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Conservation of Wood-Inhabiting Biodiversity – Semi-Natural Forests as an Opportunity

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Press

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ABSTRACT

Intensive management of forests for timber production reduces the amount and diversity of deadwood, which is an essential substrate for a large part of forest biodiversity. Semi-natural forestry, which is based on natural regeneration and multiple forest values, might provide better opportunities for deadwood inhabiting biodiversity. This thesis describes the habitat value of Estonian forest environments created by semi-natural forestry. I compared functionally important structural features in old-growth and commercially managed forests of five site types, analysed responses of beetles to such habitat qualities, and their possible cascade effects to bird assemblages.

Stand structure as well as biota of *old growth* sites appeared to vary widely at all spatial scales. For example, the volumes of deadwood in the studied hemiboreal forests exceeded published values for south-boreal and north-temperate zones; late-successional deciduous tree species were restricted to certain site types and formed a distinct successional stage on eutrophic sites; beetle assemblages were clearly segregated between dry-boreal pine and spruce-mixedwood forests; and swamps had a distinct bird assemblage.

Deadwood volumes on *clear-cuts* were much higher than reported for the Nordic intensive forestry. Yet, although natural renewal techniques retained large logs, their subsequent decay was accelerated and final felling greatly reduced snag abundance. The mortality of retained live trees improved the supply of standing and downed deadwood to some extent. Clearly impoverished beetle assemblages on cutovers were not detected, even after harvesting half of logging residues. This may also explain why threshold relationships were not detectable for any beetle species separately.

In *mature stands* of the FSC-certified state forests, several structural attributes of biodiversity importance were available similarly to old growth stands. Of these attributes, high tree-species diversity and large amounts of small-diameter dead wood were evidently promoted by natural regeneration and moderate thinning intensities. However, there were large reductions in other structures: very large trees (all species; both live and dead), all late-successional deciduous trees, and logs in late stages of decay. Beetle and bird assemblages in these forests appeared to be smaller, more homogenous subsets of old-forest assemblages.

In conclusion, semi-natural forestry, as applied in accordance with the FSC certification criteria in Estonia, is relatively sustainable in terms of habitat and species diversity, but the lack of certain scarce structures should be specifically addressed in the future.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers, which are referred to in the text with the Roman numerals **I**–**V**:

I Lõhmus, A., Kraut, A. 2010. Stand structure of hemiboreal old-growth forests: characteristic features, variation among site types, and a comparison with FSC-certified mature stands in Estonia. Forest Ecology and Management 260: 155–165. http://doi.org/10.1016/j.foreco.2010.04.018

II Lõhmus, A., Kraut, A., Rosenvald, R. 2013. Dead wood in clearcuts of seminatural forests in Estonia: site-type variation, degradation, and the influences of tree retention and slash harvest. European Journal of Forest Research 132: 335–349. http://doi.org/10.1007/s10342-012-0678-6

III Kraut, A., Liira, J., Lõhmus, A. 2016. Beyond a minimum substrate supply: sustaining saproxylic beetles in semi-natural forest management. Forest Ecology and Management 360: 9–19.
http://doi.org/10.1016/j.foreco.2015.10.016

IV Zolotarjova, V., Kraut, A., Lõhmus, A. 2016. Slash harvesting does not undermine beetle diversity on small clear-cuts containing sufficient legacies. *Under revision in Journal of Insect Conservation*

V Rosenvald, R., Lõhmus, A., Kraut, A., Remm, L. 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. Forest Ecology and Management 262: 1541–1550.
http://doi.org/10.1016/j.foreco.2011.07.002

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The contributions of the authors of the papers were as follows:

	I	**II**	**III**	**IV**	**V**
Original idea	AL	AL, **AK**, RR	**AK**, AL	**AK**, AL,	AL, RR
Study design	AL	AL, **AK**, RR	**AK**, AL	**AK**, VZ	RR
Data collection	**AK**, AL	**AK,** RR, AL	**AK**	VZ, **AK**	RR, **AK**, LR, AL
Data analysis	AL, **AK**	AL, RR	**AK**, JL, AL	**AK**, VZ	RR, **AK**, LR
Manuscript preparation	AL, **AK**	AL, **AK**, RR	**AK**, AL, JL	AL, **AK**, VZ	RR, AL, **AK**, LR

AK – Ann Kraut; AL – Asko Lõhmus; JL – Jaan Liira; LR – Liina Remm; RR – Raul Rosenvald; VZ – Valentina Zolotarjova.

ABBREVIATIONS

CWD – coarse woody debris
DBH – diameter at breast height
DW – deadwood
FWD – fine woody debris
GLM – general linear model
GLZ – generalized linear model
MRPP – multi-response permutation procedure
NMS – non-metric multidimensional scaling

1. INTRODUCTION

1.1. The global forest biodiversity challenge

Forests cover 31% of Earth's land surface (FAO, 2010). A broad distribution implies that forest ecosystems are extremely diverse – along the climatic and soil gradients from tropical to boreal biomes, and due to a diversity of disturbance regimes, successional pathways and evolutionary histories. Such habitat variation supports a vast number of plant, animal, fungal, and microbe taxa globally. Losing forest diversity means – on top of its intrinsic value – also reduced opportunities for human welfare through decreasing supply of necessary goods and ecosystem services (Hassan et al., 2005). Biodiversity conservation has therefore become a major component of many national and international forest-management agreements and networks, such as the United Nations International Arrangement on Forests and the REDD+ (Reducing Emissions from Deforestation and Forest Degradation) programme, Forest Europe, and International Tropical Timber Agreement. The negative environmental impacts of forestry are also addressed through certification, a non-state market driven form of environmental governance, which uses public purchasing power to create shifts in industry (Cashore, 2002).

Loss of forest biodiversity can take place at different scales, which form a continuum from large-scale deforestation to local degradation that only affects certain elements of forest. Clearing of forests to acquire arable land and pasture is currently the main process that reduces global terrestrial biodiversity (Gibbs et al., 2010; FAO, 2012). In addition to direct habitat loss, it exposes the remaining forests to increased edge effects, reduces forest interior areas and connectivity, or even isolates the residual patches. In the last 25 years, the global forest area has declined by 3%, but the decline has concentrated to the tropical forests. Boreal and sub-tropical forest areas have suffered less, while temperate forests have even expanded (FAO, 2015).

At a more local scale, diverse assemblages of forest species depend on the availability and relative abundance of various structural elements (i.e., stand structural complexity), which provide the necessary microhabitats and substrates . There are many studies about such dependencies, although the research is often incomplete, focusing on direct substrate relationships only. Key structural characteristics of biodiversity importance in forests include, for example, tree species composition; canopy cover and foliage arrangement; tree spacing, height and size; understorey vegetation; and deadwood (McElhinny et al., 2005). Collectively, these characteristics can be used as indicators of forest habitat quality (Marchetti, 2004; Liira et al., 2007) and it is obvious that timber extraction and other silvicultural activities can change that quality. In brief, forest habitat value or its supply of ecosystem services can deteriorate even when the tree-covered area persists. In boreal and temperate regions, such structure-mediated impoverishment constitutes the main current threat on forest biodiversity (e.g. Hanski, 2000).

Simplification of tree-species composition and stand structure are well documented for intensive wood-production systems (Esseen et al., 1997; Hanski and Ovaskainen, 2000; Angelstam et al., 2004; Thompson et al., 2013). Such degradation can be slow, accumulating across subsequent tree generations as a result of different forestry practices (e.g., harvesting and thinning operations; intensive stand-renewal techniques; prevention of natural disturbances; deadwood removal for biofuel and for "forest health"). However, some consequences, notably the loss of old-growth characteristics (large old trees and dead trees), can be drastic already in the first generation of managed stands.

1.2. Deadwood as a vulnerable forest habitat

Deadwood (DW) is an integral component of natural cycles of energy, carbon, nutrients and water in forest, and it provides a basis for complex food webs and promotes specific adaptations of organisms. DW amount and characteristics depend on stand productivity, tree species present, decay rates, and disturbances affecting the input rate and stand succession (Harmon et al., 1986). Additional diversity of DW habitats emerges because of the small-scale variation in microclimate, chemical composition, and other inhabiting species that can serve as prey or hosts (Lindhe et al., 2005; Johansson et al., 2007). Decline of specific DW habitats and their variability has a negative impact to forest "health", although it can appear slowly (Sasaki and Putz, 2009).

At stand scale, DW amounts normally constitute 10%–40% of live-tree volume, being lower in tropics and higher in boreal and temperate forests (Jonsson and Siitonen, 2012). Large DW concentrations are created by severe disturbances like storms, snowbreak, fire, flood, epidemics and pest outbreaks. In the course of successional dynamics, DW volume then declines to be lowest in the middle of succession (a typical rotation age in intensive forestry), and then increases to another peak in old-growth forests (Clark et al., 1998; Lee, 1998; Siitonen, 2001).

In timber-production forests, intensive thinnings, clear-cutting, biofuel harvesting, and salvage logging after natural disturbances all reduce DW amount – often as much as by 90% compared to natural levels (Linder and Östlund, 1998; Siitonen, 2001; Uotila et al., 2002). Such reductions inevitably decrease also DW diversity and the connectivity and continuity of DW habitats in space and time (Nordén and Appelqvist, 2001). Especially vulnerable are those DW fractions that take long time to develop or do not emerge until in the late-successional stage of the forest (Rhemtulla et al., 2009). Recurrent harvest entries amplify these effects (Lindenmayer and Franklin, 2002). Substantial reduction of DW poses a threat to *saproxylic species*, i.e. the species dependent on deadwood habitats or other wood-inhabiting species during some stage of their life cycle (Speight, 1989). Saproxylic species make up around 25% of all forest-dwelling species (Siitonen, 2001; Stokland et al., 2004) and, depending on the region, up to 50%–60% of them may be of conservation concern (Schuck et al., 2005). The habitat specificity of saproxylic species varies much, but it may include special requirements regarding the tree species, size, decay stage, moisture and nutrient content, exposure to sun, bark-covered or burned substrates, cavities in the tree, and co-occurring species (prey; hosts; lack of competitors).

Due to its profound importance, the initiatives for sustainable forest management typically include *deadwood amount* among the indicators (Rametsteiner and Mayer, 2004). However, dependence of saproxylic species richness on DW amount is not straightforward. First, the latest research emphasizes the importance of certain qualities of DW instead of total amounts (reviewed by Lassauce et al., 2011) and there is an increasing literature on the modifying influences of the surrounding landscape, geographical region (Müller et al., 2013), and even particular year (Martikainen and Kaila, 2004). Secondly, both theoretical and empirical research suggests that DW-amount impacts are non-linear (Holland et al., 2005; Müller and Bütler, 2010) and can be additionally affected by historical or spatial discontinuities (Jonsson et al., 2005). These effects are related to metapopulation processes (local extinctions and recolonizations), which vary among species. Therefore, the thresholds are unlikely to provide simple conservation guidance, because even systematically close species differ in their requirements (Ranius and Jonsson, 2007).

The question of appropriate level of DW for sustaining forest biodiversity has thus probably a combined answer. Arguments in favour of total-amount guidelines may work when higher volumes are increasingly likely to contain rare fractions and poorly known or poorly detectable biota (Humphrey et al., 2005). Most forestry operations have simultaneous effects on a wide array of structural elements at the same time. On the other hand, some distinct structural elements that are known to host multiple threatened species can (and should) be explicitly considered in forest management. Such structures include, for example, large, old trees that provide essential habitat for a range of taxa through their features like rough bark, sapflows, exposed dead wood, trunk hollows, and large dead branches (Lindenmayer et al., 2012b; Stagoll et al., 2012). Finally, a set of well-detectable deadwood dependent taxa should be directly monitored, which resolves the problem that the assessment of ecological sustainability only uses indirect evidence (Lõhmus et al., 2016).

1.3. The semi-natural forestry approach

Approximately 80% of the world's forest area is neither formally protected nor used as plantations, but aimed at maintaining multiple forest values, including biodiversity (Lindenmayer et al., 2012a; FAO, 2015). The forestry systems on the less intensive end of this management gradient include the concepts of 'near-natural', 'close-to-nature', and 'semi-natural' forestry. These concepts have some regionally different interpretations (FAO, 2005) but they all include the practice of natural regeneration and an intensity gradient defined by other silvicultural decisions (e.g., Duncker et al., 2012). In this thesis, semi-natural forestry is defined based on multiple native tree species and natural regeneration, which can be combined with most silvicultural techniques (including clear-cutting, planting, thinning, and artificial drainage) at various intensities (Lõhmus et al., 2016). The biological legacies retained are generally inversely related to that intensity, except in those rare cases where silviculture (e.g. forest drainage) increases timber production more than is actually harvested afterwards. Such cases may emerge, for example, when harvesting motivations change after the initial investment – at the level of household needs, local and international markets. Under such new circumstances, the abandonment of some planned interventions may prove to be most cost-efficient in the long term (Tikkanen et al., 2012).

Since the second half of the 20th century, Estonian forestry can be considered as semi-natural due to the prevalent use of natural regeneration – 92% of present forest area is primary or modified natural (sensu FAO, 2006); 8% are forests comprising native species, established through planting, seeding or assisted natural regeneration (Raudsaar et al., 2014). At present forests cover 51% of land area, up from ca. 34% in 1939 on account of abandoned agricultural land and wetland drainage (Meikar and Uri, 2000). In the same period, various silvicultural techniques have increased timber volumes in production forests, clear-cutting has replaced selection cutting and, between 1958 and 2010, the average age of forest stands has increased from 41 to 56 years (Adermann, 2012). The principle of sustainable forest management is central to the National Forest Policy since 1997. According to this Pan-European principle, forests should be managed in a way that ensures their biological diversity, productivity, capability for regeneration, vitality and potential at present as well as in the future (Rametsteiner and Mayer, 2004). A supplementary principle of the National Forest Policy says, however, that Estonian forests should be managed economically efficiently, both in the short and long-term perspective. Currently, the main harvesting methods include clear-cutting with green-tree retention, low intensity thinnings and some slash-harvest. Disturbed areas are usually salvage-logged. Fires, historically common especially in dry boreal forests, are suppressed, and pest outbreaks are kept under control. To achieve ecological aims, managed forests are supported by a reserve network, which sets ca. 10% forest land aside from timber harvesting.

Such semi-natural forestry model can be compared with Nordic forestry, which is similarly based on native tree species, but managed at a much higher intensity – routinely including soil preparation, promotion of mainly two conifer species, recurrent thinnings, and slash-harvest including stumps (Esseen et al., 1997; Helmisaari et al., 2014). As a result, substantial reduction in DW volumes and diversity, as well as decline or local extinction of saproxylic species has been recorded in Finnish and Swedish production forests (Siitonen, 2001; Hanski, 2007). For a comparison, it should be taken into account, however, that most Fennoscandian forests belong to the boreal zone, while Estonian forests are hemiboreal. Characteristics of the hemiboreal region include the occurrence of late-successional deciduous trees on fertile soils and higher natural DW volumes, which support additional species compared to boreal forests (Nilsson, 1997). It is poorly known, how these characters, species pools, and the higher tree-growth rates combine with forestry impacts and ecosystem recovery in the hemiboreal zone.

1.4. Aims and objectives of the study

The general aim of my studies was to assess the habitat value of the forest environments created by semi-natural forestry. This general aim was addressed by analysing, in the Estonian hemiboreal forests, (i) the abundance and quality of forest structures that are known to affect the habitat value (notably DW); (ii) actual biodiversity responses – those of beetles to the habitat structures, and its possible cascade effects to bird assemblages. The results were also expected to provide a sustainability assessment for such FSC-certified forestry system. The assessment incorporated two recent modifications of the traditional final felling approach: green-tree retention and biofuel extraction at harvesting.

My first specific objective was to establish a structural 'baseline' for assessing any management-related changes in forest stands. For that, the first representative sampling of old-growth structure in the Baltic countries was carried out – incorporating four site types along the gradients of soil moisture and nutrient content (**I**). The structures addressed are known to be crucial for biodiversity, representative of stand structural complexity, and sensitive to commercial forest management.

My second specific objective was to quantify, based on the same set of structures, the differences of semi-naturally managed forests from the old-growth 'baseline'. This assessment was carried out for two contrasting successional stages: mature commercial stands (ready to harvest; **I**) and recently harvested sites (**II**). Their comparison, in turn, provides an assessment of the final felling. The analyses included a description of the DW pool; major sources of its variation during the first decade after final felling; assessments of DW dynamics including its decay, input from dying retention trees, and removal with slash harvesting (**II**).

The third specific objective was to investigate how the structural changes recorded affect saproxylic beetles both in the mature stands and in the harvested areas. The main question was whether DW-provisioning through the semi-natural approach was sufficient for the habitat quality of wood-inhabiting beetles, or are there other major (stand-scale) factors that contribute and should be addressed by managers. This question was addressed both at the species and at assemblage levels (**III**). A special study was carried out to estimate changes in whole beetle assemblages caused by DW removal by slash harvesting (**IV**). Additionally, the study addressed a possible indirect effect of forest management through the invertebrate food base to bird assemblages. The question was whether these assemblages differ in old growth and mature managed stands and, if so, what are the roles of the food base and stand structure (**V**).

Finally, practical conclusions for planning and implementing commercial management, conservation and restoration practices in semi-natural forestry were drawn.

2. METHODS

2.1. Study area

The research was carried out in mainland Estonia (Fig. 1). The region belongs to the non-oceanic section of the European hemiboreal zone, between coniferous boreal and deciduous north-temperate forest zones (Ahti et al., 1968). The average air temperature is 16.5 ºC in July and –6.5 ºC in February; the annual precipitation is 650–750 mm. The terrain in Estonia is generally flat (only two study sites were situated over 50 m a.s.l.). Estonian forest lands (over 2.2 million ha; 51% of the country) do not contain intensive plantations; thinning intensity is low; and >90% of forest area is naturally regenerated. However, 20% of the forest area is drained and, because of a long history of clear-cutting, old stands are rare (2% exceed 120 years age; Raudsaar et al., 2014).

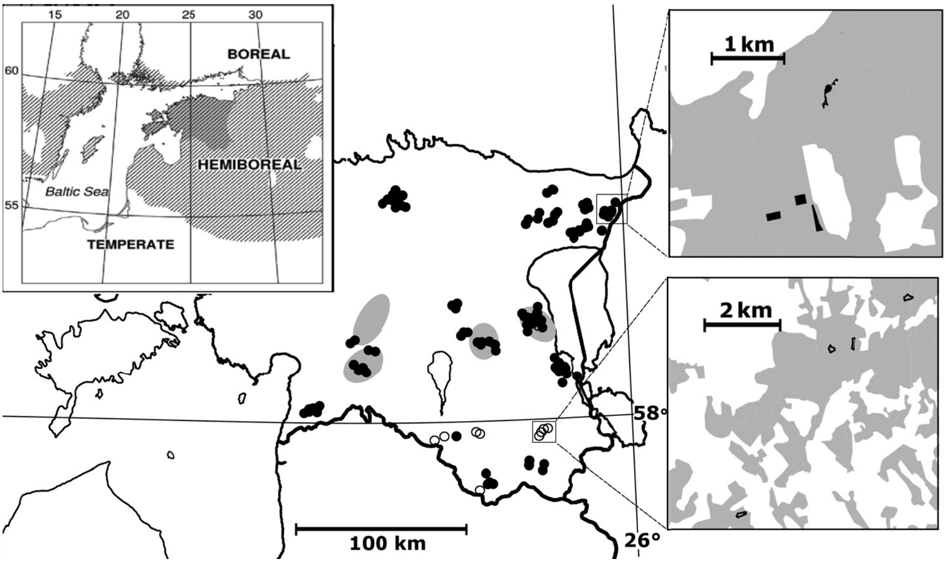

Figure 1. Locations of the study area and study sites (filled circles – basic sample; hollow circles – supplementary retention cuts; grey ovals – areas of 104 retention monitoring sites). The subgraphs on the right exemplify positions on landscape: four management stages of one replicate of eutrophic sites (a); two pairs of supplementary retention cuts (b); forest is depicted with the grey background.

In production forests, typical cut blocks are small (<5 ha) and ca. 5% of growing stock is being left as solitary retention trees since the late 1990s (Rosenvald et al., 2008). Ten percent of all forest area is now strictly protected and 15% is managed for environmental values (Raudsaar et al., 2014); additionally, the state-owned production forests (23%) are managed by the Estonian State Forest Management Centre in compliance with the Forest Stewardship Council (FSC) criteria of sustainable forestry since 2002 (Hain and Ahas, 2007).

The studies were carried out in a total of 232 forest sites. Each site represented a relatively homogeneous forest stand or its harvested area. Site selection was based on three setups:

- a block design of 116 sites (*basic sample*), including both closed-canopy forests (explored in studies **I, III** and **V**) and harvested sites **(II–IV)**, which were a part of a larger biodiversity project comparing forest management options (e.g. Lõhmus and Lõhmus, 2011; Remm and Lõhmus, 2016);
- 104 *retention cuts* (all sites in four forest districts that were harvested in 2001–2002), which were monitored for DW-provisioning from retention trees (**II**);
- a paired design of 12 retention cuts for a study on *slash extraction* **(IV)**.

The study sites included productive forests of five site-type groups (based on Lõhmus, 1984), representing a range of soil and moisture conditions:

(i) Dry boreal forests (mostly *Vaccinium*-type) on higher fluvioglacial landforms and till mounds with Podzols (pH 3.5–5.0), where water rises to the soil surface only sporadically and the top layer is periodically dry. The stands are dominated by Scots pine (*Pinus sylvestris*) (hereafter: pine) and typically yield 250–350 $m^3 ha^{-1}$ timber at felling age. Naturally, these forests would have a fire-driven natural disturbance regime.

(ii) Meso-eutrophic forests (mostly *Oxalis*-type) on till mounds or rolling plains with Podzols or Stagnic Luvisols (pH 3.2–4.2) where ground water is deeper than 2 m. The stands are conifer/deciduous mixtures, which, depending on soil productivity, contain either pine or Norway spruce (*Picea abies*) (hereafter: spruce), and yield timber volumes up to 800 $m^3 ha^{-1}$. These forests are naturally exhibiting successional dynamics after rare wildfires. *Populus tremula* is a characteristic pioneer species and an important retention tree on cutovers (Rosenvald et al., 2008).

(iii) Eutrophic boreo-nemoral forests (mostly *Aegopodium*-type) predominantly on undulating sandy till plains with favourably moist (in springtime anaerobic) Gleyic Gambisols or Luvisols (pH 4.7–6.5) and almost no organic horizon. The stands are typically mixtures of deciduous trees and spruce, which yield up to 700 $m^3 ha^{-1}$ and develop naturally through gap-phase dynamics.

(iv) Mobile-water swamp forests in lowlands and valleys along rivers or around bogs. Their thin Eutric Histosols and Fluvisols (pH 5.0–6.5) are flooded; the water level sinks 20–40 cm below ground only during longer drought periods. This study focused on sites on thinner peat, where the black alder (*Alnus glutinosa*) characteristically forms alder carrs; birch (*Betula pubescens*) dominates in case of thicker peat horizons and stagnant water. Typical stock volumes are 150–200 $m^3 ha^{-1}$.

(v) Artificially drained swamp forests (*Oxalis*-type), which represent long-term drainage effects (Lõhmus et al., 2015) and can be considered transitional from site-type group (iv) to (ii).

In the basic sample of 116 sites, four management stages (an old-growth stand; a mature managed stand; a retention cut; a clear-cut) were sampled in a factorial (block) design across all five forest site-type groups. Each factorial "block" (actually a cluster of available stands of matched site conditions within shortest possible distance; see Fig. 1) was replicated in five (swamps) or six landscapes (the other site types), resulting in a total of 29 blocks.

Among closed-canopy forests, the currently dominant live storey in most *old-growth stands* was 120–180 years old (>150 years in pine stands) but, typically, these forests were apparently (and some are well documented to be) much older. According to their classification on the Russian military maps from the 1850s, all but two stands certainly were long established forests. Most of the old-growth stands are strictly protected nowadays. For the current study, stands were considered "old growth enough" if they had no or minimal signs of previous management. Because of the rarity of such stands, the number of replicates was five (instead of six) in the swamp type. The *mature stands* were 60–100 years old, previously thinned, salvage-logged or subject to other management practices, and ready for final felling.

The cutovers included clear-cuts without trees retained and retention cuts with solitary retention trees. All the stands had been previously managed for timber production. In the basic sample, the *clear-cut* sites were studied on average eight (range 4–16) years after harvest. Soil scarification had been practiced in four dry-boreal cutovers. The *retention cut* sites were sampled on average five (range 2–13) years after harvest. The retention cuts had on average 20 m^3 ha^{-1} (range 2–69 m^3 ha^{-1}) of live retention trees at the time of sampling.

The 104 additional retention cuts monitored for the DW-provisioning study (**II**) represented a range of site conditions according to their availability in the surveyed districts. According to preharvest composition, deciduous-dominated eutrophic boreo-nemoral or pine- or spruce-dominated meso-eutrophic forests dominated among these sites. The 12 retention cut sites for the slash extraction study were organised as six site pairs of one conventionally harvested and one slash harvest site of the same site-type group (types i–iii above) and similar age (2–4 years after harvest). The final felling had been performed with a harvester; slash had been collected directly after that by forwarder operators, who determined on-site the amount of slash that was economically worth extracting.

2.2. Stand structure inventory

In each plot, we used a combination of area-based methods for estimating the densities and volumes of standing trees and the line-intersect method for volumes of downed DW. Prior to the fieldwork, we delineated a 2-ha study plot and, within each study plot, four 50-m straight sampling lines according to a standard protocol (**I:** Fig.2). In the structurally poor dry boreal forests, we added a fifth transect in order to increase the sample sizes (precision). Each transect line was marked in the field using a 50-m tape. Large structures were recorded along the whole 50-m distance: (a) live trees of ≥10 cm diameter at breast height (DBH) – within 2 m to both sides of the line; (b) standing dead trees ≥1.0 m tall and of DBH (or top diameter) ≥10 cm, as well as (c) tip-up mounds of uprooted trees, elevated ≥30 cm – within 5 m to both sides of the line; (d) downed DW of ≥10 cm diameter at intersections with the line. Small structures were recorded at six 1-m sections established at 10-m intervals: (e) low stumps and thin standing dead trees (at least 1.0 m tall), as well as (f) live seedlings and saplings (DBH <10 cm) of forest trees only – in 1 m × 1 m square plots established at one side of the line; (g) downed DW of 0.3–9.9 cm in diameter (FWD) at the intersection with the line. Hereafter, category (d) is termed 'logs'; categories (b) and (d) are collectively called '*coarse woody debris*' (CWD). Downed DW also included exposed dead roots; any woody material buried in litter or moss carpet or under water in flooded forests; as well as dead lower branches of live trees up to 2 m height. Whenever present, the diameter measurements included bark. The decay-stage classification of CWD mostly follows Renvall (1995), while that of FWD was specifically elaborated for this study following the logic of CWD classifications (**I**: Table 1).

For the retention-tree monitoring part of study **II**, all live trees and snags >1.5 m tall and with a DBH ≥14 cm were mapped in the field, and their species, diameter, height of snags, and condition were recorded. During 9–10 years, each tree was annually described in terms of its survival, cause of death, and type of damage if present.

2.3. Insect and bird surveys

The aim of the **insect** sampling was to assess the assemblage composition (**III–IV**), the supply of invertebrate prey for birds (**V**) or to establish the presence of particular beetle species at the site scale (**III**). In each site, insects were caught with two flight-intercept traps (four on slash-harvest study sites; 256 in total) consisting of two transparent plastic sheets (25×40 cm) attached vertically on top of a yellow plastic funnel with conserving solution. The traps were attached on trees or high stumps at breast height on sun-exposed side, 40–100 m from each other, and at least 20 m from stand edge. Traps were emptied monthly from May until the end of September, considering material collected on 1 June as early-summer and on 29 August as late-summer assemblage. Natural-type sites (i–iv above) were sampled in 2005 and 2006, drained forests (v) in 2009, and the 12 additional retention cuts in 2010. Additionally, for study **III**, in each of the 116 basic sites, ten-litre logs from each tree species found in the stand were collected in two springs between 2005 and 2009. The logs (1025 in total) were kept at room conditions for at least 18 months in cardboard boxes equipped with photoeclectors.

For assessing the supply of invertebrate prey (**V**) all the 83,619 arthropods captured from the basic-sample sites were classified as Hymenoptera, Coleoptera, Diptera, Lepidoptera, "other insects", or Arachnida; and further pooled into broad "palatability" classes for birds: "hard" (Hymenoptera + Coleoptera) and "soft". All individuals were assigned a size-class from 1 mm^3 to >800 mm^3 for calculating a biomass index.

For study **IV**, we identified most specimens ≥1.5 mm in length (11,948 in total), except for specimens from 3 hard-to-determine families and 14 genera. For study **III**, we first defined a set of 199 saproxylic species of potential interest (hereafter: target species) considering their identification ease and ecological diversity, and including four complete families for higher-order taxonomic representativeness (**III:** Fig. 2) We distinguished species of conservation concern (SPEC) according to the Estonian, Latvian, Finnish and Swedish Red Lists (Near Threatened or higher category) and the Estonian list of key habitat indicators (Palo, 2010). The list of putative forest pests is based on Laas et al. (2011).

Birds were surveyed on in one year between 2005 and 2009 by experienced ornithologists, who slowly walked through the stand, so that no part remained >50 m away. Each site-pair was first visited between 10 and 20 May and again between 25 May and 10 June in good weather mornings, and additionally most sites in the evenings. In the field, the position of singing males, nests or any other observations referring to nesting were recorded on a topographic map. The abundance was determined as the maximum count plus probable or confirmed nestings. To assess the amount of calcium available for birds, we estimated the relative shell mass of snails from 50 stands (five site-pairs from each site-type group). **Snails** (11,004 individuals in total) were searched from haphazardly hand-collected and sieved 1.5 l topsoil and litter samples, and also searched visually. The total weight of shells in the sample was calculated using the mean shell mass of adults and juveniles of each species.

2.4. Data processing

For forest structural analyses, the volumes and surface areas of the trunks of live trees, dead trees and snags were estimated according to species-specific diameter functions (Padari, 2004). The volume of downed DW was estimated assuming circular cross-sections (Warren and Olsen, 1964; Van Wagner, 1968). For the main types of structural elements, Shannon indices of species diversity were calculated based on the proportions of the number of items (live trees; standing DW; seedlings and saplings) or of volumes (downed DW). *Betula* spp. and *Salix* spp. were treated at the generic level. The volume of stumps was calculated with the formula of a cylinder.

In study **I**, the structural differences between old growth and mature stands were established using either (1) General Linear Models (GLMs) that incorporated the site type (a factor variable), the treatment (a repeated measure) and their interaction; or (2) in the case of non-normal distributions – using Wilcoxon's matched pairs test (supplemented with a separate Kruskal-Wallis ANOVA for the site-type effects). Significant effects were quantified by calculating the mean percentage of structures ("survival") in mature stands compared to old growth.

In study sections **IIa** and **IIb**, we estimated annual reductions of retained DW volumes in three site categories. We used GLMs comprising the cutover age and the region as a random factor. Because we lacked cutovers of <2 years age, we predicted post-harvest volumes (year 0) from these models. In similar GLM analyses, we also estimated the influence of post-harvest time on other deadwood quality characteristics. We compared the DW volumes in slash harvest sites both with those in the control cutovers of the paired design, and with the mean values that incorporated the basic sample.

In study **IIc** (retention-tree monitoring), we calculated annual volume changes of retained snags and new snags (created by the death of live retention trees); we also estimated the amounts of logs created by falling of the retention trees. We also performed an assessment of the bark and wood microhabitats in snags, which was based on field estimates of bark cover.

In study **III**, we searched for the most parsimonious set of substrate and habitat characteristics for explaining the occurrence of selected beetle species. The criteria of species selection were the known substrate specificity and sufficient representation in the samples (see **III**: Fig. 2). The species that were confined to certain site-types or management stage were additionally analysed considering such sites only. We used Generalized Linear Model (GLZ) analysis of incidence data for all species and, additionally (notably for the exploration of the shape of the substrate effect) – GLM analyses with log-transformed abundance data. The procedure included the following steps:

- omitting the site-types or management stages where the species had <10% of occurrences;
- testing for general habitat-preference (site-type; management stage; their interaction). When old growth vs. mature forests, or retention cuts vs. clear-cuts, did not differ significantly, we pooled these as "closed-canopy forests" or "harvested sites", respectively;
- building a model that related the species occurrence with the amount of its main substrate (as defined in the literature), and checking for additional effects of site-type or management type;
- testing for alternative model solutions by broadening the substrate set (e.g., all deciduous wood instead of aspen wood only) or restricting it (e.g., pine and spruce separately instead of conifers pooled);
- identifying collective patterns emerging in the best descriptive models across species.

In studies **III–IV**, we used ANOVA designs to test for treatment (resp. management stage) effects on the total abundance and species richness of analysed beetles. Site conditions were addressed by including site-type (**III**) or by a paired control-treatment design (**IV**). The treatment effects on assemblage composition were tested with multiresponse permutation procedures (MRPP) and the main compositional gradients were visualised using non-metric multidimensional scaling (NMS).

Similar procedures (GLM/ANOVA; MRPP; NMS) were used for analysing the effects of stand characteristics on avian communities and their subsets (hole-nesters; woodpeckers; **V**). In GLM analyses, we used the parameters describing the food supply (i.e., invertebrate abundance), stand structure, and landscape diversity with 'region' as a random factor. To extract significant models, we built a multivariate model with all potentially important variables according to previous univariate analyses, and then omitted non-significant variables. Last, we checked whether the site-type and management type explained additional variation if added to these models. We used the Indicator Species Analysis (Dufrene and Legendre, 1997) to define 'old-growth specific species' by broad site-type categories.

GLM and GLZ were performed in Statistica (versions 7.1 and 9.1, StatSoft Inc); NMS, MRPP and the Indicator Species Analyses were performed in PC-ORD (ver.6.07; McCune and Mefford, 2011).

3. RESULTS

3.1. Structures of biodiversity importance in old growth vs. managed stands (I) and cutovers (II)

In **old-growth forests** the volume of live trees ranged from 272±88 $m^3 ha^{-1}$ in mobile-water swamps to 473±135 $m^3 ha^{-1}$ in meso-eutrophic sites. On fertile soils (notably in eutrophic boreo-nemoral forests and the swamps), 91% of deciduous trees other than birch, aspen and black alder were of late-successional species – mainly *Tilia cordata*, *Fraxinus excelsior*, *Acer platanoides* and *Ulmus spp*. In these forests, CWD formed >50% of the live-tree volumes; that share was 32% in meso-eutrophic and only 9% in dry boreal sites. Natural regeneration was abundant in mixed-forest types (15,300–17,800 seedlings and saplings ha^{-1}), but five times scarcer in dry boreal stands.

Total CWD volumes exceeded 200 $m^3 ha^{-1}$ in six old-growth stands (**I**: Appendix 1); the average was 129 $m^3 ha^{-1}$. The total volume of standing dead trees was on average 23 – 55 $m^3 ha^{-1}$, but only 3% of those reached at least 50 cm DBH. Logs averaged from 14±12 $m^3 ha^{-1}$ in dry boreal to 143±29 $m^3 ha^{-1}$ in eutrophic boreo-nemoral stands (Fig. 2); the ≥40 cm diameter fraction was absent in dry boreal sites, but formed 18–33% of logs in other site-types. The share of well-decayed logs (stages IV and V) was 25%–37%. Uprooted trees (with tip-up mounds) had a density gradient from 2.0±4.9 ha^{-1} in dry boreal to 47.4±44.6 ha^{-1} in the swamps.

Compared to old growth, the **mature managed stands** had similar volume of live trees but significantly higher tree densities due to abundant medium-sized trees. However, late-successional deciduous trees were about three times less abundant than in old growth, and the differences were even larger for logs and large live trees (Table 1). Management generally reduced diameter variation, but not species diversity, both in live and dead trees. Very large (DBH ≥50 cm) live trees were seven times less abundant than in old growth; standing dead trees – four times in terms of volume (densities did not differ); total volume of CWD (41 $m^3 ha^{-1}$ on average) – three times, both in absolute terms and relative to live-tree volume. Logs ≥20 cm in diameter were increasingly affected by treatment (Fig. 3), particularly in eutrophic boreo-nemoral and swamp forests. DW of smaller diameter was well represented in mature managed forests.

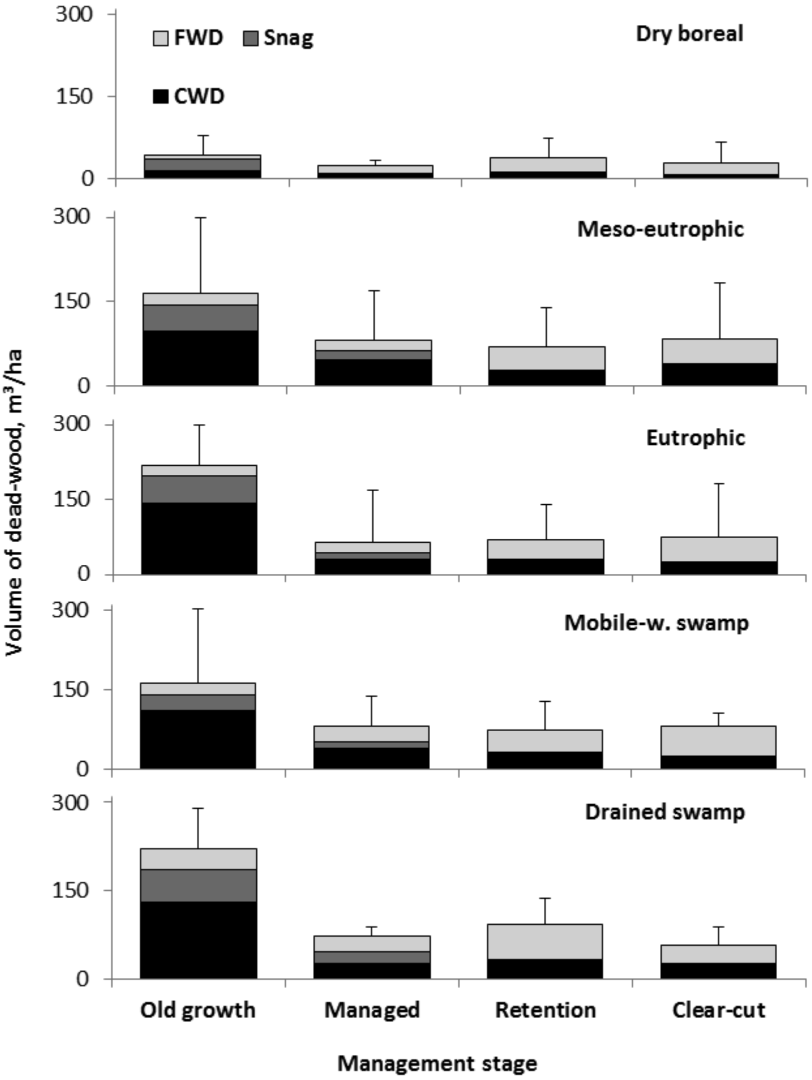

Figure 2. Mean deadwood volumes and their division by fractions (diameters: FWD 0.3–9.9 cm; CWD and snags ≥10 cm) in the 128 study sites by site type and management stage.

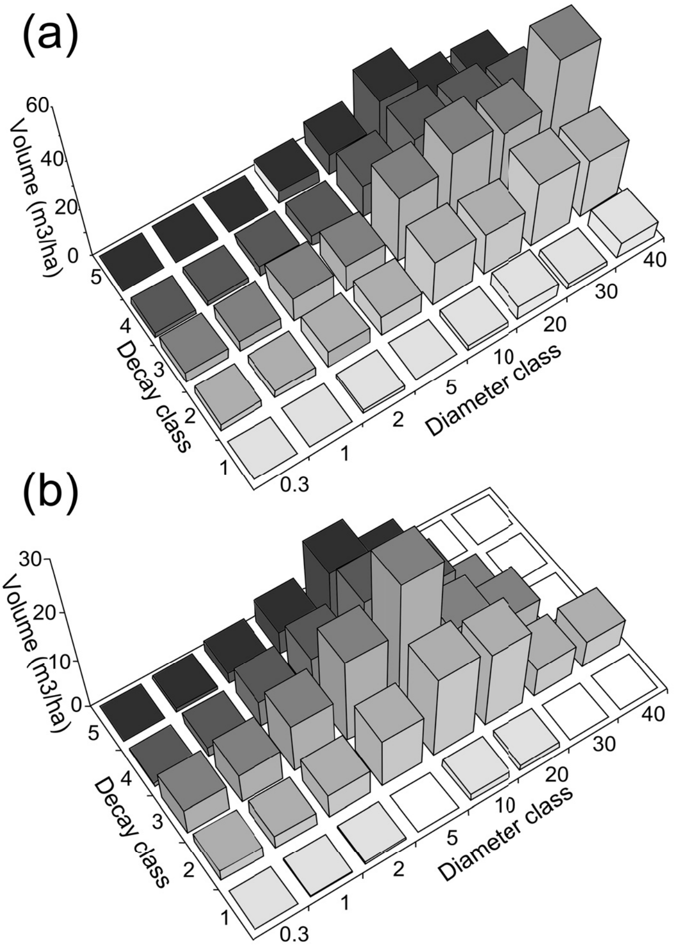

Figure 3. The average volume of downed deadwood by diameter and decay class in (a) old-growth and (b) mature managed stands across site types in Estonia (**I**).

Table 1. Mean % survived structural elements in the studied mature stands as compared with old-growth stands (**I**).

Structural element[a]	Unit[b]	Mean % survived [c]				
		Total	i	ii	iii	iv
Live trees						
Live late-successional deciduous trees [d], DBH ≥30 cm	D	5			6	
Live trees, DBH ≥ 50 cm	D	14		19	11	
Live late-successional deciduous trees [d]	D	33		0	41	42
Live trees, DBH 40...49.9 cm	D	44	26	65	47	46
Live trees, DBH 20...29.9 cm	D	204	178	182	298	199
Live birches	D	320	126	205	967	288
Live aspens	D	437		533	500	209
Deadwood						
Standing dead trees, DBH ≥ 50 cm	V	0		0		0
Logs, d ≥ 40 cm	V	2		0	0	
Logs, d ≥ 30 cm, DS III–V	V	6		9	4	11
Logs, d ≥ 30 cm	V	9		9	3	22
Logs of late-successional deciduous trees [d]	V	22			25	
Standing dead trees	V	27	9	30	26	38
Logs, DS III–V	V	32	53	43	22	34
Logs	V	34	57	49	21	38
Uprooted trees	D	49		43	54	49
Seedlings and saplings, h ≥ 1.3 m	D	38	60	30	24	63

[a] d – diameter, DBH – diameter at breast height, DS – decay stage
[b] V – volume, D – density
[c] site types: i – dry boreal; ii – meso-eutrophic; iii – eutrophic boreo-nemoral; iv – swamp
[d] *Acer platanoides*, *Fraxinus excelsior*, *Ulmus* spp., *Tilia cordata*

After **final felling**, the average estimated volumes of above-ground DW ranged from 70 $m^3 ha^{-1}$ in dry pine forests (including 58 $m^3 ha^{-1}$ downed DW) to 103–119 $m^3 ha^{-1}$ (86–96 $m^3 ha^{-1}$) in the other site types (Fig. 2; **II**). Compared with the volumes in mature managed forests, the (apparently felling-related) increase of the proportion of the finest downed DW fractions (<5 cm in diameter) was largest in dry pine forests and smallest in eutrophic forests. During the first post-felling decade, the composition of CWD (29%–56% of downed DW volume) shifted to a significantly more decayed stage than the FWD, with the only input being, on average, 5 $m^3 ha^{-1}$ from fallen retention trees (4% of the total volume of logs at the time of the surveys). Cut stumps formed largest share of standing DW items and volume (mean above-ground volumes ca. 14–20 $m^3 ha^{-1}$ in mixed forests, but only 8 $m^3 ha^{-1}$ in dry forests), while snags over 1.5 m tall only formed 9.6% of the volume. Monitoring of retained snags showed that only 37% deciduous snags and 54% coniferous snags were still standing after the first decade, but the total number of deciduous snags increased along with the death of retention trees (Fig. 4).

Slash harvesting from final-felling sites decreased the volumes of FWD and CWD roughly by half (**II**: Table 4), resulting in CWD levels lower than in mature commercial stands. However, slash harvesting decreased the share of FWD buried under litter.

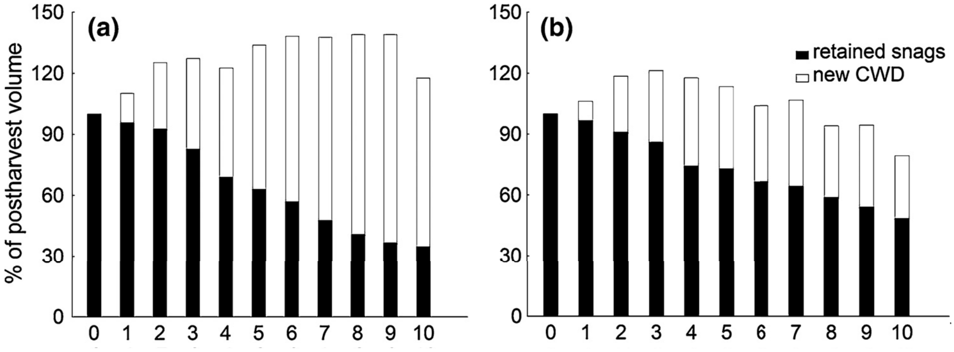

Figure 4. Development of relative post-harvest volumes of deciduous (a) and conifer snags (b). The snags retained at harvest (100% at harvest time) and the inputs from retained live trees (new CWD) are distinguished (**II**).

3.2. Habitat associations of beetles (III–IV)

Significant habitat relationships were detected for 21 of 34 saproxylic beetle species modelled (**III**: Table 1). Substrate amount had a positive effect on 12 species, but the fractions included were rather broad (mostly downed FWD or CWD of dominant tree species, or all deciduous or coniferous DW combined). In most substrate-containing models no other factor appeared significant. Forest management stage was a major factor for 25 species. Three of them were confined to closed-canopy forests; the rest occurred only or preferably in harvested sites, notably in retention cuts. Among site-type effects, dry boreal sites were distinctly preferred or avoided compared with others. Among ten significant multifactor responses detected, five species showed an association with harvested sites of the dry boreal type.

In saproxylic-beetle assemblages, total abundance explained 42% of variation in species richness (GLM: $F_{1,107}$=78.1, p<0.001), and management stage explained further 12% ($F_{3,107}$=4.8, p=0.004; Fig. 5). The contribution of forest type was marginal. Post-hoc tests showed that retention cuts were dramatically more diverse than clear-cuts (Tukey test: p=0.0001; the effect was not attributable to age or DW-amount differences), but old-growth and managed stands differed only marginally. The assemblage composition, with all site-types pooled, also differed between retention cuts and clear-cuts as well as from mature or old-growth stands (MRPP tests: A=0.03…0.07; p<0.001). Thirteen percent of target species favoured old growth, but in general, the beetle assemblages in old growth resembled those in mature commercial forest. Within management stage, the site-types (ii)–(v) appeared relatively uniform but different from dry boreal (Fig. 6a). The artificial drained-swamp type hosted a mix of beetle species of intact swamps as well as those typical of meso-eutrophic sites.

The flight-intercept trapping in the slash harvesting study (**IV**) yielded a total of 11,948 beetle specimens and 500 identified species, among them 253 saproxylic species (**IV**: Table 1). Importantly, species of conservation concern (11% of species, 3.8% of individuals) occurred regularly both in conventional and slash-harvesting sites, outnumbering putative ‘forest pest’ species (18 species; ca. 3% of individuals in both treatments). No significant influences of slash extraction on total species richness or abundance or on the number of pest or conservation-concern species were detected. Major gradients in the beetle assemblage composition (Fig. 6b) were the trapping season (MRPP test: A=0.40, p<0.001) and site type (A=0.13, p=0.013); the latter effect included co-variation with tree-species composition and deadwood volumes. Late-summer assemblages were not only distinct from early-summer assemblages, but they were also less similar across sites.

3.3. Structural vs. food-base mediated management impacts on birds (V)

In total, 62 bird species were recorded in old growth and mature managed stands, including five species of woodpeckers and 15 species of other hole-nesters. According to repeated-measures ANOVAs (**V**: Table 1) total density, density of hole-nesters and bird species richness were all higher in old growth, and distinctly low in dry boreal forests. Across site types, bird species diversity (Shannon index) was also significantly greater in old-growth compared to mature forests (t_5=–4.9, p=0.008). However, the only significant differences in the invertebrate prey base of birds were a higher abundance of “soft” arthropods in managed stands and a smaller snail shell mass in dry boreal than in other site types. The latter impact partly explained also the bird scarcity in dry boreal sites. Other environmental parameters explaining bird-community characteristics always included a positive effect of CWD, while arthropod abundance was never significant.

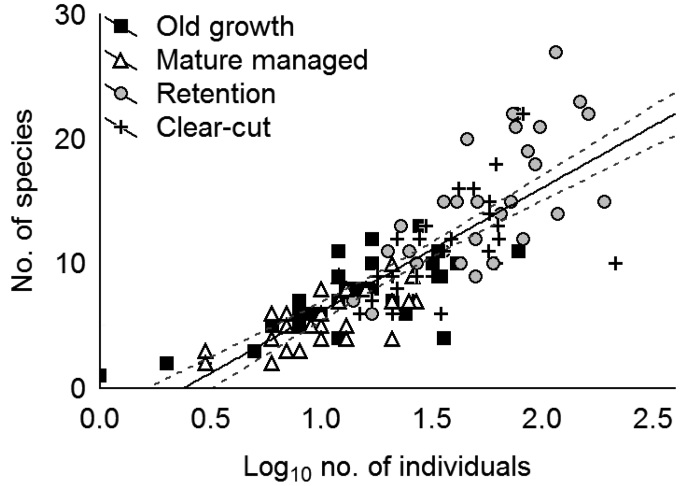

Figure 5. Regression between the numbers of beetle individuals (log-transformed) and all targeted species (n=116 sites). The four management stages have been distinguished by symbols; dashed lines are 95% confidence intervals (**III**).

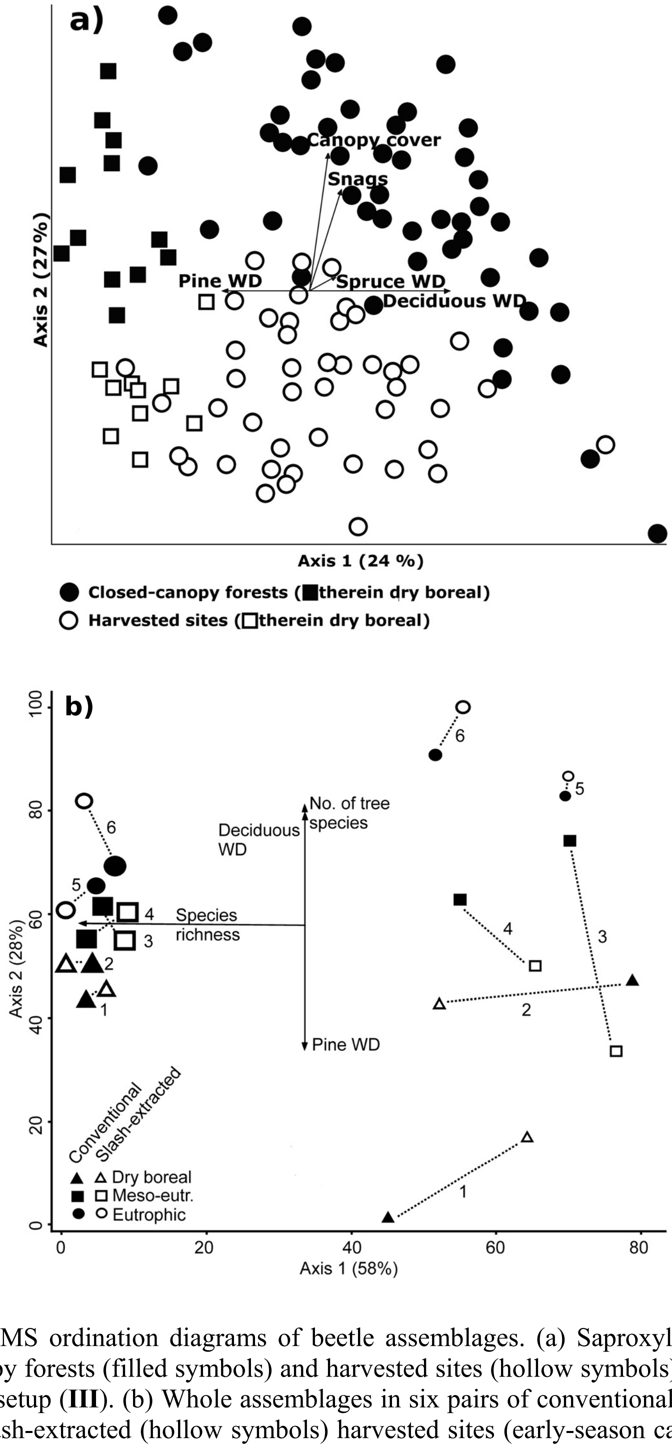

Figure 6. NMS ordination diagrams of beetle assemblages. (a) Saproxylic beetles in closed-canopy forests (filled symbols) and harvested sites (hollow symbols) in 116 sites of the basic setup (**III**). (b) Whole assemblages in six pairs of conventional (filled symbols) and slash-extracted (hollow symbols) harvested sites (early-season catches on the left, late-season catches on the right; site-pairs indicated with numbers, symbol size depicting species richness) (**IV**). The arrows on both graphs refer to the main environmental correlates (WD – downed deadwood).

4. DISCUSSION

4.1. The old-growth 'baseline'

A general conclusion, based on studies **I, III** and **V**, is that the stand structure as well as biota of old growth varies widely at all spatial scales. Such variation must be documented and taken into account, when old-growth characteristics are used for setting targets in forest conservation, restoration and management (White and Walker, 1997; Angelstam et al., 2004; Villard and Jonsson, 2009). For example, the volumes of CWD measured in Estonian mixed forests exceeded significantly the values reported for comparable south-boreal forests (Siitonen, 2001) and north-temperate forests in Europe (Hahn and Christensen, 2004). The possible reasons are related to a specific balance between primary production and decay rates (**I**). Such geographical patterns have not been possible to detect from the few local studies performed before (e.g., Kasesalu, 2001; Köster et al., 2005) or from the official statistics, which do not distinguish different forest ecosystems. Additionally, the official DW estimates for Estonia (e.g., 15 m^3 ha^{-1} average on the 'forest land'; Raudsaar et al., 2014), are apparent underestimates in terms of biodiversity since they document only a vague fraction of "economically usable" wood. Unfortunately, similar methodological bias can be also suspected in historically published research (Eräjää et al., 2010).

At landscape scale, forest structure and species communities varied notably along with site-type gradients. While beetles most clearly segregated between dry-boreal pine forests and spruce-mixedwood (**III**), distinct bird assemblages were also found in the swamp type (**V**). High site-type specificity in old forests (and its loss with the transformation of the forest into timber-production stands) has been previously recorded for Estonian bryophyte assemblages (Vellak and Ingerpuu, 2005). Although study **I** also found that structural differences between old growth and managed forests were smallest in the dry boreal site-type, this is probably an artifact: the seemingly natural dry-boreal stands probably remain impoverished by historical management. Such pine forests are generally well accessible and have highly valued wood (including fuelwood), while their recovery may be relatively slow.

At the scale of habitat complex, stand structure varies considerably between old growth sites of even the same site-type (**I**). The likely reasons include soil heterogeneity and stochastic appearance of a wide array of old-growth specific structures. The study confirmed that, in conservation planning, particular attention should be paid on the following structural elements, which require long time to develop: (1) trees of late-successional species; (2) ancient and very large live trees and snags; (3) well-decayed large downed trunks (see also Nilsson et al., 2001; Lindenmayer et al., 2012b; Aerts, 2013). In Estonia, only one late-successional species (Norway spruce) is common in production forests, due to its planting for timber. In contrast, late-successional deciduous trees are largely restricted to old-growth forests of eutrophic boreo-nemoral and swamp types, and may form distinct, rare ecosystems. Thus, study **I** suggested the existence of a three-staged succession in hemiboreal eutrophic forests (cf. similar pathways in North America; Pastor and Mladenoff, 1992), where a known 'late successional' spruce-phase is further followed by a phase dominated by *Tilia cordata*.

Population analysis of old-growth specific species was beyond the scope of this thesis. However, it is remarkable that our field sampling did not detect population-scale hotspots, i.e. particular old-growth sites with distinctly abundant occurrence of some beetle or bird species of conservation interest. This may indicate that old-growth specific species are mostly rare also in their natural habitat; for example, due to their adaptation to slowly developing transient substrates (Nordén and Appelqvist, 2001). Local rarity can potentially limit the usefulness of particular bird or beetle species as forest habitat-quality indicators, which has often been recommended (Nilsson et al., 2001; Angelstam et al., 2004; Marchetti, 2004).

Finally, the high abundance and species richness of beetles on retention cuts indicates a high proportion of species that require sun-exposed habitats. Their natural habitats are probably legacy-rich disturbance areas, where suitable conditions may last for decades, until the closing of the canopy (Swanson et al., 2011). Such natural disturbance areas thus constitute another important part of the hemi-boreal forest 'baseline conditions', which are relevant for conservation managers and require special research (e.g. Greenberg et al., 2011).

4.2. Towards more 'nature-friendly' final felling

The consequences of Nordic forestry practices have led to an understanding that final felling as such is the major threat for forest biodiversity (Berg et al., 1994; Esseen et al., 1997a). My thesis highlighted, however, that harvesting-created open habitats (cutovers) can host species-rich and distinct beetle assemblages, which are probably analogous of natural early-successional communities (**III**). This conclusion is supported by many other recent studies (Swanson et al., 2011; Perera and Buse, 2014). Hence, crucial for biodiversity is *how* final felling is performed at the stand scale (i.e., which substrates and other habitat conditions are present on cutovers), and how is a suitable landscape mosaic of different-aged stands maintained on the dynamic landscape. **Retention forestry** has been specifically introduced as an approach to resolve the problem of legacy scarcity that characterizes conventional clear-cuts (Gustafsson et al., 2012).

The strongest conflict in retention forestry is over the woody legacies (notably live trees), which are the targets of harvest. As revealed by my studies, a medium-intensity approach of semi-natural forestry can largely resolve this conflict. The main problem regarding DW was that ca. 90% of snags were destroyed during final felling (**II**), but this was rather a side-effect of the felling technique than an intention to extract snags. Since snags can be the predominant fraction of DW after natural forest disturbances (Hutto, 2006), the ecological impact of their harvest-caused reduction deserves explicit research. The general benefits of retained snags have been documented for various taxa in other studies both in Estonia (Rosenvald and Lõhmus, 2007; Runnel et al., 2013) as well as elsewhere (Junninen et al., 2007).

In contrast, the post-harvesting amount of downed DW appeared sufficient to buffer even some further removal without causing observable impoverishment of beetle assemblages (**IV**). One reason for such rich legacies on the Estonian cutovers was the practice of natural regeneration, as opposed to planting that – through the soil scarification – destroys a significant part of retained DW (Hautala et al., 2004). The resulting DW volumes are comparable with the proposed critical DW thresholds 'for most species' (Müller and Bütler, 2010). An absence of clearly impoverished sites in our samples may also explain why threshold relationships were not detectable for any saproxylic species studied in Estonia. At the same time, the occurrence of forest pests remained low despite much deadwood, and the proportion of predatory beetles was high (**III–IV**). Natural regeneration also benefits insects feeding on flowers that are promoted by the longer-open canopies (Rubene et al., 2015), and the developing deciduous thickets host distinct assemblages of fungi (Lõhmus, 2011a).

A major question of retention forestry is how to combine pre- and post-harvest legacies for temporal continuity of substrates (Hansen et al., 1991; Franklin et al., 1997). For that purpose, live-tree retention played an important role even in Estonia: retention-tree deaths stabilized the abundance of deciduous snags and provided small, but qualitatively significant amounts of large downed wood in the first post-harvest decade. This was necessary because the retained downed DW was prone to rapid to decay due to extensive ground contact (**II**). Probably, the role of retention trees is even more crucial in intensive forestry systems, where the DW legacies on cutovers are smaller (e.g., Sahlin and Ranius, 2009).

4.3. The FSC-certified mature production forests

The FSC criteria and, more specifically, the indicator of "Threatened forest species" (Rametsteiner and Mayer, 2004) imply that sustainable management activities in production forests must facilitate the persistence of as many old-growth specialist species as possible. This can be achieved by carefully combining stand-management practices with the time of final felling (i.e. duration of stand development). The habitat qualities for old-forest species are expectably highest with the least human intervention into stand development and at extended rotations (e.g. Moning and Müller, 2009; Lõhmus and Lõhmus, 2011). My studies in the FSC-certified Estonian state forests revealed that several structural attributes – the importance of which for biodiversity was confirmed in studies **III**, **IV** and **V** – were indeed similarly available in old mature stands and old growth. The development of such properties (e.g., tree species diversity; amounts of FWD and finer fractions of CWD) in production forests is evidently related to natural regeneration and moderate intensity of interventions like thinnings.

My studies of structures and assemblages also confirmed, however, that certain features of the semi-naturally managed forests remain significantly impoverished compared to old growth. Largest structural reductions were evident for very large trees (all species; both live and dead), all late-successional deciduous trees, and logs in late stages of decay. A parallel biodiversity pattern was that the studied beetle and bird assemblages in mature production stands only formed subsets of old growth, not a distinct stage. For example, bird species richness was positively related to tree-size diversity at the stand scale (**V**), and the lack of late-successional tree species reduces habitat quality for specialized saproxylic beetles (e.g. Jonsell et al., 1998) and epiphytes (Remm et al., 2013). Moreover, there are some qualities that are most characteristic in silviculturally overmature forests, with many very old and dying trees of the first tree generation (e.g. aspen; see Lõhmus, 2011b). Such forests, and the accompanying question of longer rotations, were not addressed in my study but are important for a sustainability assessment.

On the landscape scale, I observed assemblage homogenization in birds (among site-types; **V**) as well as in beetles (site-type and stand level homogenization not distinguishable; **III**). The scale of these observations suggests actual reduction of biodiversity (cf. Rooney et al., 2007), which is probably (at least partly) caused by the loss of site-specific structures and microhabitats due to management practices. It is poorly known how such site-specific effects develop, and it is also a so far open question as to how much should production forests complement the functions of protected areas. In forest certification, it appears nevertheless meaningful to monitor particular threatened species in addition to the structures.

5. PRACTICAL CONCLUSIONS

1. Structural studies of old growth stands (**I**) indicate that pine forests on mineral soils are impoverished due to past usage in Estonia, even when old live trees are present. Therefore, pine forests in reserves need appropriate management planning, which should prevent their future impoverishment and consider active creation of DW by felling, controlled burning or other methods (Halme et al., 2013).
2. Semi-natural forestry, as applied in accordance with the FSC certification criteria in Estonia, ensures the diversity of tree species through natural regeneration (**I**) and – at present management intensity – sufficient volumes of DW for most saproxylic beetle species (**III, IV**). However, the management intensities remain vulnerable to political and socio-economic changes (Lõhmus et al., 2016), and a fraction of wood-inhabiting species remains restricted to old growth (**III, V**).
3. Green-tree retention has numerous positive effects: the species richness of saproxylic beetles is significantly higher on retention cuts than on clear-cuts (**III**); the addition of CWD becomes increasingly important during the post-harvest time (**II**); and retention will presumably provide large old trees that are absent from managed forests today (**I**). In Estonia, retention of late-successional deciduous tree species should be improved (including retention of snags and 2nd storey trees; see Lõhmus and Runnel, 2014), however the >90% destruction rate of snags during final fellings (**II**) should be decreased by improving the felling techniques.
4. For beetle diversity (**III**), planning semi-natural forestry practices on a larger scale is a key element that should ensure a continuous mosaic of successional stages across landscape – including protected areas, natural swamp forests, and variablymanaged stands. In order to prevent extensive structural impoverishment, retention norms should be specified by at least broad site-type classes, considering regional descriptions of old-growth stands (**I**).
5. Moderate-level slash extraction can be integrated with other approaches of semi-natural forestry without considerably reducing wood-inhabiting biota if proper attention is given to structural legacies (**IV**). However, cutovers in general may be impoverished compared to natural post-disturbance stages; therefore further research is needed for the conservation guidance of early-successional assemblages.

KOKKUVÕTE

Puiduga seotud elurikkuse kaitse – poolloodusliku metsanduse võimalused

Metsad on erakordselt mitmekesise elustikuga maismaaökosüsteemid. Inimtegevus ohustab seda mitmekesisust mitmel moel. Troopikas on peamine metsade pindala vähenemine põllu-või karjamaaks raadamise tõttu ning sellega seotud maastikumõju (killustumine, servaefektid, sidususe vähenemine). Parasvöötmes tuleneb tänapäeval põhiline oht puistustruktuuride vähenemisest ja lihtsustumisest, mis eriti drastiliselt avaldub intensiivseks puidutootmiseks kasutatavates metsades. Olulisimad struktuurilist mitmekesisust kujundavad elemendid on eri liiki puud, nende vanuseline jaotus ja paigutus, maapinnataimestik ja kõdupuit. Nende vähenemise tagajärjed elustikule on tihti järkjärgulised ja avalduvad alles pika aja jooksul.

Kõdupuit pakub elupaika umbes veerandile kõigist metsaliikidest ning sellel on ülioluline roll looduslike metsade energia- ja aineringetes. Kõdupuidu kogus ja omadused puistus sõltuvad puude kasvu- ja kõdunemiskiirusest ning puude surma põhjustavatest häiringutest. Suktsessioonireas on kõdupuitu kõige rohkem peale tugevat häiringut (torm, üleujutus, põleng), kõige vähem keskealises ühevanuselises puistus ning sealtpeale metsa vananemisel jälle aina rohkem. Looduslikes puistutes on kõdupuitu keskmiselt 10–40% eluspuude mahust, millest valdava osa moodustavad jämedad kõdunevad tüved. Intensiivsed metsandusvõtted (raied, küttepuidu ja raiejäätmete kogumine, puude haiguste tõrje, maapinna ettevalmistamine) vähendavad üldmahtu kuni kümme korda. Ühtlasi väheneb eri puidufraktsioonide mitmekesisus ning elupaigaline pidevus ajas ja ruumis, kusjuures kujunemiseks pikka aega vajavad fraktsioonid võivad peaaegu kaduda. Niisugune vaesumine ohustab intensiivselt majandatavates metsades vähemalt poolte kõdupuitu asustavate (saproksüülsete) liikide püsimist.

Varasemad uuringud seostasid kõdupuiduelustiku seisundit peamiselt puidu kogumahuga, kuid tänapäeval pööratakse üha enam tähelepanu puidu omadustele ning ümbritseva maastiku mõjule. Saproksüülsete liikide jaoks võib puit olla kasvupind, toit, saaklooma elupaik, varje- või sigimispaik. Need tingimused olenevad sellest, kas puit on värske või tugevasti kõdunenud, koorega või ilma, varjus või päikese käes, kuiv või niiske. Populatsiooni püsimiseks on sobivat elupaika vaja piisaval määral ning on arvatud, et seda nn väljasuremiskünnist saaks kasutada looduskaitsenormatiivide väljatöötamisel. Paraku mõjutavad künnisväärtust looduses paljud tegurid, eri liikidel on künnisväärtus erinev ja kõiki asjakohaseid tingimusi ei ole praktikas ka lihtsalt võimalik jälgida. Üksmeelel ollakse põhimõttes, et kõige suurem väljasuremisoht varitseb liike, kes vajavad looduslikult haruldasi või metsa majandamisel kaduvaid substraate, nagu näiteks väga vanu puid. Siiski on kõdupuidu üldhulk jätkuvalt oluline indikaator, sest suurem hulk hõlmab enamasti ka rohkem erinevaid (sh haruldasi) elupaiku.

Käesoleva doktoritöö põhieesmärk oli hinnata seda, mil määral paraneb kõdupuiduelustiku seisund metsamajanduse intensiivsuse vähendamisel. Ligikaudu 80% maailma metsadest ei ole kaitsealad ega istandused, st neid majandatakse multifunktsionaalsetena, kasutades väga erinevaid intensiivsustasemeid ja võtteid. Doktoritöös käsitletakse Eestis viimastel aastakümnetel kasutatud pool-looduslikku (FAO: *'semi-natural'*) majandamisvõttestikku, mis on hõlmanud suurel määral (90%) iseeneslikku uuenemist looduslike puuliikidega, keskmise intensiivsusega harvendusraieid ning uuendusraieid küpsusvanustega võrreldes hilisemas eas. Alates 2002. a on Eesti riigimetsa majandatud rahvusvaheline säästva metsanduse (FSC) sertifikaadi nõuetest lähtuvalt.

Töö esimeses pooles analüüsitakse elupaigana olulise kõdupuidu hulka ja omadusi Eesti metsades ning teises pooles elustiku tundlikkust sellele mardikate ja lindude näitel (sh viimastele selgrootutest koosneva toidubaasi kaudu avalduvat mõju). Käsitletakse lõppraie, säilikpuude jätmise, raidmete kogumise ja loodusliku uuenemise rolli kõdupuiduvarus. Metoodilise võttena kasutatakse võrdlust põlismetsade kui looduslikele „referentstingimustega“, mille lisaväärtus seisneb selles, et Euroopa hemiboreaalsete segametsade struktuur on seni halvasti kirjeldatud.

Uuring **I** võrdles põlismetsade (domineeriv rinne üle 120 a vana; puistu võimalikult majandamisjälgedeta) struktuuri majandatud, raieküpsete metsadega neljas tüübirühmas (palu-, laane-, salu- ja rohusoometsad; kokku 29 puistupaari). Selgus, et põlismetsade struktuur on kõigis ruumimastaapides väga varieeruv, mida tuleb arvestada põlismetsade omadustest looduskaitseliste eesmärkide tuletamisel. Näiteks jämeda (läbimõõt ≥10 cm) kõdupuidu keskmised kogused Eestis ületavad oluliselt seni avaldatud mahte nii boreaalse vööndi lõunapoolsete kui parasvöötme põhjaosas mõõdetud metsade kohta. Puistute sisestruktuur on väga varieeruv ka tüübirühmiti ning isegi sama tüübirühmade puistute vahel. Näiteks looduskaitseliselt olulised hilissuktsessioonilised lehtpuuliigid on levinud peamiselt vanades salu- ja lodumetsades. Seejuures näib salumetsades varem hilissuktsessiooniliseks peetud kuusefaas olevat tegelikult ajutine – sellele järgneb seni kirjeldamata pärnafaas. Mardikate puhul oli põhiline tüübieristus vanade palu- ja kuuse-segametsade vahel, linnukoosluste seas eristus aga ka põline lodumets. Palumännikutes olid majandus- ja põlispuistud kõige sarnasemad, arvatavalt endisaegse raiemõju pikaajalise püsimise tõttu.

Looduslike häiringualade asemel on tänapäevaste metsade peamiseks avakoosluseks raiesmikud. Uuring **II** näitas, et Eestis raiesmike lamapuiduvaru ületab tunduvalt Põhjamaade intensiivmetsanduses kirjeldatu. Sellise soodsa seisundi üks põhjus on loodusliku uuenduse kasutamine, millega välditakse lamapuidu ja maapinna purustamist. Mardikate kohta tehtud uuringud kinnitasid, et niisugused raiesmikud võivad mõnel juhul elustiku jaoks looduslikke häiringukooslusi asendada, eriti siis, kui sinna jäetakse ka elusaid säilikpuid. Seejuures püsis kahjurmardikate esinemissagedus väike ja röövtoiduliste mardikate arvukus suur ning liigirikkust ja liigilist koosseisu ei mõjutanud oluliselt ka umbes poole kõdupuidu eemaldamine biokütteks (**III–IV**). Säilikpuude suremisel tekkiv jäme kõdupuit muutub eriti väärtuslikuks vanadel raiesmikel, kus raidmed on juba kõdunenud (**II**). Tüügaspuudest hävib lõppraietel aga u 90%, samas kui loodusliku häiringu järel võivad seisvad surnud puud olla peamine kõdupuidufraktsioon. Sellise vaesumise mõju elustikule on teadmata ning looduslikud häiringukooslused vajavad edaspidi tervikuna täpsemat uurimist.

Eesti riigimetsa majandamine vastavalt FSC-serdile säilitab osa elustikule olulist puistustruktuuri, kuid mitmete struktuurielementide hulk väheneb siiski tunduvalt. Näiteks väga suuri elus puid oli küpses majandusmetsas seitse korda vähem, hilissuktsessioonilisi elusaid lehtpuid või nende kõdupuitu kolm kuni viis korda vähem ning jämedaid seisvaid või lamapuid üle kümne korra vähem kui põlismetsades. Loodusliku uuenduse ja mõõduka majandusintensiivsuse soodsat mõju peegeldavad aga puude üldine liigiline mitmekesisus ning peene ja keskmise jämedusega lamapuidu rohkus vanades majandusmetsades, kus selle toel säilivad ka küllaltki liigirikkad mardika- ja linnukooslused. Kuna maastiku tasemel täheldati nende koosluste ühtlustumist, siis ilmselt on elustikule oluliste majandamistundlike struktuurielementide mõju kohaspetsiifiline. Näiteks majandatud salumetsades oli kõdupuitu ainult veidi vähem kui teistes segametsades, aga võrreldes põliste salumetsadega oli nii puude liigiline koosseis kui ka jämeda lamapuidu ja väga jämedate eluspuude maht palju väiksem.

Doktoritöö peamised praktilised järeldused on järgmised:

1. Kaitsealadel tuleb vältida arumännikute puistustruktuuri edasist vaesumist ning kaaluda seal kõdupuidu aktiivset tekitamist kujundusraiete või ülepõletamise abil.
2. FSC alusel serditud pool-looduslik metsamajandus on Eestis seni taganud piisava kõdupuiduvaru enamikule puiduputukaliikidele, kuid ei taga kõigi põlismetsaspetsiifiliste liikide säilimist.
3. Elusate säilikpuude jätmine lõppraiel täidab mitmeid olulisi ökoloogilisi funktsioone. Eestis tuleks senisest enam säilitada raiesmikel hilissuktsessioonilisi lehtpuid ning vähendada tüügaspuude hävimist raie käigus.
4. Mardikate (ja ilmselt teistegi puiduseoseliste organismide) kaitseks on vajalik maastikuplaneerimine, mis looks eri suktsessiooniastmetes ja eri määral majandatud puistutest ning kaitsealadest funktsionaalse terviku. Säilikstruktuuride jätmisel tuleks arvestada kasvukohatüübiga.
5. Piisava hulga säilikstruktuuride jätmisel on võimalik mõõdukas raidmete kogumine lõimida pool-looduslikku majandamisvõttestikku ilma kõdupuiduelustikku oluliselt ohustamata. Praeguste raiesmikukoosluste ’loodusläheduse’ hindamiseks tuleks teha uuringuid looduslikel häiringualadel.

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PUBLICATIONS

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Conference presentations:

European Congress of Conservation Biology, 01–05.09.09, Praha, Czech Republic, oral presentation

VIIIth Symposium of Baltic Coleopterologists, 10–12.06.2014, Kiry – Tatra National Park, Poland, oral presentation

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Kraut, A.; Liira, J.; Lõhmus, A. (2016). Beyond a minimum substrate supply: sustaining saproxylic beetles in semi-natural forest management. Forest Ecology and Management, 360, 9−19, j.foreco.2015.10.016.

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Juhendatud väitekirjad:

Valentina Zolotarjova, magistrikraad, 2012, Raiejäätmete kogumise mõju mardikakooslustele raiesmikel, Tartu Ülikool.

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