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LIINA REMM

Impacts of forest drainage on biodiversity and habitat quality: implications for sustainable management and conservation

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Impacts of forest drainage on biodiversity and habitat quality: implications for sustainable management and conservation

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Department of Zoology, Institute of Ecology and Earth Sciences
Faculty of Science and Technology, University of Tartu

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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–IV**:

I Lõhmus, A., Remm, L., Rannap, R. Just a ditch in forest? Reconsidering draining in the context of sustainable forest management. Submitted manuscript.

II Remm, L., Lõhmus, P., Leis, M., & Lõhmus, A. 2013. Long-term impacts of forest ditching on non-aquatic biodiversity: Conservation perspectives for a novel ecosystem. PLoS ONE 8: e63086.

III Remm, L., Lõhmus, A., Rannap, R. Temporary and small water bodies in human-impacted forests: an assessment in Estonia. Boreal Environment Research (in press).

IV Remm, L., Lõhmus, A., Maran, T. 2014. A paradox of restoration: prey habitat engineering for an introduced, threatened carnivore can support native biodiversity. Oryx (in press). doi:10.1017/S0030605314000271.

Author's contribution to the publications:

I – had the main responsibility for literature analysis and participated in developing the idea and the manuscript preparation.

II – had the main responsibility for data analyses and participated in developing the idea, data collection and manuscript preparation

III–IV – had the main responsibility for all stages of the studies

ABBREVIATIONS

ANOVA – analysis of variance

CWD – coarse woody debris

FSC – Forest Stewardship Council

FSL – feature selection and variable screening

ISA – indicator species analysis

MRPP – multi-response permutation procedure

NMS – non-metric multidimensional scaling

SPEC – species of conservation concern

TWBs – small and temporary water bodies

1. INTRODUCTION

1.1. Forest biodiversity in relation to water supply

All peatlands and most forests are found in regions where precipitation exceeds evapotranspiration (Wieder et al. 2006). Consequently, mosaic landscapes with forests, lentic and lotic water bodies and mires are common in vast areas of the world, and forests and aquatic habitats are tightly integrated. Reciprocal interactions between small water bodies and the forest create conditions for more abundant and diverse consumer assemblages than would be supported by either habitat type alone (Fausch et al. 2002). The biota of forested wetlands, in turn, contributes to hydrological processes and the rate of the water cycle (D'Odorico et al. 2010). Forests, due to their considerable vertical dimension into atmosphere and soil, feed back on regional hydrology and climate (Waring and Running 1998). At catchment scale forests can reduce runoff and, at larger scales, increase precipitation (Ellison et al. 2012). The examples of how organisms shape hydrological conditions also include certain plants that enhance their growth conditions by affecting soil water level and, consequently, bring about bistable systems (low *versus* high biomass; D'Odorico et al. 2010, Sarkkola et al. 2010). Beavers can create small-scale disturbance, which locally shifts terrestrial habitat to aquatic and produces spatiotemporal mosaics of unique habitat value at the landscape scale (Nummi & Kuuluvainen 2013).

Variable hydrologic conditions that harm or benefit the organisms give rise to biodiversity. The diversity arises due to different biological adaptations to the same basic hydrologic conditions (e.g. Marx et al. 2012), evolutionary differentiation along hydrologic gradients (e.g. Marks et al. 2014), and diverse biotic interactions in response to these adaptations. The role of hydrology in biotic diversification can be illustrated by species specialisation in *Sphagnum* mosses at the scale of the hollow-hummock gradient created by their own and dwarf shrubs (Rydin et al. 2006). Sphagna are keystone organisms in many peatlands: enhanced by flooded conditions, they generate harsh, nutrient poor and acidic habitat that determines the ecosystem functioning. Those harsh habitats are often rather species poor at a local scale, but they host specialized species that increase regional biodiversity (Laine et al. 1995b).

1.2. Rise of forestry drainage

Artificial drainage is a means to foster timber production in wetlands, to enable tree regeneration after watering-up and paludification of harvested sites, and to improve access to forest stands. The main drainage targets have been nutrient rich peatlands and wet areas on mineral soils with stunted tree cover, but regionally also nutrient poor and/or treeless mires (often with no success in terms of timber production). The reason for draining is that sustained flooding with stagnant water impedes tree growth via stressed respiration, photosynthesis, protein synthesis, mineral nutrition, and hormone relations, together with an increased exposure to various phytotoxic compounds and a scarcity of mycorrhizal symbionts (Kozlowski 2002). Therefore even flood-tolerant trees (e.g. *Acer saccharinum* and *Fraxinus pennsylvanica* in North-America) give place to herbaceous vegetation in prolonged waterlogging conditions (Marks et al. 2014). Moreover, the production rate or economic value of timber is often lower in flood tolerant trees (e.g. *Betula pubescens* vs. coniferous trees in North-Europe) or in flooded conditions, also because soil anaerobiosis is often accompanied with nutrient deficiency that limits tree growth.

Key conditions for forestry drainage are a climate and topography that favour paludification, but also a well developed forest industry, which has gained enough resources (or credit for subsidies) to invest in less productive land after exploiting more productive sites. This explains why most forestry draining has been carried out in northern temperate and boreal zones. Out of more than 15 million hectares of wetlands drained for forestry by the early 1990s, over 90% were situated in Fennoscandia, Russia, British Isles and the Baltic States (Paavilainen and Päivänen, 1995). Draining extensive areas of swamps for plantation in the tropics (particularly South-East Asia) can also be considered as forestry drainage. Such plantations, mainly for *Elaeis guineensis* palm oil and *Acacia* timber, covered over 3.1 million hectares (20% of regional peatlands) in Peninsular Malaysia, Sumatra and Borneo in 2010 (Miettinen et al. 2012).

In Europe, draining by hand-dug ditches for forest growth appeared locally in the 18^{th} century and it became systematic in the middle of the 19^{th} century (Paavilainen and Päivänen 1995). In Estonia, ditching started in the 1820s (Etverk 1974). In the middle of the 20^{th} century, mechanization and subsidies (by governments and the Word Bank) promoted drainage to a major role in landscape transformation (Peltomaa 2007). Landscapes that were previously scattered with (semi-)open wetlands became more homogeneous, the coverage of peat soils was reduced, and whole watersheds were transformed from wetland mosaics to linear systems. Although draining of new areas has been minimised lately, the majority of existing drainage networks are either further improved or – in the case of reduced funding or the absence of the desired silvicultural results – completely abandoned (Peltomaa 2007, Minayeva and Sirin 2009).

1.3. Environmental impacts of forestry drainage

Already historical small-scale ditching was accompanied by scientific inquiry on drainage impacts on tree stand (e.g. Ostwald 1878). Intensive study on drained forests began in the 1950s, with the main emphasis on the ecological conditions, timber production and problems of stand regeneration and management (Heikurainen 1964). An important applied task was to develop a typology of drained forests to predict future timber yields and to plan silvicultural activities. The elaborated classification systems differ among countries for cultural and natural reasons (terrain, climate, species pool etc.). However, a general conclusion has been that drained wetlands stand apart from both pristine forested wetlands and forests on mineral soil, and they additionally represent stages of post-drainage successions of different wetland types (Paavilainen and Päivänen 1995).

Because forestry drainage targets dominant living organisms (trees), it expectably has side effects on other parts of the ecosystem (summarized in Paper **I**). In just a few days the newly dug ditches start discharging the water and lowering the groundwater, but other changes appear with a delay since they are caused by slow processes (e.g. tree growth, peat decomposition and nutrient release) or by indirect mechanisms. The rearrangement of water flows and solar radiation penetrating the canopies transforms the whole vegetation and has secondary impacts on animals and fungi (Laine et al. 1995b). For example, thermophilous butterflies may be extirpated (Lensu et al. 2011) whereas mychorrhizal fungi benefit from trees and well-aerated soil (Peltoniemi et al. 2012). Ditches provide novel habitat for many species groups (Vindigni et al. 2009, Simon and Travis 2011, Zielińska et al. 2013) but, at the same time, may cause detrimental habitat fragmentation (Ludwig et al. 2008).

Impacts of modified hydrology extend beyond the drained site – to the ecosystems that receive the runoff water. The severest impacts downstream are caused by eroded and leached material and compounds (Vuori et al. 1998), not so much by changed temporal patterns in water amounts. Although such changes may be relatively small compared to, for example, intensive agriculture, their total impact in large forested regions may exceed the agricultural impact (e.g., nitrogen leaching in Finland; Kortelainen et al. 1997). While the water quality change is limited to a short post-drainage period (Holopainen and Huttunen 1998), the pollution may nevertheless become long-term in drained landscapes due to subsequent ditch cleaning and dredging activities (Heikurainen et al. 1978).

The spread of large-scale drainage soon raised concern over non-target species of economic interest, like berry plants (Huikari 1972, Veijanen 1976), mushrooms (Salo 1979) and game animals (Karsisto 1974). During the period of most intensive drainage, the studies expanded also to wider biodiversity, including invertebrates (Maavara 1955, Koponen 1985) and bird fauna (Väisänen and Rauhala 1983, Peterson 1987). Those studies were, however, often based on small samples and the effects of drainage and fertilization were not distinguishable. For many foresters, the latter appeared as a part of the same 'amelioration' activity (e.g. in Finland 30% of the drained forest was fertilized; Aarnio et al. 1997, Moilanen jt 2002). Even contemporary studies remain mainly correlative and descriptive, rarely being focused on the drainage impact mechanisms. The complexity of such mechanisms is, however, revealed by many hydro-ecological experiments unrelated to forest drainage. For example, frequent drying of forest pools has shown to reduce the nutritional quality of leaf litter (microbial biomass and nitrogen content), and therefore foraging preference by invertebrate shredders (Inkley et al. 2008). Drainage impacts remain surprisingly poorly known on a wide range of presumably sensitive organisms, such as epiphytes and (semi)aquatic biota in drained sites.

Ground vegetation in drained areas has been most thoroughly studied. It has been used as an indicator of post-drainage changes in the ecosystem, especially with regard to moisture and nutrient levels. Such studies have described successional patterns, revealing long-term vegetation convergence in different original mire types and in wet mineral-soil forests (Lõhmus 1981, Hotanen et al. 1999, Pikk and Seemen 2000), and a considerably faster succession on more fertile peat and in warmer climate (Pienimäki 1982). Dominant traits of the post-drainage vegetation change during the succession. Along with the long-term reduction in hygrophytes, there is a temporary expansion of grassland species, followed by colonization of mesophytes that eventually form a transformed, rather stable assemblage (Āboliņa et al. 2001). Because forestry drainage results in novel species assemblages and ecosystem functioning, which are poorly restorable to initial states (Haapalehto et al. 2010), it is reasonable to ask whether drained ecosystems represent novel ecosystems *sensu* Hobbs et al. (2006).

1.4. Drainage in relation to sustainable forestry and conservation

Commercial forest management is oriented on timber extraction and thus its environmental impact assessments have focused on timber harvesting techniques (e.g. Hunter 1999, Lindenmayer and Franklin 2002). Although reduction of the impacts of modified hydrology is sometimes listed as an aim, there is a lack of studies on the effectiveness of water-related measures and prescriptions (Johansson et al. 2013). The main measures, which include the aim of biodiversity protection in relation to forestry drainage, can be grouped as follows.

(i) Ceasing the establishment of new ditch networks. This has been a general trend during the last two decades in developed and/or intensively drained countries. For example, drainage is acknowledged, but not endorsed, as a means for increasing timber productivity of forested wetands in Ontario (Jeglum et al. 2003). In Sweden, forestry drainage is not subsidied any longer and it is regionally allowed only by special permits (Päivänen and Hånell 2012). In the Estonian state forests (36% of forests) the construction of new drainage systems is prohibited based on the Forest Stewardship Council (FSC) certification scheme. Most Baltic FSC-standards promote a long-term shift to more nature friendly management regarding drainage, though extent of the restrictions varies among countries (FSC 2006). A remaining administrative and legalisation problem outside the certified forests is a lack of environmental impact assessments, which is related to an assumption that the environmental impacts are modest (Leibak and Paal 2011).

(ii) Sedimentation traps. In the recent decades, sedimentation traps on the outflow of drainage networks have been prescibed in many countries. However, most drainage networks have been established earlier as directly connected to a river or lake. Furthermore, some trap designs used to improve the situation have proven to be ineffective, especially during high flows (Joensuu et al. 1999, Liljaniemi et al. 2003, Vuori and Joensuu 1996).

(iii) Establishment of protected areas. A large part of the remaining undrained wetlands are now protected. For example in Finland, one-third of undrained peatlands lie within protected areas (Similä et al. 2014). In Estonia 47%–83% (depending on site type) of present open and sparsely wooded mires are under protection; however, their total area has decreased about three times since the 1950s (Leibak and Paal 2011). While, in general, mires and wet forests are protected better than drier forest habitats (Lõhmus et al. 2004, Leibak and Paal 2011, Tuvi et al. 2011), a large part of protected wetlands are drained.

(iv) Restoration of degraded wetlands.Those currently protected wetlands, which have been historically drained, are increasingly targeted for restoration by ditch blocking. Restoration actions are typically single interventions, which aim at initiating long-term developmental processes, like tree and dead tree successions, or paludification. In Finland, about 20 000 ha of peatlands, most drained for forestry, have been restored in 1989–2013 using particularly the financial support from the European Union (Similä et al. 2014). Monitoring has shown that the return of species typical to pristine mires is slow, compared to ecosystem processes such as nutrient cycling (Haapalehto et al. 2010). In Russia and the Baltic States, the restoration of areas drained for forestry has not become widespread yet (Minayeva and Sirin 2009).

(v) Integrating drained forests to conservation networks. Post-drainage succession can apparently produce habitat for certain threatened species, but explicit assessments and realization of such potential are still lacking. For example, Estonian forest reserves contain a large proportion of drained peatland, but it is unknown to which extent could these forests compensate the under-representation of some natural forest types and old-forest specific biota in general (Lõhmus et al. 2004, but see Lõhmus and Lõhmus 2011, Rosenvald et al. 2011).

(vi) Stream restoration. Such programmes have largely been motivated by the sport fisheries and conducted by provisioning of in-stream structures and channel remeandering. However, sound monitoring of results has been rare (Louhi et al. 2011). In Finland, extensive restoration programmes (mainly targeted on salmonids) were initiated already in late 1970s; in recent decades wider approaches and new sites have been added (Muotka and Syrjänen 2007). A few first attempts of similar kind have also been made in Estonia.

1.5. Objectives of the thesis

(i) To integrate the knowledge base of biodiversity studies in relation to forestry drainage, to identify gaps of knowledge, and to develop a practical workflow that could introduce those conservation concerns to ditching practices. Although drainage is suspected to significantly affect ecosystem functioning, the biodiversity concern has been only loosely linked with environmental prescriptions. These aspects were addressed through a literature synthesis (**I**).

(ii) To provide a systematic conservation assessment on late-stage, nutrient-rich, drained forests. Post-drainage vegetation succession within one tree generation in boreal pine-mires is rather well understood, while the knowledge is scarce for nutrient rich sites and for taxa other than plants. Therefore, the three case-studies were focused on less studied species groups and habitats: alder swamps in comparison with their second generation drained counterparts (**II**), and temporary and small water bodies (**III–IV**). The main response studied was a change in species composition – it was seen as a product of species turnover (**II**) and changes in key environmental variables, measured as differences between drained and undrained sites.

(iii) To describe novel habitat values of drained sites. In general, anthropogenic novel ecosystems should gain more research attention and consideration in conservation practise (Hulvey et al. 2013). An objective of the thesis was to find out which species and habitat qualities drained sites support also after the subsequent timber harvesting, which is the ultimate purpose of forestry drainage (**II–IV**).

(iv) To extract focal species and habitat characteristics for management. This included identifying sets of drainage sensitive species and habitat types both in terrestrial and aquatic habitats (**II–III**) and exploring further engineering of water bodies as a mitigation means (**IV**).

2. METHODS

The objectives of the study were addressed using literature synthesis and three case studies. The focal species groups (lichens, plants, selected invertebrates and amphibians) and habitat components (small and temporary water bodies, terrestrial and arboreal substrates) were selected based on their proposed drainage sensitivity and lack of previous knowledge.

2.1. Literature review

Literature search for paper **I** was focused on case studies that document the impacts of forestry drainage on biota. In the case of trees and undergrowth vegetation (plants and epigaeic lichens), which appeared to be better studied, the aim was to find the most rigorous studies for generalization; for other taxon groups the search was meant to be comprehensive. The initial effort was based on major reference databases, covering both electronically available journals as well as older hardcopy material in English. In a later stage, the searching was extended to reference lists and to regional publications, including articles in Finnish, Estonian, Russian and German. The articles found were classified according to species groups, the impacts measured, and the inclusion of threatened species.

2.2. The area and design of original studies

The original studies (**II–IV**) were conducted in Estonian forests and fens. Estonia is a lowland country (on average, 50 m above sea level) in the hemiboreal vegetation zone. The amount of precipitation (on average 646 mm/y) exceeds evaporation (400 mm/y) and the runoff is slow because of the flat terrain. The average temperature in January is –4°C, and in July +16.7°C. Of the total Estonian land area of 4.4 million ha, forest land encompasses 2.2 million ha (The Estonian Environment Agency 2013) and non-forested fens ca. 80,000 ha (Leibak and Paal 2013). This area has been heavily drained with open ditches: forestry drainage systems encompass over 0.6 million ha, although their current functioning varies. In this thesis, open bogs were not addressed because they do not constitute a target for forestry drainage.

Most forestry drainage systems in Estonia have been constructed between the 1950s and the 1980s. In recent years, reconstruction of existing systems and improvement of their effectiveness by digging supplementary ditches has been affecting about 10,000–15,000 ha annually in state forests (data by the State Forest Management Centre). According to one estimate, almost all paludifying forests and 82% of existing peatland forests have been historically drained (Ilomets 2005). As a result of long-run succession over 0.3 million ha of drained forest has been transformed to the decayed peat type (Aderman 2009). Drainage of naturally open fens has been similarly devastating but no precise estimates exist in terms of current forests. While the initial aim was often to expand agricultural land (Ilomets 2005), those lands may have been abandoned and afforested later on.

Ninety percent of the Estonian forest land is currently managed for timber production (including 15% where the environmental values place specific restrictions on the silvicultural techniques) and 10% is strictly protected (The Estonian Environment Agency 2013). The timber production is based on clear cutting (>95% of the volume of regeneration fellings) and mostly natural regeneration. Typical cut blocks are small (<5 ha) and, on average, 6% of growing stock is left as solitary retention trees on clear cuts since the late 1990s (Rosenvald et al. 2008).

The case studies on drainage impacts focused on mobile-water swamp forests (comparing undrained and drained condition) and on small and temporary water bodies. (i) Mobile-water swamp forests are typically located on thin, seasonally flooded, well-decomposed Eutric Histosols and Fluvisols, with a peat layer ≥30 cm (pHKCl 5.0–6.5) (Lõhmus 1984). The undrained sites were characterised by abundant black alders (*Alnus glutinosa*) in the tree layer. The long-term drained sites (ditching >50 years ago) were selected in comparable conditions in terms of the topographic position and historical wetland status (confirmed from maps), the incidence of floods in spring and similar basic sets of tree species (confirmed in the field). These forests represent the decayed-peat *Oxalis* type on well decomposed peat soils (pHKCl 4.0–6.5) and tree stands adapted to the novel soil conditions (Lõhmus 1984). (ii) The water bodies studied were temporary and/or small: depressions with water surfaces between 25×25 cm and 200 m^2, and brooks narrower than 8 m. The set of artificial ponds explored in the Hiiumaa island (study **IV**) were ca. 1 m deep, had an area of up to 0.3 ha and a shallow northern bank to provide sun-warmed water.

The case-studies were based on comparative (space-for-time substitution) designs and ranged over three spatial scales (Fig. 1):

(i) Water body scale. Study **IV** compared water bodies available on random transects with the ponds specifically engineered to mitigate drainage impact on biodiversity. Thirteen random water bodies (some of which comprised several puddles) and 16 ponds were sampled on Hiiumaa island. Study **III** analysed water-body characteristics and breeding of brown frogs (*Rana temporaria* and *R. arvalis*) in relation to water body characteristics and habitat type.

(ii) Stand scale. Study **II** on non-aquatic organisms was carried out on 44 two-hectare plots (20 undrained, 24 drained), which represented a balanced design of four management types (old growth, mature forests, clear cuts with and without retention trees) in mainland Estonia.

(iii) Landscape scale. A country-wide sampling of aquatic habitats in forests and fens was performed on ca. 2-km long random transects (**III**). The transects were organized as clusters (4 transects in cardinal directions; 92 km in total), which were stratified by 13 landscape regions according to Arold (2005).

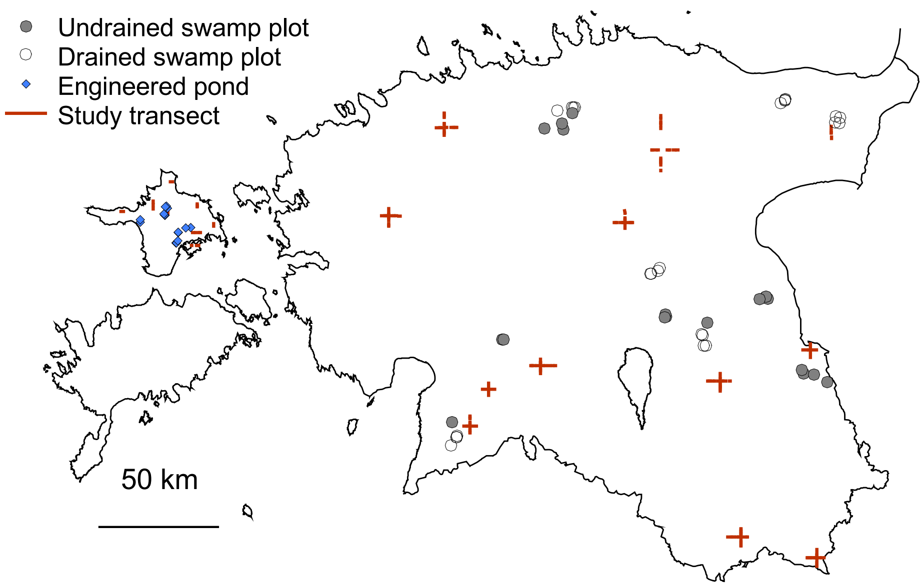

Figure 1. Locations of the study sites in Estonia.

2.3. Field methods in terrestrial habitats (II)

The stand scale surveys of vascular plants, bryophytes and lichens followed a fixed-area, fixed-effort approach (Hunter and Webb 2002, Lõhmus and Lõhmus 2009). Each of these three taxonomic groups was surveyed for all species separately by the same observer. The survey spanned all over the 2-ha stand for four hours in a suitable season between 2005 and 2010. For lichen and bryophyte species, a five-point abundance scale was used, based on the number of records: one record (1); 2–5 records (2); 6–15 records (3); 16–100 records (4); and >100 records (5). For herbaceous plants and dwarf shrubs, a ten-point abundance scale was used, ranging from one shoot (score 1) or 2–3 scattered shoots or a clone (score 2) to local dominance (score 8) or total dominance (score 9 for <80% total cover, score 10 for >80% cover). In addition to lichenised fungi, "lichens" also included lichenicolous and some saprotrophic fungi (such as calicioids) traditionally surveyed by lichenologists. For the snail survey, 3 litres of litter and topsoil, passed through a sieve with a 1 cm mesh, were collected from different microhabitats of each plot once in late summer 2008 or 2009. The material was collected as six 0.5-litre subsamples. That volume method was combined with a visual search. Snail, lichen and bryophyte specimens not identifiable in the field were collected for routine laboratory examination.

Species of national conservation concern (SPEC; listed in Supplementary Tables S1,S2, S3, S4 in **II**) were distinguished as those: (1) on the Estonian Red List (categories RE, CR, EN, NT, VU and DD; Estonian Red List of Threatened Species 2008); (2) rare or little known (up to 10 records in Estonia); or (3) established as old growth indicators: Holien 1998, Nitare 2000, Coppins and Coppins 2002). The criteria (2) and (3) were available or meaningful for lichens and bryophytes only.

The habitat structure was measured along four straight 50-m transect lines in each plot (see Lõhmus and Kraut 2010 for details). The methods included: (i) area-based assessments of the densities of live and standing dead trees (≥10 cm diameter at breast height; including broken-top snags ≥1 m tall); (ii) line-intersect approach for volumes of downed logs (≥10 cm diameter at intersections with the line) and the ground cover of bryophytes; and (iii) visual point estimates (at 10% accuracy) of canopy cover at 10-m intervals. Shannon indices of the species diversity of live trees (based on their numbers) and of decay-stage diversity of CWD (i.e., snags and logs; based on volume distribution among five decay stages) were calculated. The latter was interpreted to indicate continuity of the CWD input in time.

2.4. Field methods for water body surveys (III–IV)

In study **III,** water bodies were described on 10 m wide strip transects (or 4 m strips in the case of water bodies smaller than 3 m^2) in spring and/or autumn 2011 or 2012. The areas having significant drainage impact were delineated on the map in the field, based on the vegetation composition, distance from ditches, and ditch condition.

Waterbody abundance along the landscape transects was explored by habitat types, which were identified based of maps, ortophotos and field notes (**III**). Soils were classified as rich or poor, and as wet or dry-to-moist. 'Rich' soils had fertility comparable to or higher than in Gleyic Luvisols, Rendzinas or in transitional bog soils shallower than 1 m. 'Wet' soils were those considered economically as drainage targets (Jürimäe 1966, Lõhmus 1984). Land cover was categorized as forest, clear-cut or open fen. By definition, 'open fen' only occurred on undrained wet soil; its dominant woody vegetation had to be <1.3 m in height and to provide <30% canopy cover. 'Clear-cuts' included young regenerated stands with dominant trees <4 m in height and up to 6 cm in diameter at the breast height.

A random sample of the water bodies found (**III–IV**) and the engineered ponds of study **IV** were characterised in terms of their origin, shape, pH, electrical conductivity, temperature, water colour, shade, vegetation cover (%), open water in shade (%), the bottom substrate, and surrounding land cover. In each vernal water body, breeding of brown frogs was checked by visual searching for egg-clusters or with ten dip-net sweeps for larvae. In study **IV** also macroinvertebrates were collected by dip-netting for 5, 10 or 15 seconds (depending on water body size).

2.5. Data analysis

The main questions addressed in data analyses were (1) differences in biota and habitat characteristics between anthropogenic and natural habitats (2) the habitat qualities that could explain those differences and (3) overall abundance of small and temporary water bodies in Estonian forest and fen landscapes in a point of time.

Differences between swamp and drained plots as well as among the management types (**II**) were tested using (i) split-plot ANOVAs or Mann-Whitney U-tests for species richness, the number of SPEC, abundance of snails, and stand structural features; and (ii) multi-response permutation procedure (MRPP) and the indicator species analysis (ISA; Dufrêne & Legendre 1997) for assemblage composition. Pearson correlation was used to relate stand characteristics with species richness, abundance and species assemblage ordination axes in non-metric multidimensional scaling (NMS). The stand structural characteristics, which significantly correlated with species richness, were further included to general linear models to explore hidden effects of drainage (as no such effects were detected by split-plot ANOVA).

For the transect data of study **III**, Wilcoxon matched pairs tests were used to explore the effects of drainage and clear-cutting on the total area of small and temporary water bodies (TWBs), on the area and mean depth of natural lentic TWBs, and the effect of clear-cutting on the area of wheel rut puddles. As the area of water bodies was dependent on soil type, the analyses were carried out separately for wet and dry-to-moist soils. To describe the impacts of drainage on the characteristics of individual water bodies, feature selection and variable screening (FSL) procedure was used separately for ditches vs. natural lentic TWBs as well as for natural lentic TWBs on drained vs. undrained areas. The effects of drainage, clear-cutting and anthropogenic origin of water bodies on the breeding of brown frogs were established in a sequence of univariate to bivariate logistic regressions.

In paper **IV**, random water bodies and engineered ponds were compared in terms of macroinvertebrate assemblages (MRPP combined with ISA) and habitat characteristics (Mann–Whitney U tests with the Bonferroni correction).

The analyses were carried out in Statistica 8 and PC-ORD vers. 6.07 (McCune and Mefford 2011). Spatial autocorrelation and spatial variation were addressed through various procedures. Clustering of the study **II** plots was included as a random factor in species richness and abundance analyses. In study **III**, all patches of the same habitat type within a transect cluster were pooled, so that a cluster × habitat type combination served as a sample unit. To compare drained vs. undrained sites or clear cuts vs. forests within a cluster, only those transect clusters were included where both habitat types covered ≥0.4 ha (dry-to-moist areas) or ≥0.1 ha (wet areas). In the brown frog analyses – if breeding sites were located within 0.5 km from each other, only the one hosting most larvae/egg-clusters was included. Also, the non-breeding sites with shallower water than observed in breeding sites were excluded. On the transects of study **IV**, similar adjacent water bodies were treated as one and no more than five samples per km were collected.

3. RESULTS

3.1. Succession patterns and biodiversity knowledge (I)

The literature analysis revealed that drainage impacts can be largely irreversible and cascade after the initial ditching effort. Based on dominant environmental drivers, five post-drainage phases can be defined: (i) ditch establishment, (ii) stand development, (iii) peat decomposition, (iv) disturbance regime shift, and (v) stand replacement (Fig. 1 in **I**). The succession may be further modified by (vi) various socio-economic processes that keep drained forests under intensive use. The main biodiversity concerns vary among the phases. Several positive feedback mechanisms have been discovered that enhance the succesion and its irreversibility (Table 1 in **I**).

Although the general impact of forestry drainage is rather well known and studied during at least 150 years, the main focus has stayed on vegetation, especially on tree growth. Compared with over 46 studies about drainage impacts on ground vegetation (and much more on trees), there are only 68 studies on all other species groups (Fig. 2). Moreover, studies on species of conservation concern (SPEC) form only 4–13% among the biodiversity studies. In general the mechanisms driving the post-drainage changes in biodiversity have been only proposed, not tested or even not measured.

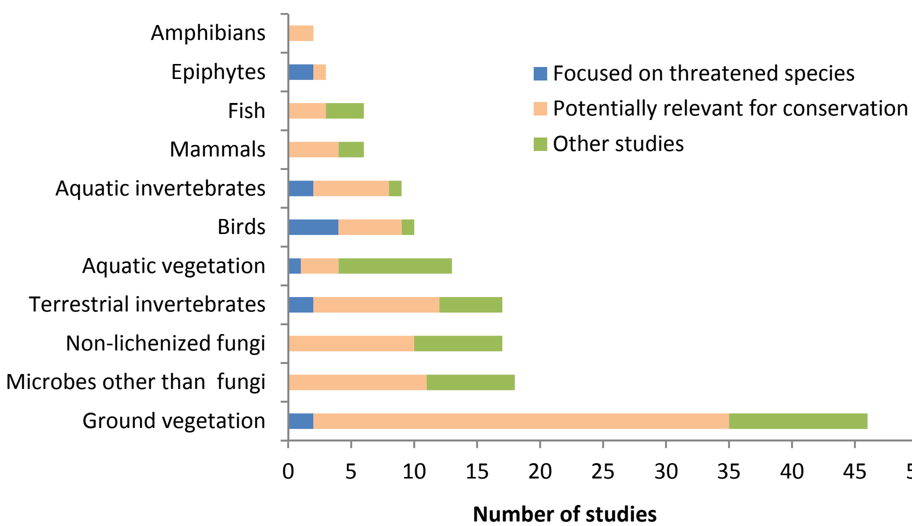

Figure 2. The number of forestry drainage studies documenting biodiversity impacts, and their presentation of species-level data of conservation relevance (threatened-species studies; potentially relevant i.e. assemblage studies). Note that the effort for searching studies on ground vegetation was much smaller than for studies on the rest of the biota. Data extracted from Table 2 in paper **I**.

3.2. Species turnover and loss in drained swamp forests (II)

Drainage affected stand-scale species richness in swamp forests only weakly (in contrast to the strong effect of clear cutting; Fig. 2 in **II**) but it profoundly changed assemblage composition. In every studied taxon group, the species composition differed significantly in undrained and drained plots of at least one management type (Table 3 in **II**). High species turnover was seen also in total numbers of species that were characteristic or unique to either undrained or drained state (Table 1).

All taxonomic groups combined, undrained swamps hosted on average 25 SPEC (range 13–45) compared to 18 (5–36) SPEC per drained plot. Negative drainage impact was clearest for cryptogams (bryophytes and lichens) in closed stands. Among all significant indicators of undrained sites, forest-dwelling lichens formed the largest group with 42 species; undrained forests were also preferred by the majority of specialist hepatics. Seven SPEC were significant indicators of old growth swamp forests: the hepatic *Geocalyx graveolens*, macrolichens *Lobaria pulmonaria* and *Menegazzia terebrata*, and microlichens *Arthonia byssacea*, *A. leucopellaea*, *A. vinosa* and *Pertusaria flavida*. Among vascular understory plants and snails, no indicator species of undrained old growth were detected, but drainage modified their general assemblage composition in forests (except in snails in old growth).

In cutover sites, lichen species composition responded to drainage as well, and this effect was also observed for hepatics in retention cuts and for plants in clear cuts. The two detected significant indicator SPEC for cutovers – the fern *Dryopteris cristata* and the snail *Carychium minimum* – characterized undrained sites (Table 3). In general, seven of the nine significant indicators among snails were characteristic to undrained swamps, notably to cutovers. Sedges (*Carex* spp.) also tended to prefer natural swamps: there were seven indicator species for undrained and only two for drained sites.

Table 1. The extent of post-drainage turnover in mobile-water swamps: the total species numbers of herbs, dwarf shrubs, bryophytes, lichens, and snails recoded in study **II**. There were altogether 857 species, including 155 species of conservation concern (SPEC). Significant indicators of either drained or undrained plots (according to indicator species analysis; ISA) can be tentatively considered as disappearing and appearing after drainage, respectively.

Site type	No. of species (no. of SPEC)			
	Total	Significant indicators		Unique[b]
		n	%[a]	
Undrained (20 plots)	709 (103)	130 (27)	22	98 (25)
Drained (24 plots)	750 (117)	112 (7)	18	135 (50)

[a] of all species included to ISA
[b] excluding significant indicators

Table 2. The species with highest significant indicator values (according to ISA) for combinations of drainage and management type in swamp forests (extracted from the supplementary tables S1-S4 in **II**, see table 4 in **II** for futher details about the analyses).

Habitat type	Indicator species and the indicator value			
	Herbs and dwarf shrubs	Bryophytes	Lichens	Snails
Undrained swamps	*Myosotis scorpioides 52*	*Campylium stellatum* 49	*Cladonia digitata* 62	*Cochlicopa lubrica* 59
Forest	*Menyanthes trifoliata* 54	*Pylaisia polyantha* 52	*Sarea resinae* 54	*Nesovitrea hammonis* 35
old growth		*Riccardia palmata* 68	*Opegrapha varia* 72	
mature	*Filipendula ulmaria* 31	*Calliergonella cuspidata* 41	*Caloplaca flavorubescens* 49	
Cutover	*Typha latifolia* 63	*Drepanocladus aduncus* 34	*Micarea denigrata* 55	*Euconulus alderi* 48
Drained swamps	*Melica nutans* 50	*Brachythecium rutabulum* 56	*Psilolechia clavulifera* 29	
Forest	*Actaea spicata* 50	*Chiloscyphus polyanthos* 37	*Micarea prasina* 43	
old growth	*Epilobium montanum* 57	*Ptilium crista-castrensis* 52		
mature	*Fragaria vesca* 50	*Eurhynchium pulchellum* 48	*Lepraria jackii* 50	
Cutover	*Calamagrostis epigeios* 35	*Ceratodon purpureus* 41	*Rinodina pyrina* 48	*Vallonia costata* 40

Table 3. The species of conservation concern with highest significant indicator values (according to ISA) for combinations of drainage and management type in swamp forests (extracted from the supplementary tables S1-S4 in **II**, see table 4 in **II** for futher details about the analyses).

Habitat type	Indicator species of conservation concern and the indicator value			
	Herbs and dwarf shrubs	Bryophytes	Lichens	Snails
Undrained swamps	*Carex disperma* 37	*Callicladium haldanianum* 57		
Forest		*Neckera pennata* 39	*Chaenotheca ferruginea* 56	
old growth		*Geocalyx graveolens* 67	*Menegazzia terebrata* 67	
mature				
Cutover	*Dryopteris cristata* 45			*Carychium minimum* 50
Drained swamps		*Campylium halleri* 40		
Forest		*Nowellia curvifolia* 47	*Chaenotheca stemonea* 48	
old growth				
mature			*Pertusaria pupillaris* 56	
Cutover				

3.3. Conservation value of drainage-created habitats (II–III)

Drainage-created ecosystems served as suitable habitats species that either survived despite the drainage impact or colonised the area after the ditching. Among the non-aquatic species found from undrained swamps, about 78% appeared rather indifferent to drainage (Table 1). The aquatic model taxon, brown frogs, also seemed to represent survivors: no difference was detected in brown frog preferences for breeding in drained vs. natural areas, and 40% of the breeding sites were in ditches (20% in natural water bodies; **III**).

The colonisers of drained terrestrial habitats typically represented post-disturbance, successional, and generalist species that readily occupy cutovers and managed forests; they included only seven SPEC. Vascular plants of the understory comprised the largest group, particulary on cutovers (Table 4 in **II**). Thirty-four species of vascular plants appeared as significant indicators for drained cutovers and 33 species (some of them rarities that did not pass the ISA) were only found there. Most of these species are characteristic of dry meadows or disturbed areas in Estonia. Drained cutovers also had 13 species of indicator lichens (mostly on deciduous tree regeneration, logging residues and stumps) – considerably more than drained old growth (4 indicator lichens). Most of the 18 indicators of drained mature stands were sparsely growing plants of eutrophic forests or lower-trunk inhabiting lichens. These same two types of indicator species were represented among the general drained-forest indicators (old growth and mature stands pooled) (Table 2 and 3).

3.4. Habitat features explaining the drainage impact

Soil characteristics were apparently the main factor affecting the distribution of TWBs in Estonian forest and fen landscapes (**III**). Water bodies were distinctly scarcer (<280 m^2 open water ha^{-1}) on dry-to-moist and nutrient-poor wet soils than on nutrient-rich wet soils (>320 m^2 open water ha^{-1}; Table 1 in **III**). Drained sites had a different set of small water bodies than undrained sites, but their total area and mean depth did not differ. On drained wet soils, ditches became dominant, partly replacing natural TWBs (Fig. 3); the median total cover of natural lentic TWBs being 32 and 146 m^2 ha^{-1}, respectively (Wilcoxon test: P=0.071). Ditches, compared with natural lentic TWBs, had generally more peaty sediment and were deeper (informative predictors in five out of seven clusters, FSL). Ditches were also more permanent: in six out of seven double-checked transects, ditches formed a larger proportion of total water cover in drier season, while natural lentic TWBs were relatively abundant in wetter season.

Those drainage-affected characteristics were not significantly related to the incidence of breeding of brown frogs. Instead, the frogs preferred anthropogenic water bodies and clear cuts in the surroundings (univariate logistic regression: P=0.010 and P=0.024, respectively). Bivariate logistic models, which combined co-varying factors, indicated that the preference for clear cuts was well explained by less shading and also by a greater proportion of anthropogenic water bodies (Appendix 3 in **III**). The frogs' preference for anthropogenic water bodies, however, remained independent of other habitat factors.

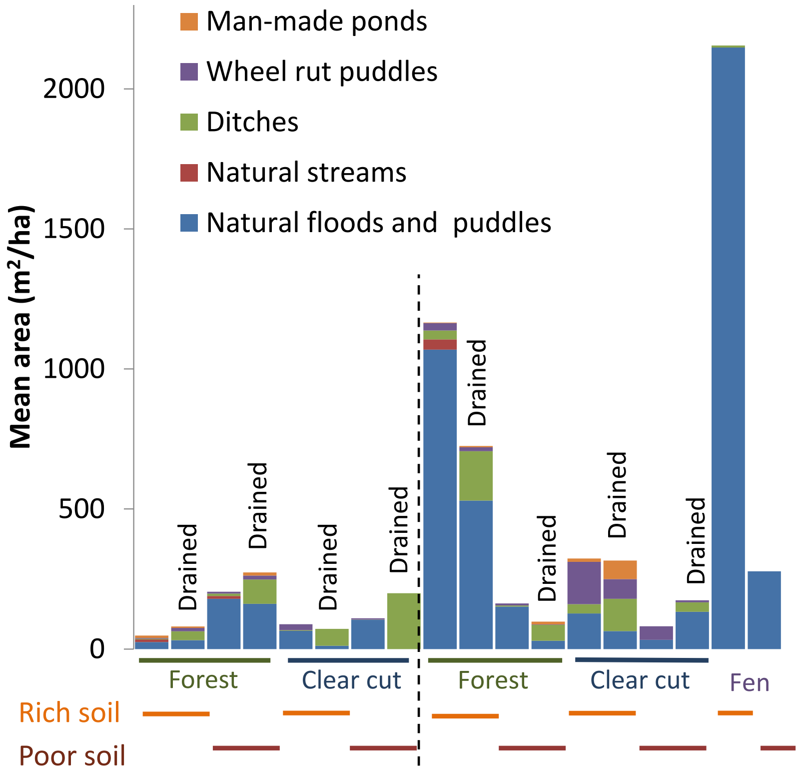

Figure 3. Mean area of different types of water bodies by habitat type on random transects in Estonia. Dashed line separates habitats on dry-to-moist soils (left) and wet soils. Data extracted from Table 1 in **III**.

Old drained swamp forests had a reduced canopy-tree diversity and CWD continuity compared with undrained old growth. A similar comparison for managed forests showed changes in tree species composition: fewer black alders and more Norway spruce in drained stands (Table S5 in **II**). At least one of these drainage-sensitive structural characteristics was significantly related to assemblage composition in every taxonomic group explored (Fig. 4; Table S5 in **II**). In forests, eight stand-structural characteristics also correlated significantly with species richness; cryptogam SPEC being clearly most structure-dependent (Table S6 in **II**). Combining these effects with the incidence of drainage in general linear models revealed the appearance of a marginal main negative effect of drainage for lichen SPEC ($P<0.1$) when either tree species diversity or the volume of logs was accounted for; a similar tendency was observed for hepatic SPEC ($P=0.1$) when accounting for the volume of logs.

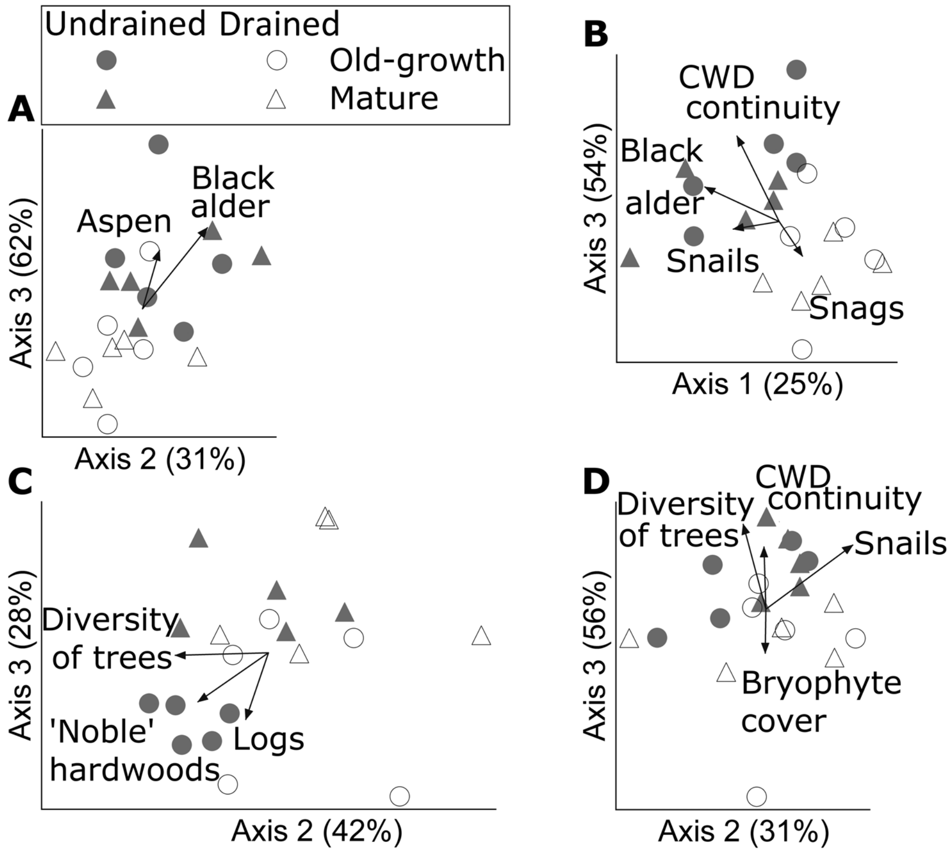

Figure 4. NMS ordination diagrams of the species' assemblages in swamp forests (**II**). (A) herbs and dwarf shrubs, (B) bryophytes, (C) lichens, (D) snails. The two most representative axes (% variance explained indicated in titles) of the 3-dimensional solutions and environmental factors correlated with these axes at combined $r^2 > 0.2$ are shown (all factors are listed in Table S5 in **II**). Note that the factor 'Snails' refers to total snail abundance. Assemblage differences between undrained and drained sites and swamp sites for a given management type were always significant (except for snails in old growth).

3.5. Indicators and focal species for drainage management

Out of the 884 species recorded in Study **II**, four forest cryptogams were extracted as potential focal species to provide conservation guidance in drainage management: two epiphytic lichens (macrolichen *Menegazzia terebrata*, microlichen *Arthonia vinosa*), the hepatic *Riccardia palmata* that inhabits well-decayed fallen trunks, and highly moisture-dependent hepatic *Trichocolea tomentella*. There were two stand structural characteristics that mitigated the drainage-caused reduction of lichen and hepatic biota in swamp forests: higher tree species diversity and volume of logs.

For brown frogs and macroinvertebrates, man-made ponds (to a smaller degree also ditches and wheel rut puddles) seemed to serve as alternative habitats in drainage-transformed landscapes (**III–IV**). Macroinvertebrate assemblages differed significantly between the mitigation ponds and random water bodies (MRPP: $P<0.001$). Twenty-three families recorded in the ponds were not found in the random forest water bodies, and eleven families were significantly more common in the ponds (Table S1 in **IV**). Dragonflies and damselflies were found only in the the ponds, including two species of European conservation concern: *Aeshna viridis* and *Nehalennia speciosa*. The difference seemed to be caused primarily by a greater depth and thus longer hydroperiod of the ponds, although mineral sediment (sand/clay), less acidic water and shade possibly contributed as well (Table 1 in **IV**).

4. DISCUSSION

4.1. Threatened species and crucial habitat components in drained forests

Most studies about forestry drainage impacts on biodiversity have been conducted in climatic zones and site types with modest tree diversity and/or document short-term effects only. This explains why the importance of overstorey composition and stand structure have rarely been assessed (**I**). The case study (**II**) clearly showed that, in temperate alder swamps, the main drainage influence (notably on cryptogams) is mediated by specific microhabitat changes. In the studied case, the economically desirable increase of Norway spruce was accompanied with decreases in the black alder and “noble” hardwoods. The latter was a keystone structure for swamp-forest lichens, including many rare species (e.g. nationally protected *Pyrenula laevigata*, and *Arthonia byssacea*). Those findings about epiphytic cryptogams in swamp forests indicate a major role of tree species replacement in mediating the drainage impact (phase 5 in Fig. 1 in **I**). Additional mechanisms, proposed for ground lichens in sparsely wooded mires (Sarasto 1961, Laine et al. 1995a), include an initial increase after water level lowering and Sphagnum decline (phase 1) and a later decline due to canopy shade (phase 2).

Old swamp forests are known to be cryptogam diversity hotspots (Ohlson et al. 1997) but study **II** indicated that after long-term ditching such forests can lose species of conservation concern (notably lichens and hepatics) even without logging. The sensitivity of swamp-forest cryptogams in **II** was further confirmed by the fact that the clearcutting origin of forests (i.e., the difference between old growth and mature stands) mattered more in undrained than drained sites. The latter concurs with what Rosenvald et al. (2011) reported for birds.

The dominance of Norway spruce is a typical convergent feature in North-European post-drainage successions (**I**, and references therein), which might have broad influence on several species groups such as understory vegetation and birds (Table S1 in **I**). Unexpectedly, spruce abundance was not related to assemblage characteristics in any taxonomic group studied (**II**). Apparently, spruce was present in the study plots (at least in the undergrowth) in sufficient numbers to host its specific species; an alternative explanation is that its substrate value changed with drainage. The influence may also depend on other tree species in these typically mixed stands; for example, snails respond to the variation from broad-leaved to needle-dominated litter (Kralka 1986). This might explain a distinct drainage impact on snails in drained mature stands, where the increase of spruce was greatest and accompanied with a loss of black alder (a small sample size may explain why the significance of those changes was not confirmed by the NMS analysis).

A potentially influential feature that was not measured in Study **II**, was a change in temporary water bodies within drained sites (**III**). This factor may be responsible for the reduction of aquatic and hydrophious terrestrial molluscs, e.g. *Euconulus alderi* and *Carychium minimum* (Table 2–3), which often occur in such habitats (**IV**). Draining seemed to shorten the hydroperiod of temporary water bodies (**III**), which definitely is a key factor for their biota and functioning (Colburn 2004). The studies about the impacts of drainage on water bodies within the drainage system are rare. The existing data suggest, however, that decreased persistence of small water bodies in drained forests may transform them to ‘ecological traps’ for amphibians (Suislepp et al. 2011) and unsuitable for specialist invertebrates (Ilmonen et al. 2012).

The impact of forest drainage on the breeding of brown frogs is multifaceted (**III**; Suislepp et al. 2011). As these frogs prefer sun-exposed breeding waters, the invasion of woody vegetation due to drainage, and decline of grazing and mowing in wetlands (Sjöberg and Ericson 1997) can worsen the conditions for larval development. In addition to a full loss of natural water bodies, hydroperiods may become shorter and less predictable, so that larvae dry out more probably before the metamorphosis. On the other hand, ditches and other anthropogeneous water bodies can provide novel habitats suitable for amphibian reproduction (also **IV**). The net effect on breeding sites of brown frogs has not been explicitly documented (Elmberg 1993). Study **III** indicated that the negative and the positive effects can balance each other. However as the number of individuals and breeding success was not estimated, the detailed impact of forestry drainage on brown frogs remains to be studied.

4.2. Mitigating drainage impacts on biodiversity

The biodiversity target and the habitat management options constitute the two strategic decisions, necessary for any systematic approach to integrating forestry draining with conservation aims. Both these decisions depend on landscape context (Fig. 2 in **I**). To operationalize the biodiversity target, it is further necessary to select representative ‘focal species’ from sets of sensitive species (Lambeck 1997). Such practices have been lacking because studies on drainage-impacted threatened species remain scarce, even on otherwise well studied plants (**I**). Based on a large number of species, the study **II** accomplished such a procedure – first defining the sensitive (‘indicator’) species and then extracting conspicuous, moderately rare species of conservation concern as potential focal species. It appeared that at least in alder swamps (but probably elsewhere as well), epiphytes should gain more attention and that long species lists should be examined to identify a few practical focal species. The proposed focal lichens, *Menegazzia terebrata* and *Arthonia vinosa*, are relevant for European boreonemoral hardwood-spruce swamps. The hepatic *Riccardia palmata* might be suitable also in Fennoscandian spruce swamps, as it grows both on fallen conifer and alder trunks. The hepatic *Trichocolea tomentella* represents moisture dependent species in hardwood-spruce swamps.

The case studies on species rich taxon groups, stand structure and water bodies showed that habitat quality of drained forests is not unambiguously impoverished, and that the occurrence of threatened species depends on the remnant or novel structures. Thus, some focal species can be sustained in managed forests that are not in intensive use (see 2.2).

High total species richness in combination with massive long-term turnover after drainage indicates a multitude of positively and negatively affected species in drained landscapes (**I–II**). Obviously, those individually responding species cannot be protected with the same management approaches. Support to such high turnover rates comes from bird studies in the same sites as study **II** (Rosenvald et al. 2011) as well as from vegetation studies in Finnish spruce swamps (Maanavilja et al. 2014) and Latvian mixotrophic sites. In the latter, the major change in vegetation took place already in the first post-drainage years (Āboliņa et al. 2001).

In order to assess the contribution of drained forests that are situated in protected areas, it is important to know whether drained forests can host species of conservation concern. Study **II** showed that drained old growth hosted very few specific species compared to undrained sites. Thus such stands cannot provide quality habitats for old growth species of drier forest types and/or such species cannot colonise drained forests within two forest generations (the forest-age criterion in study **II**). Those species still need forest-type specific set-asides. On the other hand, drained old-growth hosted several threatened species that are less demanding in relation to site type. Long-term monitoring is needed to establish whether such old, slow-changing drained stands could sustain such target species in a long run (Lõhmus and Kull 2011).

More generally, biodiversity planning would benefit from assessing the values of various anthropogeneous habitats (Hulvey et al. 2013; Fig. 2 in **I**). How to assess, for example, the habitat value of clear cuts – widespread consequences of modern forestry, in combination with ditching impacts? Both conceptually (Fig. 2 b–c in **I**) and based on the case studies **II–III**, there appear to be two broad types of habitat values. First, the occurrence of water bodies can make clear-cuts suitable for the breeding of brown frogs (**III–IV**). Secondly, wet clear cuts were preferred by some plants and snails of conservation concern. These included the fern *Dryopteris cristata* and land snails *Carychium minimum* and possibly also the rare *Vertigo angustior* and *V. lilljeborgi*. For such species it would be necessary to tolerate watering up in clear cuts (Fig. 2 in **II** e). In order to provide habitat for multiple species groups, including sensitive plants and deadwood dwellers, full scarification of cutover sites is not recommended (**II**).

At the water-body scale, abundant wheel rut puddles on wet clear cuts (Fig. 3, Fig. 2 c in **I**) might replace treefall pit puddle habitats. The latter were rare in clear cuts (**II–III**), but probably prevail in natural forests shaped by wind disturbance. In contrast, ditches are characterized by novel features, when compared to the small natural lentic and lotic water bodies that are reduced after drainage (**III**). Indeed, ditches do not provide quality habitats for those fish species that are specialized to natural streams (Rosenvald et al. 2014). However, in homogeneously drained forests, ditches provide distinct habitat qualities – aquatic and wet terrestrial habitat, open conditions and exposed soil (Table S2 in **I, II–IV**).

In order to enhance biodiversity value of drained forest, special mitigation tools should be developed for structural key components, such as tree stand and ditch network structure (Fig. 2 d, f in **I**). Ideally, the mitigation measures would enhance biodiversity more than they reduce timber production. A general way to address this is to target the measures simultaneously at multiple species and to distribute them to spatially most effective sites (**IV**). Selection of the most appropriate conservation tools is facilitated by best practice frameworks and decision trees, which have been elaborated, e.g., for specific sedimentation traps (Marttila et al. 2010). Good examples also exist for restoration activities (Armstrong et al. 2009, Similä et al. 2014). Case studies testing the effectiveness of drainage-mitigation measures on biodiversity remain scarce. However, the effectiveness of well-designed ponds for amphibian and aquatic invertebrates rehabilitation has been shown (Brown et al. 2012, Rogers 1998, **IV**). More frequent vegetation removal under power lines in drained areas can generate alternative habitat for mire butterflies (Komonen et al. 2013, Fig. 2 b in **I**). For swamp forest lichens and hepatics of conservation concern, retaining abundant deadwood and diverse canopy, is a possible drainage mitigation tool probably due to enhanced ground-habitat heterogeneity and substrate provision (**II**). In fact, most cryptogam SPEC preferring drained forests (but also occurring in undrained swamps) were confined to well-decayed fallen trunks.

The general implication based on this thesis is to apply appropriate management approaches according to landscape context. The impacts of forestry drainage cannot be simply eliminated: they transform the whole ecosystems and landscapes, including species assemblages, and the change are hardly (if ever) reversible over management time-frames. It is therefore important to acknowledge the valuable habitat components and associated threatened species found in drained forests. The research to support biodiversity conservation practises includes assessing less studied but potentially sensitive species groups, details of the impact mechanisms, searching for and testing of focal-species and habitat management approaches.

5. CONCLUSIONS

(i) Research on the impacts of forestry drainage on biota has mainly been focused on vegetation, especially on tree growth, whereas threatened species have gained very little attention. Drainage impacts remain surprisingly poorly known on a wide range of presumably sensitive organisms, such as epiphytes and (semi)aquatic biota within drained sites, and the mechanisms driving the post-drainage changes are not well established.

(ii) The changes caused by forest drainage are complex and occur at varying severities, so that one cannot speak about 'general drainage impact'. Ditching initiates a chain of largely irreversible changes, which can be divided into five phases based on dominant environmental drivers: (1.) ditch establishment, (2.) stand development, (3.) peat decomposition, (4.) disturbance regime shift, and (5.) stand replacement. The succession may be further modified by (6.) various socio-economic processes that keep drained forests under intensive use.

(iii) Drainage profoundly affects species assemblage composition, but not necessarily site-scale species richness. There are large numbers of positively and negatively affected species over different time frames; these species cannot be protected using a single management approach. Hence, biodiversity conservation can be conciled with forestry drainage only through planning on the landscape level.

(iv) Vast number of species should be examined to identify a few representative biodiversity targets for drainage mitigation programmes. At least in swamps, epiphytes and dead wood dwellers should gain more attention as possible focal species.

(v) Old swamp forests were rich in threatened lichens and bryophytes – the taxon groups that were in general more sensitive to the changing stand structure than snails and vascular plants. In general, stand structural changes (e.g. dead wood qualities and amounts) mediate the drainage impacts to a large proportion of forest biota.

(vi) Effectiveness of drainage mitigation can be increased by preferring multi-functionality techniques. In this study, the ponds initially designed for brown frogs, also provided quality habitat for macroinvertebrates that were uncommon in the surrounding forests.

(vii) Temporary and small water bodies are an integral part of forest and fen landscapes and their distribution varies mostly according to soil conditions. Forest management primarily changes the features of such water bodies rather than their total abundance. Some novel aquatic habitats that are created by forest management seemed to (partly) substitute natural ones for brown frogs. However, their quality for population survival and for other aquatic and semi-aquatic species remains to be studied.

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* * *

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KOKKUVÕTE

Metsakuivenduse mõju bioloogilisele mitmekesisusele ja elupaikadele: järeldused säästlikuks majandamiseks ja looduskaitseks

Sood ja enamik metsadest asuvad piirkondades, kus sademed ületavad oluliselt aurumise. Selle tulemusena on suurel osal maismaast tüüpiliseks loodusmaastikuks metsa, soode ja veekogude mosaiik, kus mitmekesised hüdroloogilised tingimused suurendavad elurikkust. Märgi metsi kuivendatakse puidutootlikkuse suurendamiseks, raiesmike soostumise takistamiseks ja metsamasinate liikumise hõlbustamiseks. Kuivendamise eeldusteks on soostumist põhjustav kliima ja reljeef, kuid ka arenenud metsandussektor, millel on endal suutlikkust või toetajaid, et vähem tootlike metsade majandamisse investeerida. Seepärast on peamiseks kuivenduspiirkonnaks olnud Fennoskandia, Briti saared, Venemaa Euroopa-osa ja Balti riigid, aga tänapäeval ka Kagu-Aasia troopilised soometsad. Peamiselt on kuivendatud toitainerikkaid hõreda puistuga soid ning märgi arumaid, kuid paiguti, sageli edutult, ka lagesoid. Labidatööna kuivendati metsi mõnel pool Euroopas juba 18. sajandil. Ulatuslikuks maastike kujundajaks sai kuivendus aga 20. sajandi keskel, muutes maastikke ühtlaselt metsasemaks, vähendades turvasmuldade pindala ning vormides terveid valgalasid lineaarseteks kraavivõrkudeks.

Metsakuivendus mõjutab ökosüsteemi võtmekomponente – hüdroloogiat ja domineerivaid organisme (puid, turbasamblaid) – ning nende kaudu kogu elukooslust ja ökosüsteemi toimimist. Põhjavee tase hakkab langema kohe pärast kraavide kaevamist. Paljud teisesed ning aeglastest protsessidest, nagu puistu kasv ja turba lagunemine, tingitud muutused ilmnevad aga pika viibega. Mõju elustikule ongi reeglina aeglane, liigiomane ja sageli kaudne, kuid suhteliselt hästi on kirjeldatud ainult selle majanduslikult olulised aspektid, nagu puude kasv, marja- ja seenetoodang, aga ka muutused alustaimestikus, mida on kasutatud praktilises metsanduses kasvukohtade klassifitseerimiseks.

Kuivendusmõju leevendamiseks on seni kasutusel all-loetletud meetmed. 1. Tugevalt kuivendatud metsadega ja/või arenenud riikides on üldiselt loobutud uute kuivendussüsteemide rajamisest. 2. Kraavivõrkude väljavooludele on hakatud settelõkse rajama. 3. Suur osa säilinud looduslikest märgalakompleksidest on võetud kaitse alla. 4. Kuivendatud märgalade looduslikkust püütakse taastada, eriti kaitsealadel. 5. Kaitsealade koosseisu on haaratud kuivendatud metsi, kuna need paistavad sobivat mõnedele ohustatud liikidele, kuid selle mõju elurikkuse püsimisele on täpselt teadmata. 6. Lõheliste populatsioone on püütud taastada õgvendatud ojade voolusängide mitmekesistamisega.

Käesolev töö koondab ja süstematiseerib senised teadmised metsandusliku kuivenduse mõjust elurikkusele. Koguti uut olulist teavet kuivenduse mõjude leevendamisvõimalustestest ning pikaajalise kuivenduse mõjudest väikestele metsaveekogudele, toitainerikastele märgadele metsadele ja nende elustikule.

Töötati läbi asjakohane teaduskirjandus (**I**) ja viidi läbi kolm uuringut Eestis (**II–IV**). Eesti sobib hästi pikaajalise kuivendusmõju uurimiseks oma soise maastiku ja pika metsandusajaloo tõttu. Enamik Eesti metsakuivendussüsteemidest on kaevatud 1950. ja 1980. aastate vahel ning 300 000 ha metsi on pikaajalise kuivenduse tulemusena jõudnud juba kõdusoo staadiumini.

Uuritavate liigirühmade (samblikud, taimed, selgrootud ja kahepaiksed) ning elupaigakomponentide (väiksed ja ajutised veekogud, lodumetsade puistuelemendid) valik lähtus nende eeldatavast kuivendustundikkusest ja senisest vähesest uuritusest. Kasutati võrdlevaid meetodeid kolmes mastaabis. Veekogu mastaabis käsitleti pruunide konnade (raba- ja rohukonn; *Rana arvalis, R. temporaria*) sigimiseelistusi Eesti metsamaastikel (**III**) ja võrreldi Hiiumaale kuivendusmõjude leevendamiseks rajatud tiikide faunat tavaliste metsaveekogude omaga (**IV**). Puistu mastaabis uuriti puistu struktuuri ja maismaaelustikku loodusliku veerežiimiga lodudes ja neist tekkinud jänesekapsakõdusoodes, käsitledes eraldi põlismetsi, küpseid majandusmetsi ning lage- ja säilikraiesmikke (**II**). Maastiku mastaabis uuriti vee-elupaikade hulka ja omadusi metsa, madal- ja siirdesoo juhutransektidel üle Eesti.

Kirjanduse ülevaade osundas, et kraavitamine vallandab suuresti pöördumatute muutuste ahela, mille võib lähtuvalt peamisest ökosüsteemi kujundavast keskkonnategurist jagada viide järku: 1. kraavide kaevamine, 2. puistu kasvu hoogustumine, 3. turba lagunemine, 4. häiringurežiimi teisenemine ja 5. puistu koosseisu teisenemine. Pöördumatust põhjustavad mitmesugused ökoloogilised ja sotsiaalmajanduslikud tagasisidemehhanismid. Näiteks tihenenud puistu võrastik püüab suure osa sademetest kinni enne, kui need maapinnale jõuavad (seetõttu kuiveneb muld veelgi) ja vajadus teenida tagasi kraavituse kulud toob kaasa intensiivse majandamise. Ainult väike osa seni metsakuivenduse elustikumõju uurinud töödest on pööranud tähelepanu ohustatud liikidele ning sageli on toimemehhanisme vaid oletatud.

Taimede, samblike ja tigude liigirikkus kuivendatud ja looduslikes lodudes (**II**) ei erinenud oluliselt, kuid viimastest leiti rohkem looduskaitseliselt tähelepanuväärseid liike. Seitse sellist liiki olid põliste lodumetsade indikaatorid: maksasammal haisev maakarikas (*Geocalyx graveolens*), suursamblikud harilik kopsusammal (*Lobaria pulmonaria*) ja harilik poorsamblik (*Menegazzia terebrata*) ning pisisamblikud rant-tähnsamblik (*Arthonia byssacea*), valkjas tähnsamblik (*A. leucopellaea*), puna-tähnsamblik (*A. vinosa*) ja lumisamblik *Pertusaria flavida*. Kokku 884 leitud liigi seast valiti välja potentsiaalsed suunisliigid, kellest lähtuvalt metsakuivendust looduskaitseliselt korraldada: harilik poorsamblik ja puna-tähnsamblik ning maksasamblad kämmalrikardia (*Riccardia palmata*) ja viltjas udesammal (*Trichocolea tomentella*).

Ükski leitud soontaime- ega maismaateoliik põliseid lodumetsi statistiliselt oluliselt ei eelistanud, kuid kuivendus mõjutas nende liigilist koosseisu metsades (v.a. tigudel põlismetsades). Raiesmikelt leiti kaks iseloomulikku looduskaitseväärtusega liiki: suga-sõnajalg (*Dryopteris cristata*) ja väike kääbustigu (*Carychium minimum*), kes mõlemad olid omased kuivendamata lodudele.

Kuivendatud alad polnud üheselt vaesunud, vaid neil leidus väärtuslikke elupaigakomponente ja palju ohustatud liike. Sealses elustikus eristati kuivenduse suhtes vähetundlikud liigid ja liigid, keda kuivendus soosib. Viimaste seas moodustasid valdava osa niisugused raiesmikelt leitud soontaimed, mis üldiselt kasvavad kuivadel niitudel ja häiringualadel (**II**). Vähetundlike liikide hulka hinnati 78% lodudest leitud liikidest (**II**) ning – vee-elustikus – pruunid konnad, kelle sigimisveekogudest 40% olid kraavid ja 20% looduslikud lombid. Pruunid konnad eelistasid kudemiseks inimtekkelisi veekogusid ning raiesmikke. Sellised laialt levinud inimtekkelised elupaigad ilmselt osaliselt asendavad kuivendusega hävinud avatud märgalasid, aitavad tasakaalustada looduslike veekogude kuivamise negatiivset mõju, seega täiendavad looduskaitsemeetmeid.

Looduskaitsemeetmeid kasutatakse sageli just karismaatiliste liikide kaitseks, neid on aga võimalik ühendada muude looduskaitseeesmärkidega (**IV**). Hiiumaale konnade sigimise soodustamiseks ja sellega euroopa naaritsa toidubaasi suurendamiseks kaevatud tiigid täitsid oma põhieesmärki ning lisaks pakkusid elupaika mitmekesisele selgrootufaunale, mis erines metsaveekogude omast. Erinevus oli tingitud peamiselt tiikide suuremast sügavusest, aga võimalik, et ka päikesele avatusest, liivasemast-savisemast põhjast ja vähem happelisest veest. Näiteks leiti tiikidest Euroopas ohustatud rohe-tondihobu (*Aeshna viridis*) ja pisiliidrik (*Nehalennia speciosa*).

Ajutiste ja väikeste veekogude pindala Eesti metsades, siirde- ja madalsoodes mõjutasid eelkõige looduslikud mullatingimused (**III**). Veekogude kogupindala oli väiksem (<280 m^2 ha^{-1}) kuivadel ja toitainevaestel märgadel muldadel kui toitainerikastel märgadel muldadel (>320 m^2 ha^{-1}). Kuivendatud aladel oli veekogude kogupindala sarnane, aga looduslikud seisuveekogud olid osaliselt asendunud kraavidega, mis olid seejuures turbasema põhjaga, sügavamad ja püsivamad.

Suurele osale elustikust mõjub kuivendus puistuga seotud mikroelupaikade aeglase muutumise kaudu (**II**). Põhja-Euroopas on tüüpiline erinevate kuivendatud metsade muutumine kuusikuteks (**I**), kuid uuring **II** eristas olulise mõjuna ka vanade lodumetsade mitmekesisema puuliigilise koosseisu ja jämeda kõdupuidu kõduastmeti ühtlasema jaotuse. Vähemalt üks kuivendustundlik puistu struktuuri tunnus (kuigi üllataval kombel mitte kuuskede tihedus) seostus liigilise koosseisu varieerumisega kõigis vaadeldud liigirühmades. Samblad ja samblikud olid puistu struktuuri muutumise suhtes kõige tundlikumad, kusjuures puistu mitmekesisus ja lamapuude rohkus vähendas kuivenduse negatiivset mõju ohustatud liikide arvule nendes rühmades. Seda asjaolu tasub arvestada kuivenduse mõju leevendamisvõimalusi välja töötades.

Töös kirjeldatakse esmakordselt süsteemset lähenemist metsakuivenduse ühendamiseks looduskaitse eesmärkidega. Selleks tuleb maastikust lähtuvalt valida elustiku sihtrühm, piiritleda seal suunisliigid, ning jaotada maastikuplaneerimise kaudu puistud nelja peamisse majandamisvõtete gruppi (**I**). Väheste sobivate suunisliikide leidmiseks tuleb läbi analüüsida sadade liikide leiuandmed, kuid vähemalt lodumetsa kuivendusmõjude puhul osutusid kõige perspektiivsemateks epifüüdid ja kõdupuiduelustik (**II**). Kuna kuivendatud metsamaal soovitakse elurikkuse säilitamise kõrval tavaliselt ka puitu toota, tasub valida eriti tõhusad looduskaitsevõtted, suunata need võimalikult paljudele sarnaste nõudlustega liikidele ja maastikus kõige tõhusamatesse paikadesse ning tulemusi seirata (**IV**). Edasine teadustöö peaks keskenduma väheuuritud, kuid tõenäoliselt tundlikele liigirühmadele, täpsematele mõjumehhanismidele ning otsima ja testima suunisliike ja säästliku majandamise võimalusi.

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PUBLICATIONS

CURRICULUM VITAE

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Honours and Awards:

III prize in Contest for Students' Scientific Research, organised by the Estonian Ministry of Education, 2011

Research interests: conservation biology, sustainable forestry, ecology of terrestrial and freshwater snails and amphibians

Publications:

Remm, K., Linder, M., **Remm, L.** 2009. Relative density of finds for assessing similarity-based maps of orchid occurrence. *Ecological Modelling*: 220: 294–309.

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Conference presentations and courses:

Remm, L., Lõhmus, A., poster presentation "Soil conditions affect land snail community more than disturbances caused by non-intensive forestry activities", Student Conference on Conservation Science, 22–24 March 2011, Cambridge, Great Britain.

Remm, L., Lõhmus, A., Lõhmus, P., Leis, M., oral presentation "Drainage impact on forest biodiversity: Long-term artificial forest drainage affects terrestrial forest biodiversity by cumulative indirect effects", European congress of Conservation Biology 28 August – 1 September 2012, Glasgow Great Britain.

Participation in field course "Educative and Participative Monitoring for Amphibian Conservation", 9–15 June 2014, Białowieża and Narew, Poland.

Remm, L., Lõhmus, A., Rannap, R., oral presentation "Temporal and small water bodies in modern forests: a landscape-scale assessment in Estonia" International Wetlands Conference Wetlands Biodiversity and Services: Tools for Socio-Ecological Development, 14–18 September 2014, Huesca, Spain.

Dissertation supervised:

Maarja Vaikre, Master's Degree, 2012, "Impact of forest drainage on macroinvertebrates of small water bodies", University of Tartu.

Other interests and affiliations:

Kiristaja, P., Ehlvest, A. Remm, L. 2014 "Eesti kojaga maismaatigude määraja" Loodusajakiri 2014. Tallinn (Identification guide to terrestrial snails of Estonia).

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Teaduspreemiad ja -tunnustused:
III preemia Eesti Vabariigi Haridus ja Teadusministeeriumi üliõpilaste teadustööde riiklikul konkursil, 2011

Peamised uurimisvaldkonnad: looduskaitsebioloogia, säästev metsamajandus, maismaa- ja magevee tigude ja kahepaiksete ökoloogia

Publikatsioonide loetelu:

Remm, K., Linder, M., **Remm, L.** 2009. Relative density of finds for assessing similarity-based maps of orchid occurrence. *Ecological Modelling*: 220: 294–309.

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Konverentsiettekanded ja kursused:

Remm, L., Lõhmus, A., posterettekanne "Soil conditions affect land snail community more than disturbances caused by non-intensive forestry activities", Tudengite looduskaitsebioloogia konverents (SCCS) 22–24 märts 2011, Cambridge, Suurbritannia.

Remm, L., Lõhmus, A., Lõhmus, P., Leis, M., suuline ettekanne "Drainage impact on forest biodiversity: Long-term artificial forest drainage affects terrestrial forest biodiversity by cumulative indirect effects", Euroopa looduskaitsebioloogia kongress (ECCB) 28 august – 1 september 2012, Glasgow, Suurbritannia.

Osalemine kahepaiksete looduskaitse välitöö kursusel "Educative and Participative Monitoring for Amphibian Conservation", 9–15 juuni 2014, Białowieża ja Narew, Poola.

Remm, L., Lõhmus, A., Rannap, R., suuline ettekanne "Temporal and small water bodies in modern forests: a landscape-scale assessment in Estonia" konverentsil "Wetlands Biodiversity and Services: Tools for Socio-Ecological Development", 14–18 September 2014, Huesca, Hispaania.

Juhendatud väitekirjad:

Maarja Vaikre, magistrikraad, 2012, "Metsakuivenduse mõju pisiveekogude suurselgrootutele", Tartu Ülikool.

Muud tegevused ja liikmelisused:

Kiristaja, P., Ehlvest, A. Remm, L. 2014 "Eesti kojaga maismaatigude määraja" Loodusajakiri 2014. Tallinn.

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