single-trait values within a given community (Ricotta and Moretti 2011).

Functional diversity: "The range and value of those species and organismal traits that influence ecosystem functioning", the latter defined as "the rate level, or temporal dynamics of one or more ecosystem processes such as primary production, total plant biomass, or nutrient gain, loss, or concentration" (Tilman 2001).

Functional heterogeneity: “Spatial and temporal heterogeneity in biological legacies and physical conditions that is produced by ecological disturbances (and) will function to increase coexistence among assemblages of species” (Odion and Sarr 2007). This increase in species coexistence is given at intermediate frequencies of ecological disturbance, as predicted by the intermediate disturbance hypothesis (Connell 1978).

Prescribed burning: forest controlled burning which “is currently used in some protected areas as an active management tool to enhance and maintain habitats for biodiversity outcomes in boreo-temperate forests” and “is also commonly used for the purpose of mitigating wildfire risk by managing the accumulation of fuel in forests when and where necessary” (Eales et al. 2018). This definition refers to prescribed burning used for restoration purposes. Prescribed burning can also be used in managed forests as a silvicultural method, to modify soil structure after clear-cut and to promote establishment of the new tree cohort (Graham and Jain 1998).

Retention forestry: “Forest management approach based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest at the time of harvest (with) the aim of achieving a level of continuity in forest structure, composition, and complexity that promotes biodiversity and sustains ecological functions at different spatial scales” (Gustafsson et al. 2012; Lindenmayer et al. 2012).

Sustainable forest management: “The stewardship and use of forests and forest lands in such a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, and vitality, and their potential to fulfil, now and in the future, relevant ecological, economic, and social functions at local, national, and global levels, and that does not cause damage to other ecosystems” (WGCICSMTBF 2014).

1. INTRODUCTION

1.1 Background

Sustainable forest management, as assessed by the Montréal Process and followed in essence by most international forest research organizations, comprehends a set of criteria that address in explicit form the conservation of forest biodiversity and multiple ecosystem services (WGCICSMTBF 2015; Parvianen and Västilä 2011). The potential for ecologically sustainable forest management can be fulfilled on those forests which are neither formally protected nor intensively dedicated to wood production (Lindenmayer et al. 2012). These multiple-use forests encompass most of the forest area, with as much as 76% of the global forest, and 88% of the forest area in Finland (FAO 2015; Kortesmaa and Jokela 2017). These forests can be managed for the supply of multiple goods and services, such as provisioning (e.g. wood and non-wood forests products), regulating (e.g. carbon sequestration, pollination and biological control), supporting (e.g. habitat for species) and cultural (e.g. recreational and spiritual experience) services (TEEB 2010).

However, forest management is usually intensive in these forest areas, securing the provision of a single commodity, wood biomass for fuel, pulp and timber. In order to maximize wood provision, this managements leads to forest simplification (e.g. mono-specific, even-aged plantations) and the suppression of natural disturbances, compromising biodiversity, (Puettmann et al. 2009; Thom and Seidl 2016), and forest multi-functionality (Nocentini et al. 2017).

Fennoscandian boreal forest have been severely impacted trough intensive forest management and the suppression of wildfires from World War II on, leading to fairly homogenous, younger and even-aged stands with relatively short rotation cycles (Keto-Tokoi and Kuuluvainen 2014). This management has had profound impacts on forest structure and dynamics, with rotation cycles shorter than natural disturbance (i.e. wildfires) frequency, leading forest outside its intrinsic rate of variability (Cyr et al. 2009; Shorohova et al. 2011), and transforming a landscape dominated by old forests in a compartment-wise landscape mosaic dominated by young forests stands (Kouki et al. 2001, Kuuluvainen and Siitonen 2013). Moreover, in Finland, only 12% of the forest area is formally protected (Kortesmaa and Jokela 2017), most of it corresponding to poorly productive areas, as it is the case with reserves worldwide (Margules and Pressey 2000), and with the majority of protected areas located in the northern part of the country. These forest reserves are not representative of the full regional diversity (Bengtsson et al. 2003), making “off-reserve” conservation within managed forests highly needed (Fischer et al. 2006).

Forest homogeneity because of intensive forest management and the suppression of natural disturbances has an overly negative effect on boreal forest biodiversity (Niemelä 1997; Rassi et al. 2010; Junninen and Komonen 2011), and on ecosystem services maintained by forest diversity (Bengtsson et al. 2000). Forest biodiversity supports multiple ecosystem services (Thompson et al. 2011), and provides temporal and spatial insurance in ecosystem service delivery against environmental fluctuations (e.g. disturbances; Tylianakis 2010). Despite its relevance, the role of diversity in the provision of forest ecosystem services remains widely understudied (Mori et al. 2017). This is especially true regarding regulating services provided by insects (e.g. pollination and natural pest control; Pohjanmies et al. 2017), which are essential for human well-being. As an example, more than 75% of crop plants require animal-mediated pollination (Klein et al. 2007), while estimated economic valuation of pest control amounts to roughly 4.5 billion $ for the US alone (Losey and Vaughan 2006).

This knowledge gap on the ecological and functional basis of pollination and natural biological control services in boreal forests present a challenge for an effective conservation of these ecosystem services (Kremen 2005; Cadotte et al. 2011). Research on drivers affecting community structure at multiple scales of management (Kremen et al. 2007; Winfree et al. 2018), and on functional diversity of service providers is then critical for a better understanding of the effects of diversity on the maintenance of service provision (Klein et al. 2009; Peralta et al. 2014), and for a correct assessment of disturbance effects on ecosystem service delivery (Blüthgen and Klein 2011; Mouillot et al. 2013; Perović et al. 2018).

Additionally, the emphasis of wood production in intensive forest management has led to an under-development in the management of non-wood forest products (NWFP; Calama et al. 2010), despite their importance in interrelating environmental with provisioning and socio-economic sustainability criteria (Lund et al. 1998). Finnish boreal forest provides with several non-timber goods, among them: recreational activities, game, lichen, Christmas trees, mushrooms and berries (Matero and Saastomoinen 2007). In Finland, berries are mainly produced by forest dwarf-shrubs of the family Ericaceae, in particular (because they attain the highest covers on understory layer) bilberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.) (Uotila et al. 2005; Uotila and Kouki 2005). The importance of both shrubs in sustainable forest management becomes apparent as they provide socioeconomic and provisioning services (recreation, household income and food; Turtiainen et al. 2011), supporting services (habitat for insectivorous birds and herbivorous insects; Atlegrim 1991; Lakka and Kouki 2009), and regulating services (pollination; Ranta 1981), constituting also one of the main drivers in boreal ecosystem dynamics (Nilsson and Wardle 2005).

In spite of their importance, bilberry and lingonberry have decreased their coverage over 50% since 1950's, because of management practices such as clear-cutting harvest that increases direct light and soil drought; tillage, that destroys shrub rhizomes; and fertilization, that decreases shrub cover by lowering its competitive ability with nitrophilous plant species; Reinikainen et al. 2000; Strengbom and Nordin 2008). Additionally, forest density and the proportion of young forests have increased in the same period, with negative effects for cover of both shrubs (Hedwall et al. 2013), while there is no available evidence on how intensive forest management has affected ecosystem services supported by both shrubs.

Under this scenario (i.e. reduction in biodiversity, multi-functionality and NWFP because of intensive forest management), the incorporation of silvicultural practices aiming to promote functional heterogeneity through the emulation of natural disturbances and the conservation of biological legacies hold promise for the conservation of biodiversity and multiple ecosystem services in managed boreal forests.

1.2 Managing forest disturbance for functional heterogeneity

Under natural circumstances, boreal forests are subjected to disturbance regimes based mainly on wildfire, windstorms and biotic disturbances (Kuuluvainen 2009), with wildfires as the main natural force driving forest dynamics in northern boreal areas (Kouki and Niemelä 1997). The effect of natural disturbances on boreal forest dynamics vary depending on forest structure and fuel load, and on disturbance extent, frequency and intensity, leading to three main types of forest dynamics: a) succession after stand replacing disturbance, b) gap dynamics caused by death of individual trees or patches of trees, and c) cohort dynamics related to tree survival after partial disturbance (Angelstam and Kuuluvainen 2004). These three categories represent a continuum in natural forests, producing and maintaining heterogeneity at multiple spatial and temporal scales (Angelstam 1998), with stand replacing disturbances far less common than gap and cohort dynamics (Kuuluvainen and Aakala 2011).

Wildfires and other natural disturbances provide with large quantities of dead wood and other natural legacies (Franklin et al. 2000; Kouki et al. 2001; Swanson et al. 2011), increasing structural heterogeneity at multiple spatial scales. As such, the application of management methodologies directed to the promotion of biodiversity through the emulation of natural disturbances (Lindenmayer et al. 2006), i.e. prescribed burning and retention forestry, was set to alleviate negative effects of intensive forestry during the 1990s (Gauthier et al., 2009). This management practices should be ideally applied at multiple spatial scales, mimicking natural disturbance regimes (Halme et al. 2013), and their application have the potential of increasing forest functional heterogeneity, with associated positive effects to biodiversity and multiple ecosystem services (Odion and Sarr 2007; Lindenmayer et al. 2012).

Open forests areas created after fire provide suitable areas for bilberry and lingonberry recovery and re-colonization (Hancock and Legg 2012). The application of prescribed fire to mature forests create gaps which are main sites for lingonberry regeneration (Hekkala et al. 2014), while bilberry finds its optimum at open, mesic conditions (Parlane et al 2006). Low to intermediate intensity fires allow the survival of both shrub rhizomes, releasing them from competition with rhizomatous grasses (Schimmel and Granström 1996) and from crowberry (Nilsson and Wardle 2005). On the other hand, retention patches provide continuity in forest function and structure (Gustafsson et al. 2012), acting as “life-boating” element for post-disturbance recovery (Swanson et al. 2011). Thus, both shrubs are likely to benefit from improved shelter from tree retention after forest harvesting. Additionally, early successional post-fire forests attract large quantities of flower-visiting insects, offering them flowering and nesting resources (Potts et al. 2003; Moretti et al. 2004; Grundel et al. 2010). Pollinator abundance is fundamental for both shrubs, as they are obligatorily insect-pollinated, having extremely reduced fruit set in the absence of pollinators (Jacquemart and Thompson 1996; Nuortila et al. 2002).

Pollination services are not restricted to bilberry and lingonberry alone, with an estimated 87% of all angiosperm species requiring animal-mediated pollination (65% for the boreal zone; Kevan et al. 1993; Ollerton et al. 2011). Bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphydae) are main pollinators in most ecosystems (Larson et al. 2001; Michener 2007). Response to disturbance by both groups is dependent on larval and adult resource-use, degree of specialism, body size, behavior and habitat-use traits (Williams et al. 2010; Rader et al. 2014; Moquet et al. 2018), with post-disturbance pollinator assemblage composition modulated by their functional composition (Schweiger et al. 2007; Moretti et al. 2009). Besides the positive effect of open areas on forest pollinators (Hanula et al. 2015; Hanula et al. 2016), natural disturbance increases spatial and temporal heterogeneity, which allows habitat and phenological complementarity in resource use, increasing pollinator diversity at landscape scale (Ricarte et al. 2011; Rubene et al. 2015) and over the course of the growing season (Mandelik et al. 2012; Rollin et al. 2015).

The combined influence of prescribed fire and retention forestry does not only affect bilberry and lingonberry, but the whole plant community. Both silvicultural practices have an effect on plant community composition in early managed forest ecosystems (Fredowitz et al. 2014; Johnson et al. 2014). Changes in the first trophic level may cascade up to the third trophic level (i.e. predators and parasitoids), as consumer survival could depend on the community structure of lower trophic levels (Fenoglio et al. 2012; Peralta et al. 2017). Natural biological control is carried by species from the third trophic level, with insect parasitoids among the most effective agents in regulating forest herbivore insect populations (Lill et al. 2002; Eveleigh et al. 2007). Disturbance management increases variability in species and functional composition of plants because of augmented structural heterogeneity (Pidgen and Malik 2013; Baker et al. 2015), affecting parasitoid species composition and diversity in several ways. Structural complexity of vegetation is of outmost importance for parasitoid behavior and development, providing shelter, adult food in the form of nectar, and physical and chemical cues for host finding and oviposition (Kaiser et al. 2017). At the local scale, parasitoid diversity has been positively related with plant diversity (Sperber et al. 2004; Sääksjärvi et al. 2006) and habitat structure (Stireman et al. 2012; Di Giovanni et al. 2015), with heterogeneity at landscape scale driving parasitoid diversity by increased habitat diversity (Fraser et al. 2007; Kendall and Ward 2016). Responses of parasitoid community structure to forest disturbance are modulated by parasitoid body size (Roland an Taylor 1997), specialization (Komonen et al. 2000), life-history and resource use traits (Hilszczański et al. 2005; Maleque et al. 2010). Therefore, the study of parasitoid communities from a functional point of view offers a valuable perspective for assessing management effects on natural biological control (Perović et al. 2018).

1.3 Aims of the thesis

This thesis explores the effect of functional heterogeneity created by prescribed fire, retention forestry and the preservation of old-growth forests, on ecosystem services linked with bilberry and lingonberry, on spatiotemporal variation in pollinator community composition, and on functional diversity and functional composition of parasitoids, more than 10 year after harvesting. Percent cover and flowering of bilberry and lingonberry were assessed in relation to combined disturbances, as well as the effect of conservation practices on provisioning (i.e. berry yield) and regulating (i.e. pollination) services linked with both dwarf-shrubs (**I**). Processes driving spatiotemporal variation in pollinator community composition and diversity were investigated by studying the effect of structural heterogeneity at multiple spatial and temporal scales on wild bee and hoverfly communities (**II**). Parasitoid functional diversity and functional composition was compared among habitats shaped by disturbance management and in association with vegetation functional diversity and composition (**III**).

The main research questions addressed in this thesis are:

1. What is the effect of tree retention and the heterogeneity provided by biological legacies on dwarf-shrub performance and berry yield? (**I**).
2. What is the effect of combined disturbances on biological legacies providing feeding and nesting resources to wild bees on bilberry and lingonberry flowering seasons? (**I**).
3. What is the effect of structural heterogeneity mediated by disturbance on pollinator diversity, composition, and spatial and temporal species turnover (β diversity)? (**II**).
4. How do parasitoid functional diversity and composition respond to disturbance mediated heterogeneity at local and landscape scales? (**III**).
5. Do parasitoid and plant variability in functional composition match in their response to functional heterogeneity promoted by fire, retention and old-growth forest preservation? (**III**).

2. MATERIAL AND METHODS

2.1 Study area and experimental design

This thesis makes use of a large-scale ecological experiment “FIRE” established in 2000, where tree retention level and prescribed fire were manipulated and replicated according to a factorial design (see http://forest.uef.fi/jarikouki/project_fire.htm). The experiment is located in Lieksa, Eastern Finland (63°10′ N, 30°40′ E), 5–35 km from the Russian border, in the transition zone between the south and middle boreal vegetation zones (Ahti et al. 1968). The experimental design included 24 sites located within a 20 × 30 km area, ranging in size from 2 to 8 ha and averaging 1.96 ± 1.24 km (mean ± SD, range 0.612–4.48 km) between nearest neighbor sites (Fig. 1). The landscape in the area consists mostly of a mosaic of managed forest plantations of different development, fragmented by mires, clear cut areas, small water bodies, and an extensive road network. Although most of the forest area is considered multiple-use forests, mostly managed for timber production, there are also some protected areas, with Patvinsuo National Park (10 500 ha, of which 3700 ha correspond to upland forests) as the largest.

All study sites were ca. 150 years old boreal forests dominated by Scots Pine (*Pinus sylvestris* L.), with Norway spruce (*Picea abies* (L.) Karsten) and two birch species (*Betula pendula* Roth and *B. pubescens* Ehrh.) as the most abundant admixed species. All sites had some signs of low-intensity selective felling, although no cuttings had been done at the study sites during the last ca. 100 years before the experiment. All study sites were predominantly growing on sub-xeric soils of *Vaccinium* (VT) or *Empetrum-Vaccinium* (EVT) types (*sensu* Cajander 1949), with a variable proportion of moister and nutrient-rich patches. The 24 study sites were randomly allotted and subjected to different treatments according to a factorial design (Fig. 2). Study sites were harvested during the winter of 2000–2001, following four levels of tree retention: clear-cut, 10 m^3 of retention trees per hectare—which was chosen to be close to silvicultural recommendations during mid-1990s, about 5–10 trees/ha (Hyvärinen et al. 2005)—, 50 m^3 of retention trees per hectare and control (old-growth uncut forests). Trees were mostly retained in groups (range = 6–65; mean ± SE = 17.98 ± 1.41 trees per group) but a few of them were also scattered as single trees. Half of the sites were burned during summer of 2001, leaving three sites per each of the eight treatment combinations (retention level × fire). Further details on the prescribed burning procedure can be found in Hyvärinen et al. (2005). No other silvicultural measures typical of Fennoscandian boreal forests (Valkonen 2011), such as soil harrowing and mounding, or planting were used to enhance regeneration of the study sites. Hence, at the time of sampling in year 2013, all harvested sites were 13 years old, naturally regenerated.

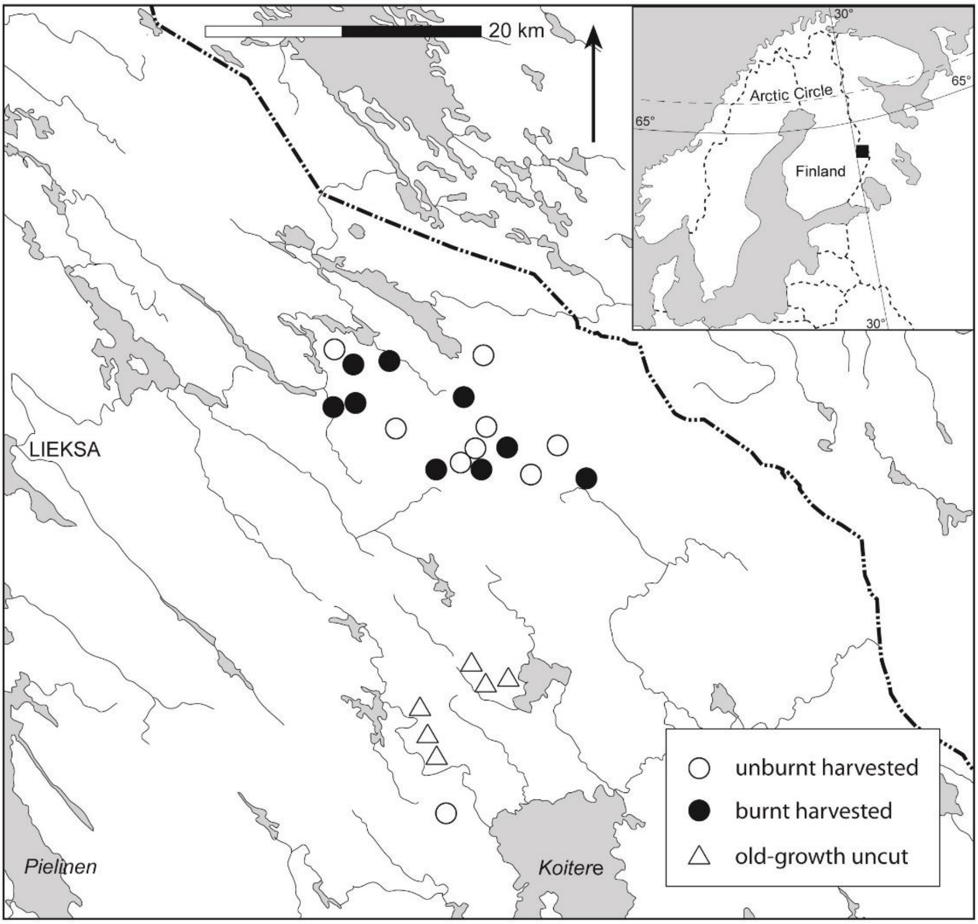


Figure 1. Map of the experimental area, showing study sites.

2.2 Dwarf-shrub and insect sampling

Data on bilberry and lingonberry percent cover, number of flowers and berry yield was collected from May to August 2013 during peak flowering and berry ripening times for both shrubs and when the annual vegetative growth for leaves and shoots was over. Vegetation characteristic from both shrubs were sampled on eight 1 m^2 quadrats arranged on perpendicularly crossed 32 m transects in clear-cut and old-growth forest sites, and by three quadrats inside retention patches and four quadrats outside retention groups in study sites with retention (vegetation sampling schematized in Fig. 2) (**I**).

Bees (Hymenoptera: Anthophyla), hoverflies (Diptera: Syrphidae), and parasitoid flies (Diptera: Tachinidae) were sampled during four periods on May to August 2013, covering most of the flowering season in the area. The four sampling periods are: a) Spring (late May to early June), covering bilberry peak flowering, b) Early summer (mid-June), corresponding to peak lingonberry flowering season, c) Midsummer (early July), corresponding to the peak flowering period of fireweed (*Epilobium angustifoulium* L.) and common cow-wheat (*Melampyrum pratense* L.), plus heather early flowering period (*Calluna vulgaris* (L.) Hull), d) Late summer (late July to early August), covering the heather late flowering period. Insects were sampled by pan traps placed on the ground consisting of twenty-one 500 ml colored bowls per study site (painted fluorescent blue, yellow and left as original white), filled with water and few drops of detergent. Traps were arrayed on transects covering cleared areas and retention patches in sites with 10 and 50 m^3 of retention trees per hectare, while traps were arranged on two 40-m crossed transects intersecting in the center of the study site in control forests and in clear-cuts (insect sampling schematized in Fig. 2) (**I, II** and **III**).

All insect groups were identified to species level. Workers and queens from the *Bombus lucorum* complex cannot be reliably identified by morphological characters and were therefore collectively referred as *B. lucorum* group (Carolan et al. 2012). Species traits were taken into account for the interpretation of dwarf-shrub ecological patterns in response to fire and variable retention (**I**), and for assessing the effects of flowering and nesting resources on pollinator community composition (**I**, **II**). An explicit trait-based approach was used for evaluating congruency in plant and parasitoid functional composition regarding habitat diversity (**III**). Insect traits were obtained from direct measurements and from the literature: a) nesting habitat for bees (**I**, **II**), b) larval biology for hoverflies (**II**); c) body size, host taxonomic order, specialization, host micro-habitat, host location, oviposition strategy, oviposition location, and flight phenology for tachinid flies (**III**). Plant traits related with leaf physiology and morphology, together with plant life form and architecture, were mainly retrieved from the TRY database (Kattge et al. 2011). (**III**).

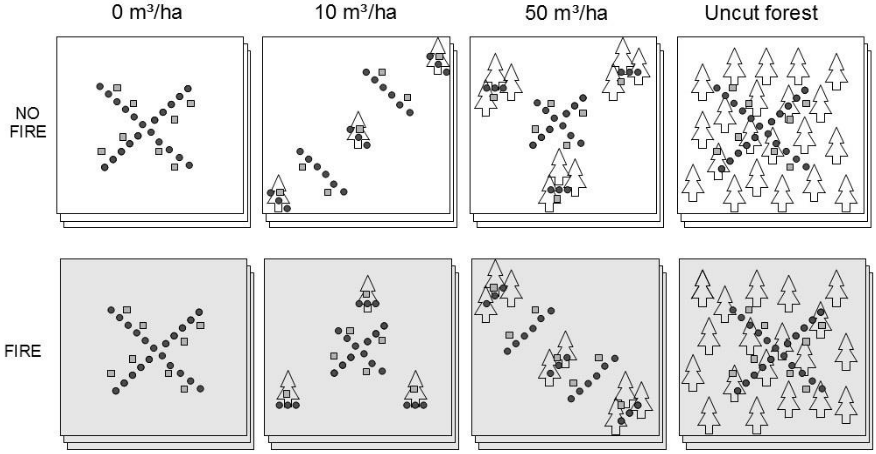


Figure 2. Experimental design and sampling scheme. Grey squares indicate the location of sampling quadrats for vegetation and black dots indicate location of pan traps (schematically).

2.3 Environmental data and analysis

Bee nesting resources were measured on 2013, using the same quadrats for sampling bilberry and lingonberry characteristics: % cover of grasses, % cover of soil litter and % cover of rocks. Data on coarse woody debris (CWD, dead wood with diameter > 10 cm), collected in 2011, was used for calculating CWD diversity index (Siitonen et al. 2000), and the number of CWD logs/ha, with dead wood as important nesting resource for trap-nesting bees (Westerfelt et al. 2016). Nesting and flowering resources were used as predictors for bee abundance, richness, diversity and evenness in ordinary least squares (OLS) models and in generalized linear models (GLM). The effect of flowering and nesting resources on bee species composition was assessed by redundancy analysis (RDA; Borcard et al. 2013). Bilberry and lingonberry percent cover, number of flowers, berry yield and % fruit set were modeled by generalized linear-mixed effect models (GLMM) with fire, retention level, CWD diversity, elevation, and surrounding forest influence (from harvested sites; Baker et al. 2013) as explanatory variables (**I**).

The predictive power of fire and tree retention on bee and hoverfly community composition was assessed by multivariate regression trees (MRT; De'ath 2002). Rarefaction/extrapolation curves based on equal sample completeness were used to compare pollinator species richness among habitats defined by MRT analysis, following procedures in Chao et al. (2014). Partitioning of β diversity within habitats was performed by additive partitioning of regional diversity excess (Tuomisto 2010), and β diversity among habitats was assessed by decomposing dissimilarity in species composition in its turnover and nestedness components (Baselga 2010). Percent cover of herbs, deciduous and coniferous tree regeneration (number of stems/ha, as measured in 2012; Bakker 2014), volume of CWD (m^3/ha), and the % of aquatic habitat within 400 m radius, were added to environmental variables in (**I**) as important habitat requirements for hoverfly larvae (Speight 2017). The relative importance of environmental variables, spatial processes and season in explaining variability in pollinator species composition (β diversity) was assessed by variance partitioning based on partial redundancy analysis (pRDA; Peres-Neto et al. 2006) (**II**).

Data on ground vegetation was sampled on 2011, measuring the percent coverage of all ground living vascular plants (including tree seedlings) per site within 15 plots of 4 m^2 in size (Johnson et al. 2014). Distinctive habitats shaped by disturbance and forest management were characterized by using *k*-means partitioning (Borcard et al. 2013) on vegetation data. Percent cover of charred soil, variation in humus depth (after experimental burning; Laamanen 2002), % of tree retention, % cover of litter, and number of stumps/ha were used as predictors for plant species composition in harvested sites (RDA model) to further validate habitat classification. Parasitoid species richness, distance-based functional diversity (${}^1D(Q)$; Chiu and Chao 2014) and functional dispersion (FDis; Laliberté and Legendre 2010) were compared among habitats and in relation to environmental variables (plant ${}^1D(Q)$, plant FDis, % herbs, % grasses, % shrubs, elevation, deciduous and conifer regeneration, and average number of flowers), by GLM and OLS models. Dissimilarity in parasitoid functional composition was assessed by permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), and association between parasitoid and plant functional composition was evaluated by co-inertia analysis (Dray et al. 2003). The effect of functional heterogeneity on parasitoid functional composition was assessed by redundancy analysis of community weighted mean trait values (CWM-RDA; Kleyer et al. 2012), and individual traits were analyzed by fitting OLS models and general linear models (GLS) for each CWM versus habitat (**III**).

Statistical methods are described in detail in the original articles (**I**, **II** and **III**).

3. MAIN RESULTS AND DISCUSSION

3.1. Contrasting responses of bilberry and lingonberry to prescribed fire and retention level after more than 10 years of treatment application (I).

Bilberry reach its maximum development with much higher cover, flowering and yield in old-growth forest stands, independent of prescribed fire. This pattern is consistent with the negative effects of forest harvesting on bilberry through increased drought and light intensity (Parlane et al. 2006; Miina et al. 2009) (**I**).

Lingonberry shows much higher resistance to harvesting and it is well adapted to drier conditions and higher light levels (Parlane et al. 2006; Turtiainen et al. 2013). Lingonberry cover showed a positive relationship with CWD diversity (Fig. 3a), associated with higher diversity of sites with improved microclimatic environment near dead wood (Lampainen et al. 2004). Lingonberry flowering had a positive relationship with prescribed fire on high retention harvested sites (Fig. 3b). The higher structural heterogeneity in these sites provide shelter and suitable substrate for post-disturbance recovery of lingonberry shrubs (Hautala et al. 2001; Hekkala et al. 2014), while clearings in burned old-growth forests improve lingonberry regeneration and performance. Conversely, the absence of shelter within burned clear-cut sites lowers lingonberry performance greatly (Fig. 3b).

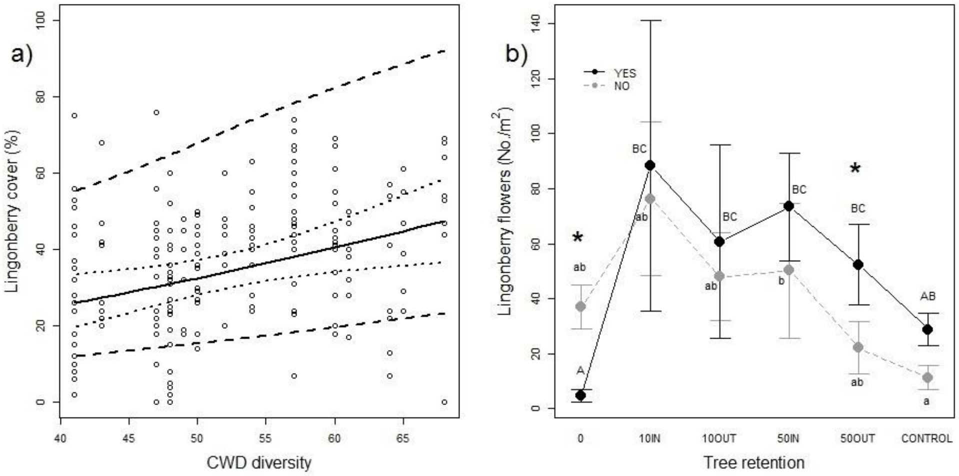


Figure 3. (a) Relationship between CWD diversity and percent cover of lingonberry. Fitted line from the logistic regression model plotted. Dotted lines show ± 2 SE for fixed predictor and dashed lines show the added variation because of random intercept at site level. (b) Lingonberry flowers (average ± SE) as a function of retention level and fire. Unburnt retention levels not connected by the same lowercase letter are significantly different in the model. Burned retention levels not connected by the same uppercase letter are significantly different in the model. Asterisks indicate the presence of significant interaction between fire and retention level. Tree retention labels: 0 (clear-cut), 10IN (10 m^3/ha inside retention patches), 10OUT (10 m^3/ha outside retention patches), 50IN (50 m^3/ha inside retention patches), 50OUT (50 m^3/ha outside retention patches), CONTROL (old-growth uncut forests).

3.2. Biological legacies provide nesting and flowering resources on burned harvested sites with retention (I).

Queen bumblebee abundance during bilberry season is 64% higher (75% higher, considering dominant bumblebee species) on sites with 50 m^3 of retention trees per hectare compared with uncut forests. This situation represents a decoupling of bumblebees from flowering resources, as bilberry flowering is 80% less on high retention sites compared to old-growth forests. This pattern is explained by the higher availability of bumblebee nesting resources provided by increased structural heterogeneity from high retention sites (Løken 1973; Korpela et al. 2015).

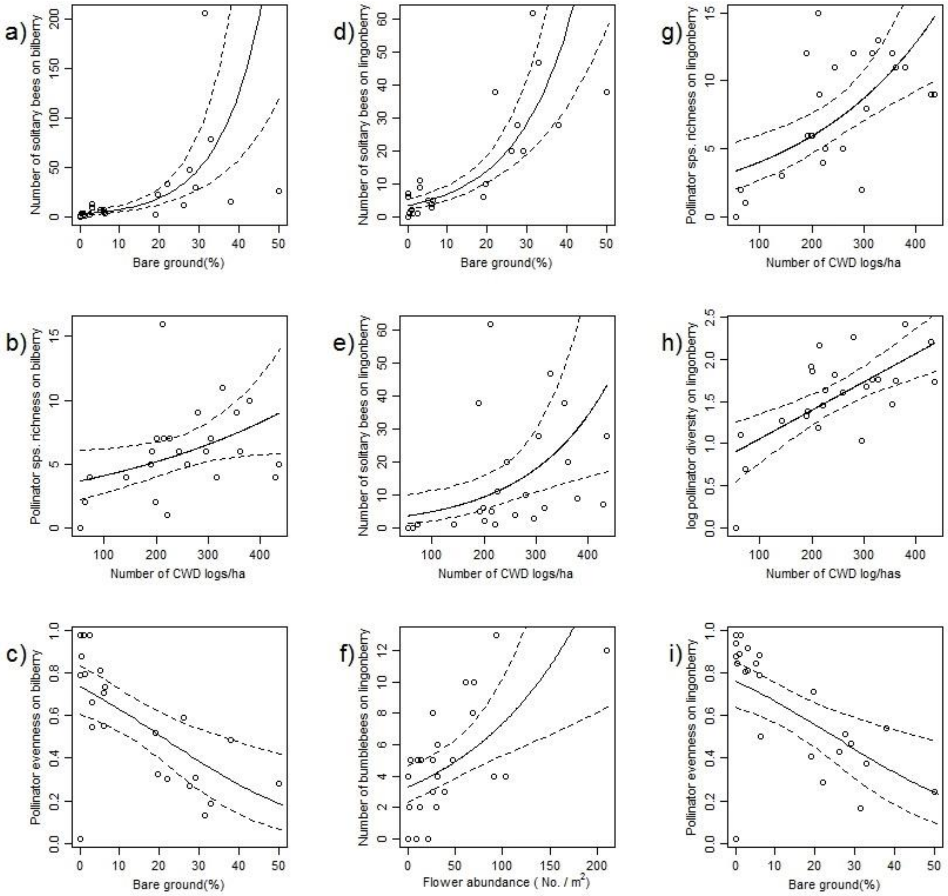
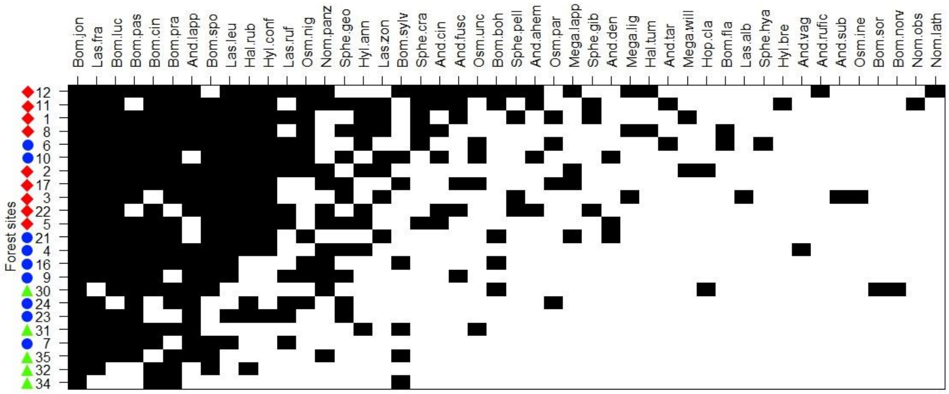


Figure 4. Relationship of pollinator community structure with significant continuous predictors retained in best models. Plots (a-c) for bilberry sampling and plots (d-h) for lingonberry sampling. For simplicity, in plots (b), (d), (e) and (g) the fitted line of the univariate relationships were plotted for the significant predictors retained in the full multivariate model. Dashed lines show ± 2SE.

Bee community composition on bilberry and lingonberry season was mainly determined by biological legacies providing nesting resources in the form of bare ground and CWD logs. Burnt sites had 81% more bare ground than old-growth forests in average, providing an important resource for Andrenid and Halictid ground nesting bees, which become overly dominant in burnt harvested sites (Potts et al. 2005; Campbell et al. 2007; Proctor et al. 2012). Hence, the higher abundance and species richness, coupled with lower pollinator evenness in relation to % bare ground (Figs. 4a, 4c, 4d, 4i). The number of CWD logs was fairly abundant in harvested sites, providing nesting habitat for bumblebees (Korpela et al. 2015) in bilberry season and nesting resource in the form of saproxylic beetle cavities for trap-nesting bees (Sydenham et al. 2016) on lingonberry season (Figs. 4b, 4e, 4g, 4h). Lingonberry season was nest provisioning time for bumblebee workers in harvested sites (Fig. 4f), with bumblebees tracking the most rewarding patches of dominant flowering species (Pengelly and Cartar 2010).

3.3. Pollinator community composition is controlled by structural heterogeneity at multiple spatial and temporal scales (II).

Bee communities along season were structured in three habitats: Burnt harvested forests (BHF), unburnt harvested forests (UHF), and old-growth forests (OGF), with additional effects of temporal turnover in species composition. In turn, hoverflies communities were mainly structured by the turnover of species along time.



N_{rows} = 72.81; $N_{columns}$ = 56.19; NODF = 59.45; $p < 0.001$

Figure 5. Matrix of bee species composition and forest sites showing nested pattern (sites with fewer species contain a subset of the species in more diverse sites). Nestedness was calculated using the nestedness metric based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008). N_{rows} and $N_{columns}$ indicate the average paired nested degree for rows and columns. Black squares within the matrix represent species presence and white squares represent species absence in each forest site. Observed NODF was tested for significance against 999 null matrices generated by the null model described in Patterson and Atmar (1986). Habitat type is indicated by red diamonds (burnt harvested forests), blue filled circles (unburnt harvested forests), and green filled triangles (old-growth forests). Abbreviations for species names are made by taking the three first letters of the generic name, followed by the three first letters of the specific name from the taxonomic list in (**II**).

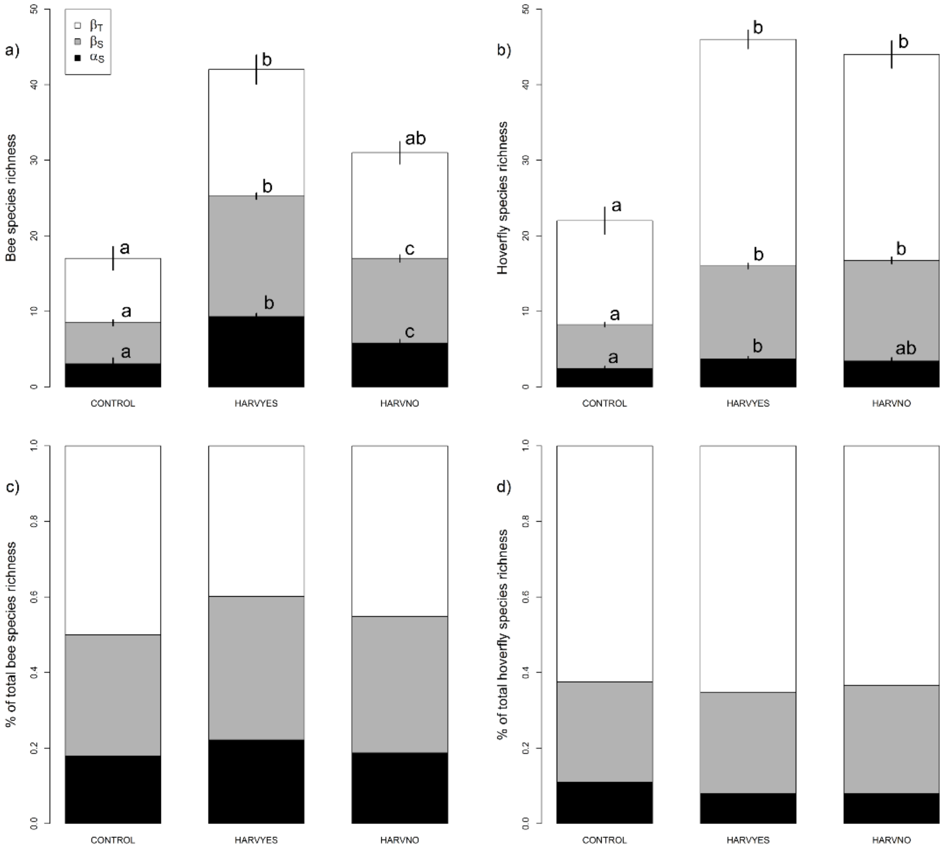


Figure 6. Mean α- and β-diversity values for bee (a) and hoverfly (b) species richness ± SE (among sites and among seasons). Proportion of total (γ) species richness partitioned into α and β components for bees (c) and hoverflies (d). β stands for regional diversity excess, computed among sites (β_S), and among sampling periods (β_T) for each habitat. Hierarchical diversity partitions are shown for old-growth forests (CONTROL), burnt harvested sites (HARVYES) and unburnt harvested sites (HARVNO). Different lowercase letters indicate significant differences between diversity components between each habitat type.

Variation in species composition along the growing season is a feature typical of bees (Oertli et al. 2005; Rollin et al. 2015), and hoverflies (Martínez-Falcón et al. 2011), increasing pollinator β diversity greatly and warning against partial sampling schemes, not covering the whole sampling season (Tylianakis et al. 2005). Spring to early summer communities were dominated by solitary bees (as seen above, in point 3.2), while bumblebees were present during the whole growing season, showing changes in their relative abundance among habitats because of the tracking of flowering resources (Ranta and Vepsäläinen 1981).

Bee and hoverfly species richness were higher on BHF and UHF than in OGF, with no differences in species richness between harvested habitats. Hoverfly β diversity was equally attributed to turnover and nestedness, with bee β diversity pattern among habitats attributed to lower species richness of OGF containing a subset of species from UHF, which in turn are nested in BHF sites (Fig. 5). Within habitats, pollinator diversity was mainly attributed to spatial and temporal β diversity (Fig. 6). Average diversity per site (α), diversity among sites

(β_S), and diversity among sampling seasons (β_T), were all higher for BHF in bee communities (Fig. 6a). Hoverfly diversity was mainly determined by temporal turnover (Fig. 6d), with β_S and β_T higher in harvested sites (Fig. 6b). Most of the variables explaining bee and hoverfly β diversity were spatially structured (% bare ground, number of CWD logs, % grasses, % herbs, amount of edge habitat), following the disturbance gradient. Variation in pollinator community composition was determined by the interaction of spatial and temporal variation, as pollinators use spatially dispersed resources along the growing season, underscoring the importance of disturbance-mediated forest heterogeneity in driving species diversity (Odion and Sarr 2007).

3.4. Conservation of old-growth forests and emulation of natural disturbance dynamics in harvested forests promote parasitoid functional diversity (III).

Diversity of forest management, combining variable retention and prescribed burning in harvested forests with the preservation of old-growth forests, shaped four distinctive habitats based on understory plant composition:

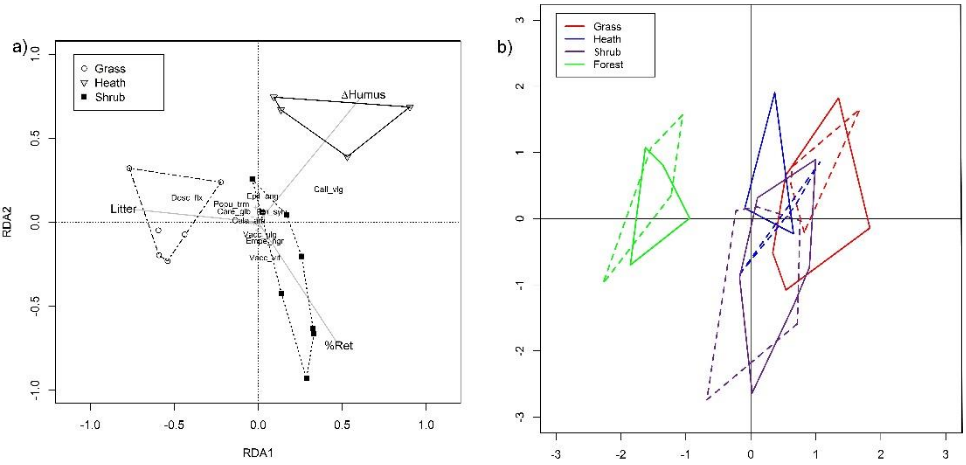


Figure 7. (a) Results of constrained ordination (RDA) showing the relationship of ground vegetation species composition in harvested sites with management related predictors. Each symbol represents one study plot; labeled arrows refer to explanatory variables. For clarity, some species names have been omitted. Labels for explanatory variables are: *Litter*, percent cover of litter; *ΔHumus*, variation in humus depth; *%Ret*, % of tree retention. Labels for species are: Cala_arn, *Calamagrostis arundinacea*; Call_vlg, *Calluna vulgaris*; Car_glb, *Carex globularis*; Desc_flx, *Deschampsia flexuosa*; Empe_ngr, *Empetrum nigrum*; Epil_ang, *Epilobium angustifolium*; Pin_sylv, *Pinus sylvestris*; Popu_trm, *Populus tremula*; Vacc_ulg, *Vaccinium uliginosum*; Vacc_vit, *Vaccinium vitis-idaea*. (b) Overlap of habitats defined by forest management, represented as convex hull overlap for plant traits (dashed line) and parasitoid traits (continuous line) in the new ordination space from co-inertia analysis. Habitat labels: Grass (young grass forests), Heath (young heath forests), Shrub (young dwarf-shrub forests), and Forest (old-growth forests).

a) Mature un-harvested forests dominated by bilberry, b) Early successional forests rich in grass, especially *Deschampsia flexuosa* (L.) Trin., c) Early successional forests rich in heather (*Calluna vulgaris* (L.) Hull), and d) Early successional forests with mixed cover of ericaceous dwarf shrubs, including bilberry, lingonberry, bog whortleberry (*Vaccinium uliginosum* L.) and crowberry (*Empetrum nigrum* L.). Disturbance processes driving this habitat typology are depicted in figure 7a. Grassy habitats were defined by high amount of logging residue, low intensity or absence of burning and very low tree retention, all characteristics giving a competitive advantage to *D. flexuosa* (Foggo 1989; Schimmel and Granström. 1996).

Young heath forest habitats were characterized by low logging residue and high fire intensity, allowing the germination of heather in post-fire calcium-rich soils (Schimmel and Granström 1996; Uotila et al. 2005). Young dwarf-shrub forests were defined by low logging residue, moderate to low fire intensity and moderate to high tree retention, with *Vaccinium* shrubs dominating in burnt sites and *Empetrum* dominating in unburnt sites (Nilsson and Wardle 2005; Uotila et al. 2005).

Increased structural complexity in disturbed sites is expressed by higher plant functional diversity and increased deciduous regeneration, with positive effects on parasitoid species richness and functional diversity, respectively.

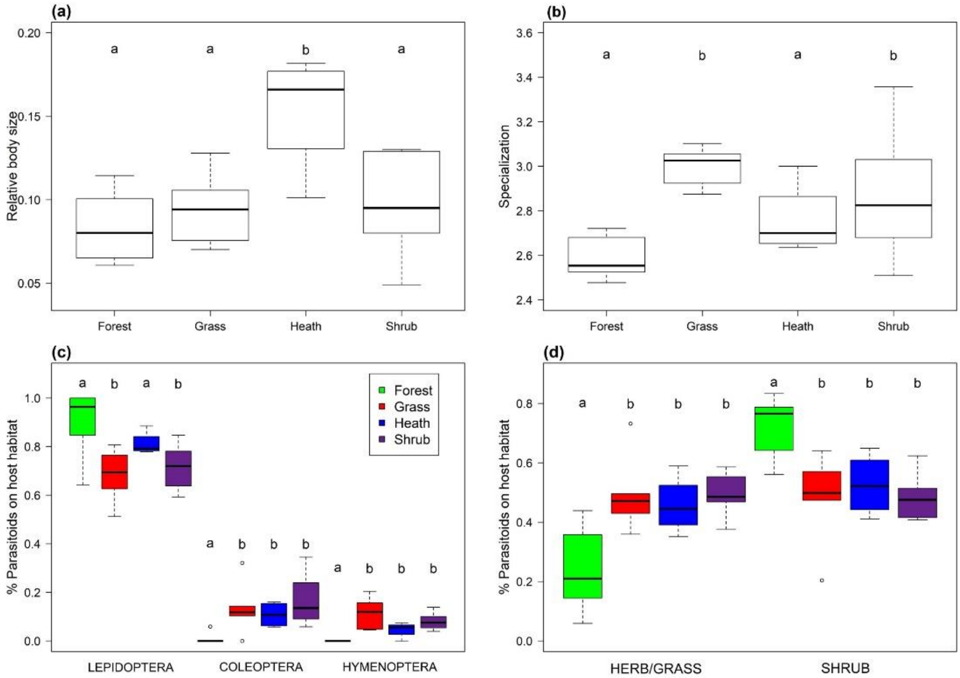


Figure 8. Relationship between community weighted mean trait values (CWM) and habitats defined by forest management: a) Relative body size, b) Specialization, c) % of parasitoids attacking different host orders, d) % of parasitoids on different host micro-habitats. Significant differences indicated by letters relative to old-growth forest as the baseline habitat for comparison with other habitats. Habitat labels as in Fig. 7.

This pattern is consistent with the positive effect of plant diversity on insect host availability mediated by niche diversity (Fenoglio et al. 2012; Staab et al. 2016), and with the rich fauna of suitable insect hosts on birch (Atkinson, 1992), the deciduous tree showing the highest regeneration in early successional forests (Hynynen et al. 2010), especially on young heath and dwarf-shrub forests. The different habitats shaped by disturbance management have distinctive parasitoid functional composition. Moreover, habitats showed congruency in post-disturbance plant-insect functional composition (Fig. 7b), a pattern consistent with earlier findings (Moretti and Legg 2009; Aubin et al. 2013) and theoretical expectations (Gripenberg and Roslin 2007). Parasitoid functional traits get filtered by habitat, increasing parasitoid functional diversity at the landscape scale. Old-growth forests provide a relatively stable environment for Geometrid and Noctuid caterpillars feeding on bilberry (Niemelä et al. 1982; Robinson et al. 2010), which is exploited by generalist tachinid species like *Oswaldia muscaria* (Fallén), attacking caterpillars of both lepidopteran families on shrubs (Tschorsnig 2017). Early successional forests contain more specialized tachinids, attacking a wider diversity of host herbivores, as indicated by higher parasitoid functional diversity in these habitats (Figs. 8b, 8c, 8d). Young heath forests, rich in heather and deciduous regeneration, host an assemblage of large polyphagous caterpillars (Robinson et al. 2010), which makes possible for a higher presence of larger parasitoid flies (Stoepler et al. 2011).

4. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The majority of global forest area, corresponding to multiple-use forests, is nevertheless utilized for maximizing a single ecosystem service, the provision of wood biomass, with harmful consequences for forest biodiversity and sustainable forest management. In these forests, understanding the relationship among multiple ecosystem services, the impact of disturbances on this relationship (Bennett et al. 2009), and the functional ecology of ecosystem service providers (Luck et al. 2009), are fundamental for a sound and sustainable management of multiple ecosystem services. Multiple-use of forests where the production of a single commodity, wood biomass, is emphasized often leads to simplification of forest ecosystems, with negative consequences on biodiversity. Based on this observation, the main objective of this thesis was to assess the effect of functional heterogeneity on biodiversity and selected ecosystem services. Main results from this research underscore the significance of incorporating natural ecosystem dynamics into forest management at large spatial and temporal scales for an effective conservation of biodiversity and multiple ecosystem services in boreal forests. The application of different levels of forest disturbance at the stand-scale aggregates at larger scales, promoting habitat diversity and multiple ecosystem services at the landscape scale.

The conservation of mature forests promotes bilberry yield in managed boreal forests, while cover of lingonberry increases with higher levels of biological legacies in the form of CWD diversity. The combination of prescribed burning and high levels of retention has a strong positive effect on lingonberry flowering in harvested forests, whereas the creation of gaps in old growth forests also increases the number of lingonberry flowers, directly affecting berry yield and population performance of this shrub. Hence, increased heterogeneity at local scale has a positive effect on lingonberry, and the preservation of natural old-growth and early successional forests (increasing heterogeneity at landscape scale), makes for an effective conservation strategy of the multiple ecosystem services related to bilberry and lingonberry in Fennoscandian boreal forests (**I**).

This thesis brings up substantial new knowledge to the prominence of insects as providers of ecosystem services (Schowalter et al. 2018), providing information about the effects of forest disturbance and heterogeneity on the variation in pollinator community structure (**I**, **II**), and on the functional ecology of parasitoids (**III**) in boreal forest ecosystems. This information is key to advance on the conservation of ecosystem services provided by insects (Cardoso et al. 2011). Prescribed fire and retention applied at harvesting provide nesting resources for bees in the form of bare ground and CWD logs, plus flowering resources for all pollinator species along the growing season, when mature and early successional forests are taken into consideration with a landscape perspective. Based on my results, the conservation of pollinators and pollination services require the incorporation of natural disturbance dynamics in multiple-use forests into the conservation planning, instead of relying on static forest reserves alone, which appears as an inadequate strategy for conserving the full array of pollinator services in boreal forests (**I**, **II**).

Large-scale structural heterogeneity caused by variability in tree retention and fire intensity at harvesting, plus the conservation of natural old-growth forests translate into higher variation of plant and parasitoid responses to combined disturbances (Schowalter 2012). Parasitoid functional diversity increases at local scale because of higher structural complexity driven by disturbance, in the form of higher plant functional diversity and higher deciduous regeneration. Habitat diversity generated by old-growth forests and the application of disturbance management further begets functional diversity, through an increase in the range of parasitoid functional traits at the landscape scale (**III**).

In conclusion, this thesis provides strong support to the positive relationship between functional habitat heterogeneity and the provision of ecosystem services (Tylianakis et al. 2008; Brockerhoff et al. 2017), with natural disturbance as the main provider of functional heterogeneity in forest ecosystems (Odion and Sarr 2007). Results emphasize the value of preserving both natural old-growth and early successional boreal forests for the conservation of biodiversity and forest integrity (Kouki et al. 2001; Swanson et al. 2011; Kuuluvainen and Gauthier 2018). The research developed in this thesis points out further hypotheses about the effect of biodiversity on the delivery of ecosystem services (Noriega et al. 2018). In particular, based on my findings, I hypothesize that: (1) Bilberry within mature forests neighboring burned harvested stands with retention benefit from improved pollination, services, reaching higher % fruit set than in mature forests near clear-cuts or young forests; (2) Between-year variation in pollination services on bilberry and lingonberry are stabilized by higher pollinator diversity near burned harvested sites; (3) Higher parasitoid functional diversity on burned harvested forests improves natural biological control of naturally regenerated forest in these stands; and (4) Large-scale parasitoid functional diversity is positively correlated with parasitoid-host interaction diversity and parasitism rate. Finally, my results give guidelines for the implementation of silvicultural practices that mechanistically connect stand-scale and landscape-scale processes in boreal forests. Such development has the potential to bring production forestry closer to multi-functionality (Granath et al. 2018) and quantifiable sustainability targets.

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