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The impact of forest drainage on macroinvertebrates and amphibians in small waterbodies and opportunities for cost-effective mitigation

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The impact of forest drainage on macroinvertebrates and amphibians in small waterbodies and opportunities for cost-effective mitigation

UNIVERSITY OF TARTU
Press

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

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LIST OF ORIGINAL PUBLICATIONS

This thesis is the summary of the following papers, which are referred to in the thesis by their Roman numerals **I–IV**. The author of the thesis is highlighted in bold type. All published papers are reprinted here with permission from the copyright owners.

I **Vaikre, M.**, Remm, L., Rannap, R. 2015. Macroinvertebrates in woodland pools and ditches and their response to artificial drainage in Estonia. *Hydrobiologia* 762: 157–168.

II **Vaikre, M.**, Remm, L., Rannap, R., Voode, M. 2018. Functional assemblages of macroinvertebrates in pools and ditches in drained forest landscape. *Wetlands* 38: 957–964.

III Remm, L., **Vaikre, M.**, Rannap, R., Kohv, M. 2018. Amphibians in drained forest landscapes: Conservation opportunities for commercial forests and protected sites. *Forest Ecology and Management* 428: 87–92.

IV **Vaikre, M.**, Remm, L., Rannap, R. 2020. Forest ditch maintenance impoverishes the fauna of aquatic invertebrates: opportunities for mitigation. *Journal of Environmental Management* 274: https://doi.org/10.1016/j.jenvman.2020.111188

Author's contribution to the studies (* denotes a moderate contribution, ** a high contribution, *** a leading role).

	I	**II**	**III**	**IV**
Original idea	**	***	**	***
Study design	**	***	**	***
Data collection	***	***	**	***
Data analysis	**	**	**	**
Manuscript preparation	***	***	**	***

ABBREVIATIONS

ANOVA – Analysis of Variance
BACI – Before-After-Control-Impact
DD – drainage ditches
DNM – ditch network maintenance
FFG – functional feeding groups
FI – filterers
FSC – Forest Stewardship Council
GA – gatherers
GLM – General Linear Models
GLMM – General Linear Mixed Models
GLZ – Generalized Linear Models
GWL – groundwater level
ISA – Indicator Species Analysis
MRPP – Multi-response Permutation Procedure
NMS – Non-metric Multidimensional Scaling
nTWB-D – remnant pools, e.g. pools that still exist in drained sites
nTWB-UD – natural pools
PerMANOVA – Permutational Multivariate Analysis of Variance
PR – predators
SC – scrapers
SH – shredders
WRP – wheel rut pools

1. INTRODUCTION

1.1. Unique features of small and temporary waterbodies

Small and/or temporary waterbodies vary from phytotelmas and trails of large animals to headwater streams and larger seasonal floodplains of rivers and lakes (Cohen et al., 2016; Biggs et al., 2017). There are four main attributes of small and often temporary waterbodies that (in combination with other environmental features) make them inherently unique and valuable habitats.

First, small and temporary waterbodies can form almost anywhere where suitable conditions (topography, low permeability soils) are met and are therefore exceptionally abundant in many different ecosystems globally (Williams et al., 2001). For example, Williams et al. (2001) found that seasonal ponds were the most abundant of all the waterbody types in the New Forest in England, with an average of over 100 discrete seasonal ponds per 1 km^2. In Estonia, according to survey by Remm et al. (2015b), the total density of small lentic waterbodies in forests and fens (400 m^2 ha^{-1}) was almost equal to the cover of permanent ponds and lakes of the Estonian land area (490 m^2 ha^{-1}). The number varied mostly by soil type – abundance was greater on clay and fen peat soils and lower on bog peat and sandy soils. Their quantity and hydrological stability depend mostly on regional climate, landscape hydrology and geomorphology, e.g. rainfall and snowmelt and the resulting ground- and floodwater levels (Colburn, 2004; Williams, 2005).

Secondly, in regions with stable climate and landscape hydrology, temporary waterbodies can persist in a same location for very long time, being amongst the most long-lived aquatic habitats (Gray, 1988). The oxidation of organic matter during the dry phase prevents the accumulation of organic sediments (with the exception of flood plains and dense woodland) and overgrowth that befalls more permanent habitats such as ponds or small lakes (Williams et al., 2001). The predictability of the yearly flooding regime is subject to the water source, local geologic conditions, and the overall volume of precipitations and affects the distribution of biota and the likelihood of successful reproduction in a given year (Colburn, 2004). For example, temporary waterbodies with predictable dry phase host more specialized species than those with unpredictable dry phase (Wissinger et al., 2009). As the ecosystems of temporary waterbodies are sensitive to both increased and decreased water amounts, their numbers and distribution are strongly affected by human activities (Biggs et al., 2017).

Thirdly, the isolation (in time or space: temporary or scattered) coupled with numerical abundance of small pools in a landscape creates opportunities for biodiversity, particularly for macrophytes, aquatic micro- and macroinvertebrates and amphibians (Colburn, 2004; Cohen et al., 2016; Biggs et al., 2017). Small waterbodies vary greatly in habitat characteristics due to small isolated catchment and large shore-to-area ratio (Williams et al., 2004; Biggs et al., 2017), but even in environmentally similar waterbodies communities may substantially differ due to the stochastic nature of colonization (Bilton et al., 2009). Therefore, they greatly contribute to regional diversity (Oertli et al., 2002; Williams et al., 2004), even though the diversity at waterbody-scale may not be that high (Colburn, 2004; Biggs et al., 2017). Temporary waters can support many unique and endemic species that do not inhabit permanent waterbodies at least in in some stage of their life cycle, for instance due to sensitivity of predation by fish or requirement of rapidly warming shallow water (Zedler, 2003; Colburn, 2004; Kneitel & Chase, 2004; Biggs et al., 2017). The availability of small waterbodies in landscapes enables freshwater organisms to move between different habitat patches (Fortuna et al., 2006). For example, some beetles exploit temporary habitats for foraging and oviposition while over-wintering in permanent waterbodies (Colburn, 2004).

Finally, small waterbodies are strongly interconnected with adjacent terrestrial habitats as shifts in life-history stages (terrestrial adults) can result in significant flows of biomass across the aquatic-terrestrial threshold (Paetzold et al., 2007). Recent meta-analysis about riparian zones has shown that the proportion of aquatic subsidies in terrestrial predator diets is in general more than 50% (Lafage et al., 2019) though this proportion may vary with in-stream productivity, season and ecoregion (Murakami & Nakano, 2002; Baxter et al., 2005; Paetzold et al., 2005; Lafage et al., 2019). Emergent aquatic insects can influence the composition, abundance and densities as well as behavior and growth of riparian consumers such as birds, bats, lizards, spiders and other arthropods (Murakami & Nakano, 2002; Baxter et al., 2005; Fukui et al., 2006; Hoekman et al., 2011; Stenroth et al., 2015). As shown for swallows, the fledging success is positively associated with the availability of highly unsaturated fatty acid-rich aquatic insects whereas variation in terrestrial insects has little effect (Twining et al., 2018). Also, terrestrial subsidy is affected by the presence of predatory fish, as it can alter the biomass and trophic structure of emergent insects (Wesner, 2010). This could highlight the importance of temporary waterbodies to terrestrial consumers. For example, it has been found that the total density and biomass of emergent aquatic insects was higher in temporary streams compared to perennial streams, although taxonomic richness was greater in latter (Progar & Moldenke, 2002). Many amphibians also serve as important prey for invertebrates, other amphibians, reptiles, birds and mammals either as eggs, larva or adults. Tadpole presence in both lotic and lentic water reduces the abundance, biomass and effects community structure of algae, phytoplankton and periphyton (Hocking & Babbitt, 2014).

1.2. Artificial forest drainage and its impact on aquatic organisms

Freshwater biodiversity is declining at a much faster rate compared to marine or terrestrial biodiversity (Dudgeon et al., 2006; Collen et al., 2014) and wetland drainage is one of the main reasons (Brinson & Malvárez, 2002; Global Wetland Outlook, 2018). In Europe, where about 60% of pristine peatlands have been altered, 50% of the loss could be contributed to agriculture, 30% to forestry and 10% to peat extraction (Joosten, 1997). Most of the forest drainage (about 15 million ha) is conducted in boreal and temperate regions where positive water budget and impervious sub-soil layers promote paludification and forest industry is developed enough to operate in less productive sites. Finland and Sweden have the largest area of peatlands but also the largest proportion of drained ones (Vasander et al., 2003). In Finland, more than half of the original mires are drained for forestry and peatland forests contribute about 25% to the total annual growth of forests (Vasander et al., 2003; Päivänen & Hånell, 2012; Piirainen et al., 2017). In Estonia, small-scale ditching started in the 1820s (Etverk, 1974) and peaked in the middle of the 20th century, when mechanization and subsidies resulted in approximately 25% of drainage impacted forest area presently (Torim & Sults, 2005).

Much slower gas exchange between soil and air in water-saturated soils hampers tree growth (Sikström & Hökkä, 2016); and forestry operations with heavy machinery are encumbered on wet soils. Hence, there are three main purposes for forest drainage: (i) to remove excess water from the soil profile to improve root zone aeration and promote tree establishment and growth; (ii) to enable access for management operations especially for timber extraction and transport; and (iii) to reduce watering up and improve stand establishment after clearcutting (Skaggs et al., 2016). If drainage is successful, the potential productivity of the site shifts from a peat-forming mire plant community towards a forest ecosystem, where most of the primary production accumulates as wood (Päivänen & Hånell, 2012).

Drainage of peatlands and wet mineral soils has both short- and long-term effects on site and catchment hydrology. The major impact of drainage is the lowering of the groundwater level (GWL) after the establishment of ditch network. The hydraulic conductivity of soils decreases as the bulk density increases (Silins & Rothwell, 1998). Subsequently, the total volume of runoff from drained area often increases, intensifying the nurtient and sediment transport downstream (Päivänen & Hånell, 2012). This probably causes a decrease in the surface area of small natural waterbodies and the duration of floods, though studies about the exact magnitude are lacking. The initial drainage is amplified by feedback-regulated mechanisms in post-drainage succession (Lõhmus et al., 2015), as a well-growing tree stand has significant effect on the water balance (Koivusalo et al., 2008). Increased height and canopy cover have further drainage effect as increased transpiration and interception reduces groundwater recharge, gradually leading to a decrease in total runoff volumes (Holden et al., 2004). Even old drainage systems may contribute to considerable seasonal water loss (Price et al., 2003). On the whole, the landscape pattern and hydrology of remaining wetlands changes from a mosaic of numerous, diverse, clustered wetlands to fewer and more isolated ones (Gibbs, 2000; Blann et al., 2009). Even if the site is no longer managed, drained areas are unlikely to revert back to previous peat-forming ecosystems (without active interference) or the transformation is very slow (Price et al., 2003; Holden et al., 2004).

Ditch networks (including dredged and straightened streams) constitute a very significant aquatic habitat in densely drained areas. For example, in United Kingdom it is estimated that the length of ditch networks is four times greater than those of rivers and streams (Maltby et al., 2011). In Estonia, the total length of drainage ditches is 67 620 km (Registry of Estonian Melioration System, 2020) compared to approximately 19 000 km of rivers and streams (including canals and strengthened streams; Estonian Environmental Registry, 2020). The creation of drainage ditches and dredging of streams decreases the diversity of aquatic habitats, increases the connectivity between waterbodies, and changes the reciprocal interactions with adjacent terrestrial habitats by interrupting the pattern of regular floods, not to mention the loss of species dependent on specific micro-habitats e.g. riffles (Brooker, 1985). Compared to natural streams, straightened streams and presumably ditches have simplified substratum structure, relatively homogeneous flow patterns and reduced retention potential (Haapala & Muotka, 1998; Muotka et al., 2002). Even so, ditches can be exceptionally important for freshwater biodiversity, usually because they may constitute only available waterbodies in otherwise drained wetland environments (Armitage et al., 2003; Herzon & Helenius, 2008). The biodiversity value and whether ditches can substitute for natural waterbodies depends on their position, availability of other waterbodies in the landscape, and ditch properties such as hydroperiod and the structural complexity of macrophytes (Hinojosa-Garro et al., 2010; Chester & Robson, 2013; Biggs et al., 2017). The decline in benthic invertebrate diversity in agricultural peat ditches, for example, was associated with the gradual decline of submerged macrophytes (Whatley et al., 2014). In United Kingdom, most of the valuable and protected ditches can be found in coastal and floodplain grazing marshes where they are not subject to pollution as other farmland ditches (Biggs et al., 2017). Ditches in a chalk stream floodplain have shown to support larger number of unique macroinvertebrate species than river mesohabitats (Armitage et al., 2003). Peatland ditches in the Netherlands can provide habitat for at least similar numbers of species (incl. rare ones) as semi-natural small lakes, though ditch communities exhibit much higher assemblage dissimilarity among the individual drainage ditches (Verdonschot et al., 2011). Amphibians can also use ditches for breeding and migration between habitat patches (Mazerolle, 2005; Remm et al., 2015b). Nevertheless, only a subset of the fish species present in streams can be found in ditches (Rosenvald et al., 2014).

Not surprisingly, the hydrological effects of drainage and subsequent response of ground vegetation with the emphasis of tree growth and site-specific successional pathways in drained areas has been most thoroughly studied (Lõhmus et al., 2015). Studies about the impact of forest drainage on aquatic biota (with some exception of downstream biota), however, are rare (Lõhmus et al., 2015). Also more generally, small and temporary forest waterbodies have been mostly overlooked (Kreutzweiser et al., 2013) despite their importance to forest ecosystem integrity and performance (Penaluna et al., 2017). An overview from Lõhmus et al. (2015) reported that with over 46 studies about drainage impacts on ground vegetation (and much more on trees), 18 examined aquatic biota (9 about aquatic invertebrates, 6 about fish and 3 about amphibians). Out of these 18 studies, only two explored small lentic waterbodies (Allgood et al., 2009; Suislepp et al., 2011) and three considered the biodiversity and habitat value of ditches (Simon and Travis, 2011; Rosenvald et al., 2014; Homyack et al., 2016). Using a similar search (18.06.2020) did not render any new literature (except those covered by this thesis). The effect of ditching on aquatic species is not self-evident, since the number of available waterbodies may not change, when ditches substitute natural habitats (Remm et al., 2015b). However, their quality on the occasion of periodical ditch network maintenance still remains to be studied.

1.3. Ditch network maintenance

In recognition of the economic importance of forest drainage the maintenance of old drainage systems is a standard forestry practice in many countries with thriving forest industry. For example, in Finland ditch network maintenance (DNM) has been carried out on about 75 000 to 80 000 ha per year to sustain and improve forest growth on drained peatlands, though the estimated annual need is 100 000 ha (Päivänen & Hånell, 2012; Sarkkola et al., 2012). In Estonia DNM has encompassed around 20 000 ha of drained areas per year over the past years (Estonian Forestry Development Plan, 2018). The primary aim of DNM is to sustain or increase tree growth in already drained and established forest stands by restoring the water transportation capacity of the ditch network and is usually accompanied with the restoration of other forest infrastructure, e.g. roads. The deterioration of ditches due to subsidence of peat and blockage by vegetation (Paavilainen & Päivänen, 1995; Hökkä et al., 2000) may slightly rise GWL and soil-water content (Sikström & Hökkä, 2016) potentially hindering stand productivity. Additionally, when DNM is accompanied by clearcutting and reforesting, it facilitates the establishment and development of the new stand by lowering the temporarily raised GWL due to significantly reduced evapotranspiration (Piirainen et al., 2017). Normally, DNM encompasses the whole system (drainage object), regardless of the drainage potential of individual ditches.

DNM includes cleaning of deteriorated ditches and/or supplementary ditching, e.g digging new ditches next to the old ones (Päivänen & Hånell, 2012). It is most effective in areas where water table is closer to the ground (Koivusalo et al., 2008). The extent of lowering GWL depends on other factors as well, such as the conductivity of subsoil and the thickness of peat soil. For example, in sites with a shallow peat layer and sandy subsoil the lowering of GWL may be much greater (Ahti & Päivänen, 1997; Päivänen & Sarkkola, 2000; Koivusalo et al., 2008). When GLW is relatively low (35–40 cm from the soil surface) and stand is already well stocked, DNM is mostly redundant (Sarkkola et al., 2010; Sarkkola et al., 2013; Finér et al., 2018; Sikström et al., 2020). In addition, many ditches are not actually draining water, as Hasselquist et al. (2018), using upslope catchment area algorithms, found that 25 to 51% of ditches in Sweden did not support flow and could therefore be left unmanaged. DNM can have a similar effect to the quality of runoff water as first-time ditching – it increases the mobilization of suspended solids and solutes (Joensuu et al., 2001; Joensuu, 2002; Piirainen et al., 2017), but adequate sedimentation traps can alleviate the harmful effect to biota (Louhi et al., 2010). The impact of DNM on aquatic biodiversity inside a drainage network, however, is largely unstudied. A handful of studies conducted to date have shown that the frequency and period of dredging, the type of dredging machine, and the water depth at the time of dredging can influence the presence of the larvae of caddisflies, dragonflies and amphibians in agriculture drainage ditches (Twisk et al., 2000). Homyack et al. (2016) found that the time since ditch maintenance had little effect on the occupancy or richness of reptiles and amphibians in roadside ditches in pine plantations. However, Painter (1998) found that ditches with abundant submerged and floating macrophytes supported more Odonata larvae than newly excavated ditches with poor plant development.

1.4. Measures to mitigate the effects of forest drainage

There are three primary methods used to conserve and protect biodiversity: (i) the creation of protected areas (set-asides); (ii) restoration of altered habitats and landscapes; and (iii) modifying managing practices outside of protected areas to sustain more sensitive biodiversity than business as usual. Protected areas, which currently cover only 15% of the land area (Protected Planet Report, 2020), can maintain merely a subset of species (Wilson, 2016) and restoration is often only acceptable in set-asides. Therefore, wetland protection policies have to evolve from simple area-based strategies to incorporate methods that attempt to support biodiversity also in managed landscapes. Here I use the term mitigation in the sense of minimizing harm or making it less severe via maintaining or creating certain structures or promoting practices that help to preserve sensitive biota. In the USA, the same term is often used interchangeably with “offset” to refer to activities designed to compensate for unavoidable environmental damage and functions (Ten Kate et al., 2004).

In the beginning to middle of the 20th century, when forest drainage became systematized in many countries, mitigation measures were very rarely used. But as the extent of drained areas grew so did the concern for its environmental effects. As it became clear that drainage significantly increased the mobilization of suspended solids and, to a smaller extent, the leaching of nutrients from drained areas with undesirable consequences for downstream biota, government support for drainage ceased in many countries (Piirainen et al., 2017). In USA the expansion of drainage projects ended by 1990 due to federal wetland protection regulations. Finland ceased subsidies for new forest drainage projects in 1992, due to mostly ecological concerns (Skaggs et al., 2016). Estonia prohibited the establishment of new drainage systems in state forests due to FSC (Forest Stewardship Council) certification in 2002 and in 2004 in protected areas (Nature Conservation Act, 2004).

Several mitigation techniques are currently in use in Nordic and Baltic counties to alleviate the harmful effects of DNM. Such measures, concentrated mostly on sediment and nutrient leaching from drainage object to receiving environments, are sedimentation ponds and traps, overland flow areas, peak runoff control structures, constructed wetlands, and breaks in ditch cleaning and digging (Piirainen et al., 2017). Rarely have such measures gained ecological interests (e.g. Chester & Robson, 2013). Couple of studies about road sedimentation ponds suggest that such structures can contribute to the regional pond biodiversity (Le Viol et al., 2009; Sun et al., 2018). However, some mitigation measures for supporting (semi-)aquatic biodiversity within commercial forests have been suggested, such as enhancing ditch channel heterogeneity by creating deep-water pools and bank enlargements to support more diverse fish and amphibian assemblages in ditches (Suislepp et al., 2011; Rosenvald et al., 2014); increasing the variety of waterbodies by constructing separate ponds to ensure stable source populations of amphibians (Soomets et al., 2017); and leaving some ditch sections uncleaned to facilitate macroinvertebrate recolonization after DNM (Finér et al., 2018). Nevertheless, these methods have not yet been implemented or tested.

1.5. Motivations and objectives of the thesis

Due to large-scale habitat loss and pollution in wetland habitats, the biodiversity of insects alongside amphibians (Stuart et al., 2004) is in a worldwide decline (Sánchez-Bayo & Wyckhuys, 2019). Downward trends in invertebrates' abundance and biomass, formerly typical to agriculture or open landscapes, have now also been recorded in forests (Seibold et al., 2019) and even in protected areas (Hallmann et al., 2017). Semi-aquatic species (from orders Odonata, Plecoptera, Trichoptera and Ephemeroptera) are being replaced with habitat and dietary generalists and pollution-tolerant taxa (Sánchez-Bayo & Wyckhuys, 2019). The loss of biomass and the homogenisation of assemblages' points to a wider concern as species and functional diversity have an integral role in ecosystem functioning (Petchey et al., 2004). Thus, the loss of biodiversity and associated functional diversity may in turn lead to the loss of ecosystem functions (Vaughn, 2010) and resilience (*sensu* Holling, 1973).

In this thesis I explore the effect of drainage and DNM on waterbodies in forested wetlands and associated fauna, focusing on the potential conservation value of those ecosystems and ways to mitigate the loss of biodiversity in drained forest landscapes. The dissertation consists of four case studies exploring the biodiversity of small and temporary waterbodies in two spatial scales (landscape level: **I** and plot level: **II–IV**). By using aquatic macroinvertebrates and amphibians as focal species I aim to address four broader knowledge gaps about this previously often neglected wetland type:

(i) the impact of forest drainage on macroinvertebrates in small and temporary waterbodies and the species characteristic to drainage ditches (**I, IV**). While drainage impact on downstream biota is relatively well documented (e.g. Louhi et al., 2010; Ramchunder et al., 2012), its effect on small waterbodies within the drainage object is almost neglected. Also the habitat value and species composition of ditches as novel habitats, specifically in forest landscape, has received little attention.

(ii) functional properties of waterbodies in drained and managed forests. An objective of the thesis was to find out whether remnant pools (pools in drained sites) and ditches differ in terms of their trophic organization using macroinvertebrates functional feeding groups as a proxy (**II**). The knowledge about invertebrates in artificially drained forests is scarce and studies on functional communities virtually non-existent (Lõhmus et al., 2015). The amount of waterbodies may not change due to addition of ditches (Remm et al., 2015b), but it is not clear whether the functioning of respective communities differ;

(iii) the impact of ditch network maintenance on macroinvertebrates (**IV**) and amphibians (**III**) in drained forest waterbodies including ditches. DNM is a regular disturbance in drained and managed forest. Aside from downstream environments (Joensuu et al., 2002; Nieminen et al., 2010), the extent of this disturbance on aquatic biodiversity is poorly documented. DNM presumably sets back already well developed late-successional ditch communities, but breeding conditions for brown frogs (*Rana temporaria, R. arvalis*) may improve (Soomets et al., 2017);

(iv) the effectiveness of two conservation approaches for drained forest areas: (i) leaving the drained area for natural succession (**III**) and (ii) constructing mitigation pools during ditch maintenance works (**III–IV**). The first approach was tested in historically drained but currently protected peatlands that encompassed some sites with beaver (*Castor fiber*) activity. The second approach was evaluated in commercially managed forests with an experimental study to specifically examine the efficiency of constructed ponds and ditch enlargements in mitigating the potential negative impact of DNM using amphibians (**III**) and macroinvertebrates (**IV**) as focal groups.

Specifically I endeavor to answer following questions:

(i) Which macroinvertebrates are characteristic to small forest waterbodies (**I–II, IV**)?

(ii) Does forest drainage have an impact on macroinvertebrate diversity and assemblages in small forest waterbodies (**I, IV**)? Can drainage ditches serve as alternative habitats for these invertebrates (**I, IV**)?

(iii) Do functional feeding groups differ between ditches and pools in drained areas (**II**)? Which contemporary and local habitat factors could explain the possible differences in functional communities between ditches and pools (**II**)?

(iv) Whether deteriorated ditches (with or without beaver dams) can substitute natural floods as breeding sites for amphibians in drained protected areas (**III**)?

(v) How does DNM impact macroinvertebrate communities (**IV**) and breeding of brown frogs (**III**) in ditches and remnant pools? Which habitat characteristics facilitate the effect of DNM on amphibians (**III**) and which could explain the recovery of macroinvertebrate assemblages (**IV**)?

(vi) Does the construction of separate ponds and ditch enlargements help to mitigate the potential negative impact of ditch cleaning by providing habitat for (semi-)aquatic species (**III–IV**)? Which pond characteristics facilitate the occurrence of brown frogs' tadpoles in mitigation pools (**III**)? Are macroinvertebrate communities in mitigation pools' different from those in natural pools e.g. pools in undrained sites (**IV**)?

2. METHODS

2.1. Study area

The four case studies were conducted in Estonian forest and fen landscapes (Fig. 1). Estonia is located in hemiboreal vegetation zone (Ahti et al., 1968), where the mean air temperature varies between 16.9–18 °C in July and −1.9– −6 °C in February and the average precipitations (578–764 mm/y) exceeds evaporation (450–473 mm/y; Simm, 1975; Estonian Weather Service, 2020). The topography of Estonia is mostly of glacial origin: flat terrain with undulating moraine and glaciolacustrine plains with abundant clayey deposits and extensive postglacial paludification. About 51% (2.3 million ha) of the total Estonian land area is covered with forests (Estonian Environment Agency, 2018). Timber production (mostly based on clear cutting) encompasses 86% of the forest land and 14% is strictly protected (Estonian Environment Agency, 2018). Most of the forest drainage was conducted between the 1950s and 1980s and has resulted in approximately 723 530 ha of drained forest land (25%) with total of 67 620 km of ditches (Registry of the Estonian Melioration Systems, 2020). Almost all paludifying forests and 82% of peatland forests have been drained (Ilomets, 2005). The scarcity of fully intact wetlands has led to the incorporation of drained or partly drained wetlands into protected areas (about 45%, including both forested and open mires; Action Plan for Protected Peatlands, 2015). Although the construction of new drainage systems is prohibited in state forests, DNM on existing ditches and supplementary ditching is still practiced.

Case studies followed two main designs: (ii) comparative (space-for-time substitution) design (**I**–**III**); and (ii) partial BACI design (**IV**). Landscape study (**I**) was conducted within six landscape regions (Arold, 2005) across Estonia (Fig. 1). The study sites which were selected in frame of the DNM-mitigation experiment included three artificially drained commercial forest plots (total area 239 ha) and three comparable commercial forest plots with mostly natural hydrology (total area 216 ha), located in Peipus lowland and Ugandi plain (Fig. 1). Undrained sites were located at maximum distance of 10 km from the paired drained site. Study sites were located on Gleysols and to a smaller extent on shallow peat soils. Tree stand consisted of native species: birch (dominant on 39% of the area), pine (32%) and spruce (17%). Forest site types (Lõhmus, 1984) were *Vaccinium*, *Oxalis*, *Aegopodium*, *Filipendula*, mesotrophic bog, and stagnant water swamp. Forest drainage ditches in drained sites comprised 98% of the network of lotic waterbodies (76 m/ha) and had not been cleaned or reconstructed since the digging, therefore were mostly overgrown with Sphagnum mosses and macrophytes and with minor flow.

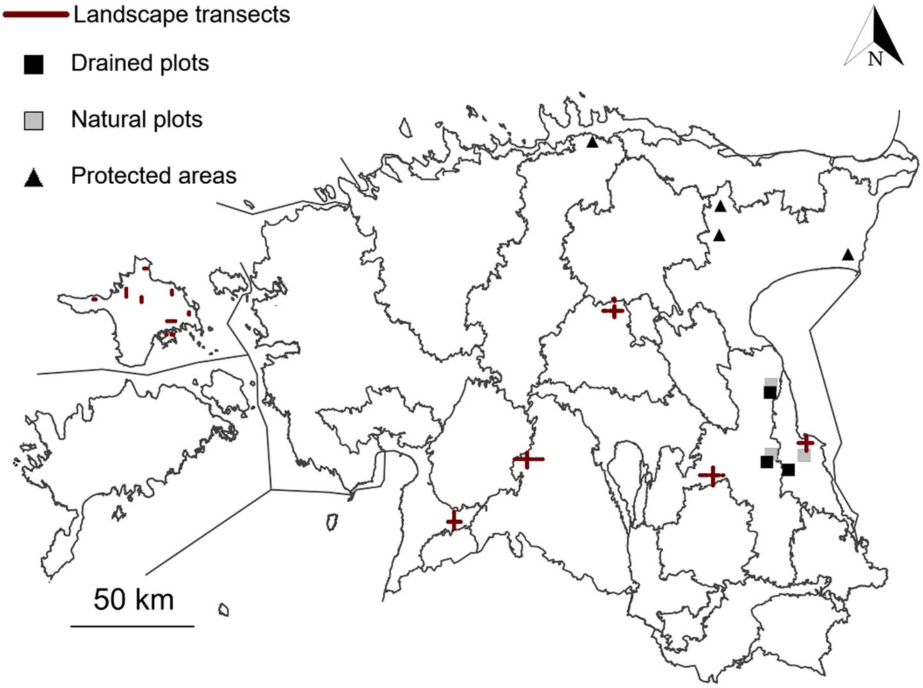

Figure 1. Landscape regions (marked with black lines) and the location of study sites in Estonia.

2.2. Data collection

In landscape study (**I**) data were collected once in April–May in 2011 or 2012 from random transect clusters in forest and fens within six landscape regions. In total 8–10 km of transects centered on a random point were examined in each landscape region. Transects were divided into areas that were considered (i) drained, when drainage system was dense and functional, and had a considerable effect on vegetation or (ii) natural, when it had mostly natural hydrology or the network of drainage ditches was sparse and/or ditches were old and overgrown. In total 181 waterbodies (25–41 from each region) from four distinct categories were sampled: (i) ditches (width < 8 m), (ii) natural temporary waterbodies (e.g., pools in natural depressions, tree fall puddles, and natural floods), (iii) wheel rut pools (both), and (iv) anthropogenic ponds (e.g., peat excavation holes) with area larger than 1 m^2, and deeper than 15 cm. Permanent waterbodies larger than 200 m^2 were excluded.

The study **III** examined the impact of drainage in protected areas at the margins of four raised bog complexes in north-eastern Estonia (Fig. 1). In total 42 sites were surveyed: (i) eight flooded sites in natural transitional mires (undrained or very slightly drained on mesotrophic peat); (ii) eight comparable drained peatland forest sites; (iii) 13 beaver-impoundments on ditches in former lagg-areas (on eutrophic peat); and (iv) 13 drained sites without beavers (Table 1).

For experimental study (**IV**) three drained forest sites were surveyed annually from 2013 to 2018 (Table 1). From each study plot we selected 10 ditches and 10 pools (natural floods, wheel rut pools etc.; with depth > 15 cm). In addition, 10 natural pools from three undrained forest plots were sampled for reference in 2015 and 2016 for the study **IV** (Table 1). For study **II** we only used invertebrate data from drained sites collected in 2013 and 2014 before DNM. The removal of brushwood from ditch banks, DNM and excavation of mitigation pools was carried out by State Forest Management Centre in early spring 2014 in Valgma and Ropka, in Kirepi the same works were carried out in 2017. Mitigation pools were constructed with various sizes and depths and were located in sun-exposed sites, e.g. next to ditch corridors and forest roads (Fig. 2). The instructions for mitigation pool creation required a construction of shallow littoral zone (width: ≥ 1 m; water depth: ≤ 30 cm); however, in one third of the cases this requirement was not followed enabling us to examine the importance of this factor. Although mitigation pools were excavated the same year as the ditch maintenance works, they were not finished by the time of fieldwork in Ropka and Kirepi. Thus, the data from the mitigation pools is available from 2015 in Valgma, 2016 in Ropka, and 2018 in Kirepi.

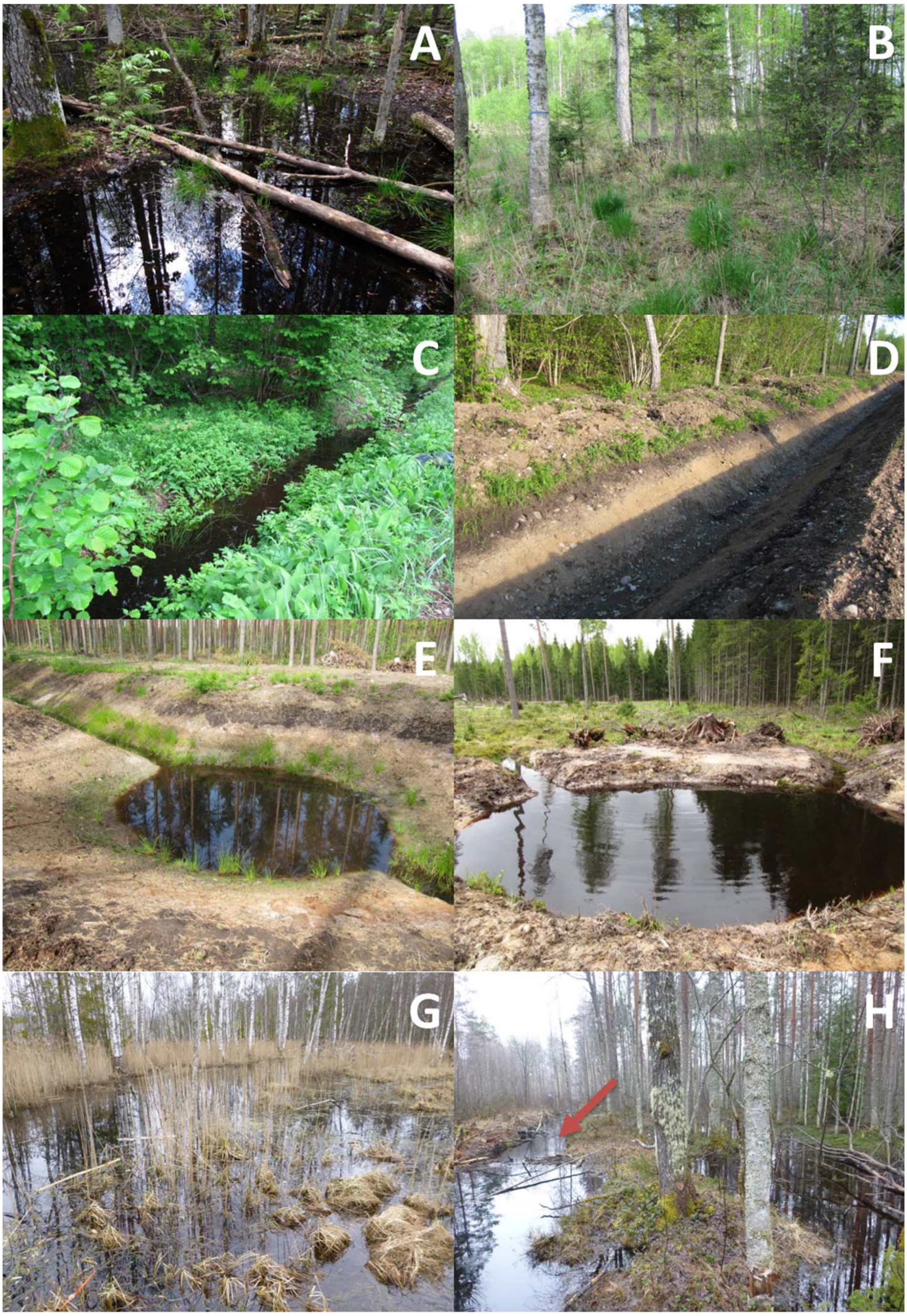

Figure 2. Examples of studied waterbodies (**II–IV**): natural pool (A); remnant pool that has dried out after DNM (B); ditch before DNM (C); the same ditch right after DNM (D); ditch enlargement (E) one year after excavation; pond (F) right after excavation; (G) flooded natural transitional mire site; and (H) beaver impoundment (arrow points to a beaver dam). Modified version of Figure 3 in paper **IV**.

2.2.1. Macroinvertebrates

Macroinvertebrates (considered here as invertebrate fauna with body size larger than 500 µm) were sampled by actively sweeping with 0.5 mm mesh D-frame net (17 × 19 cm). In landscape study (**I**) sampling effort depended positively on the size of the waterbody (5, 10, or 15 s). In studies **II** and **IV** (which were conducted within the DNM-mitigation experiment) the area of 4 m^2 was dip-netted for 20 sec in each waterbody. During the sampling, active sweeps were made covering different aquatic microhabitats, including bottom sediments, vegetated areas, and open water. Samples were preserved on-site in ethanol. All sampled waterbodies were described in terms of their origin, physical and chemical parameters and surroundings (see Table 1).

Invertebrates were sorted from the detritus, counted and identified in laboratory. Individuals were identified to lowest possible taxonomic level, mostly to species or genus: (**I**) 70% of all individuals (33% to species), except almost all Diptera, Bivalvia, Lymanaeidae, Nematoda and Platyhelminthes; (**IV**) 76% of individuals (59% to species), with the exception of some dipterans (Chironomidae, Dolichopodidae, Rhagionidae and Sciomyzidae), Nematoda and Platyhelminthes (Appendix 1 in **IV**). Therefore, taxonomic resolution in experimental study was slightly higher than in landscape study.

For functional community analyses (**II**) each taxon was assigned to functional feeding group (Appendix in **II**). Adults and larvae of the same taxon were assigned to different functional groups when feeding modalities differed between development stages. The total biomass (as dry mass) of all collected specimens (if $N < 20$; or 20 specimens and extrapolated to others) of each taxon in a waterbody was calculated from individual lengths (without the shell in case of molluscs); head widths or cylindrical volume of pieces or whole individuals (Oligochaeta) using equations from similar and geographically close habitats (Schwoerbel, 1994; Benke et al., 1999; Baumgärtner & Rothhaupt, 2003; Haas et al., 2007; Edwards et al., 2009; Méthot et al., 2012; Mährlein et al., 2016).

2.2.2. Amphibians

In the **III** study, we focused mostly on brown frogs (*Rana arvalis* and *R. temporaria*) and selected the survey time and methods accordingly, though other observed amphibians were also recorded. To determine brown frog breeding preferences and overall distribution, we surveyed spawn clumps once in April 2016 or 2017 in protected bog margins (paired sites were usually visited on the same day or at least within the next six days) and in 2017 in commercial forest plots. Commercial forest data were supported with tadpole surveys from a subset of ditches and all mitigation pools from 2013–2017. Tadpoles were dip-netted (10 sweeps in each waterbody) in late May or June. Species were determined morphologically on site (about 86% of the individuals determined to species). Additionally, in July of 2017, just before the metamorphosis of brown frogs, all studied waterbodies in commercial forest plots were visited (and dip-netted when possible*)* for the third time to determine breeding success of brown frogs; detect other late-breeding amphibian; and check whether the waterbodies had dried out during the summer. A number of environmental variables were recorded (see Table 1) to describe the breeding conditions in ditches and mitigation pools. In protected sites the mean canopy cover per site was determined using LiDAR data (Appendix A in **III**).

2.3. Statistical analyses

We compared macroinvertebrate assemblage's composition (i), taxa richness (ii) and preferences of individual species (iii) according to waterbody or management type; as well as the number of spawn clumps and tadpoles of amphibians (iv). See Table 1 for specific diversity indices for taxa richness (ii) used in different studies. One waterbody was treated as one sample unit. Analyses were performed with PC-ORD 6.07 (McCune & Mefford, 2011); STATISTICA 7 (Stat Soft Inc. 1984–2005) and R packages lme4 (Bates et al., 2015) and MuMIn (Bartoń, 2016); and EstimateS vers. 9.0. (Colwell, 2013).

(i) We analyzed assemblage composition in different waterbodies based on the abundance of species that occurred at least in three waterbodies. Differences between different management and waterbody types (**I**) were tested with Multi-Response Permutation Procedures (MRPP). Twenty groups of waterbodies were formed. MRPP was conducted over all data and also separately in each landscape region. Differences in functional group composition (**II**) between ditches and remnant pools were evaluated using two-way factorial Permutational Multivariate Analysis of Variance (PerMANOVA) with 'waterbody type' and 'plot' as grouping factors. Compositional differences between the 'before DNM' waterbody types (**IV**) were studied using One-Way PerMANOVA. Assemblage differences (**I**, **IV**) were illustrated with non-metric multidimensional scaling (NMS). The number of axes was chosen with medium autopilot mode. For the verification of the final solution, three sets of NMSs with real (and randomized) data (250 runs each) were performed manually. Linear correlations between ordination scores and environmental variables ($r^2 > 0.2$) were considered. Sørensen (Bray–Curtis) distance measure was used for all the analysis.

We also tested whether the assemblage difference between pre- and post-DNM ditches exceeded the average annual variation before DNM (**IV**), using Sørensen distance calculated in PC-ORD. Differences were analyzed with general linear mixed models (GLMM). Plot and the 'time since DNM' were included as fixed and 'waterbody ID' as random factors.

(ii) To explain macroinvertebrates' taxon richness at waterbody scale and explore correlations with habitat factors (**I–II**, **IV**) we used a variation of general and generalized linear (mixed) models (GLM; GLMM). Models were mostly built according to the following procedure: (i) test for the significance of each habitat factor ($p < 0.15$); (ii) detection of correlating habitat factors (Spearman correlation: $p < 0.05$) among significant factors; (iii) multifactorial models with non-correlating factors significant in step i; (iv) choosing the best multifactorial model based on the lowest Akaike information criterion value; (v) omission of non-significant factors from the best model ($p < 0.05$). GLMM was also used to compare diversity indices in ditches before and after DNM (**IV**) where 'time since DNM' were included as fixed and 'waterbody ID' as random factor.

One-Way (**I**) or Repeated Measures (**IV**) Analysis of variance (ANOVA) was used to detect weather diversity indices differ between waterbody and management types. To find out whether diversity indices differ in natural pools, ditches and remnant pools before DNM (**IV**), waterbody type and plot were considered as independent variables and the study years as repeated measure. To analyze the effect on DNM on remnant pool macroinvertebrates (**IV**), we compared diversity indices (averaged over the years when pool contained water) before and after DNM, including plot as an independent variable.

To describe and compare macroinvertebrates' total taxon richness in different waterbody types (**I**) we applied species richness accumulation curves (Colwell et al., 2012), computed from taxonomic lists (differentiated to genus-level or family-level in case of Diptera, Bivalvia, and Lymnaeidae) for ditches, remnant pools and natural pools separately in each landscape region, as well as for ditches, wheel rut pools, remnant and natural pools over all data.

(iii) Indicator species analysis (Dufrêne & Legendre, 1997) was performed to evaluate potential indicator taxa for different waterbody and management types. In landscape study (**I**) we sought characteristic taxa for ditches, remnant pools, natural pools (nTWB-D and nTWB-UD in **I**), wheel rut pools, and anthropogenic ponds. In experimental study (**IV**) characteristic taxa for different types of waterbodies was detected in three comparisons: (i) natural pools, pre-DNM ditches and remnant pools; (ii) natural pools and mitigation pools; and (iii) post-DNM ditches, ditch enlargements, and ponds. Analyses were restricted to the taxa that were mostly identified to species level (**I**) or for genera where at least 80% of individuals were differentiated to species-level (**IV**) and also for higher taxa (**IV**) mostly at order level.

(iv) We used logistic regression (**III**) to (i) predict the occurrence of brown frog spawn clumps in hydrologically natural versus ditched sites, and beaver-affected versus unaffected ditched protected sites. Separately we analyzed whether canopy cover differs between the two types of sites (via t-tests) and posited whether it could explain the occurrence of spawn clumps (via logistic regression); (ii) examine how DNM influences the occurrence of tadpoles in ditches and pools and which habitat characteristics explain the effect of DNM in ditches. Firstly, we identified the best subset of the full model with habitat characteristics. Thereafter, we attempted to find out which habitat characteristics explain the effect of ditch maintenance by adding the factor 'maintenance' to the best model. To study which pool characteristics facilitates the occurrence of brown frogs' tadpoles in mitigation pools, we chose the best subset of the regression model, considering the type (ditch enlargement/separated pool), water depth, and presence of shallow littoral-zone.

Table 1. An overview of case studies (**I–IV**).

<table>
<tr><th></th><th>I</th><th>II</th><th colspan="2">III</th><th>IV</th></tr>
<tr><td>Sites (N)</td><td>landscape regions (6)</td><td>drained plots (3)</td><td colspan="2">protected areas (4)
drained commercial forest plots (3)</td><td>drained plots (3)
undrained plots (3)</td></tr>
<tr><td>Studied taxa</td><td>invertebrates</td><td>invertebrates</td><td colspan="2">amphibians</td><td>invertebrates</td></tr>
<tr><td></td><td></td><td></td><td>spawn</td><td>tadpoles</td><td></td></tr>
<tr><td>Survey years</td><td>2011–2012</td><td>2013–2014</td><td>2016 or 2017</td><td>2013–2017</td><td>2013–2018</td></tr>
<tr><td>Studied water-bodies/ groups</td><td>diches
natural pools
remnant pools
anthropogenic ponds
wheel rut pools</td><td>pre-DNM ditches
remnant pools</td><td>ditches
natural floods
beaver impoundments
remnant pools
mitigation pools</td><td colspan="2">natural pools
pre- and post-DNM ditches
pre- and post-DNM remnant pools
mitigation pools</td></tr>
<tr><td>Response variables</td><td>mean number of taxa
total number of taxa
assemblages</td><td>biomass, abundance and taxa richness of FFG</td><td>number of spawn clumps</td><td>number of tadpoles</td><td>mean number of taxa
number of higher taxa
Shannon index
assemblages</td></tr>
<tr><td rowspan="3">Explanatory variables</td><td colspan="5">pH, water depth, cover of (semi-)aquatic plants, shading</td></tr>
<tr><td colspan="2">electrical conductivity,
bottom cover, clear-cuts in vicinity</td><td colspan="2" rowspan="2">shallow littoral zone</td><td rowspan="2">sediment thickness, bank inclination, bottom cover, clear-cuts in vicinity</td></tr>
<tr><td>ditch width, water area, inclination of slope, surroundings</td><td>sediment thickness</td></tr>
<tr><td>Statistical analysis</td><td>MRPP
NMS
ISA
GLM
ANOVA</td><td>PerMANOVA
GLMM
GLZ</td><td colspan="2">Logistic regression</td><td>PerMANOVA
NMS
ISA
GLMM
ANOVA</td></tr>
</table>

3. RESULTS

3.1. Macroinvertebrates

3.1.1. Macroinvertebrate fauna

In landscape study (**I**), 139 species and 52 additional higher taxa were collected from 181 waterbodies. Mean diversity varied between 10 and 15 per waterbody depending on its type and was significantly different between landscape regions (Fig. 2 and Table 3 in **I**). Six year experimental study (**IV**; 471 samples) revealed 312 species and 68 additional higher taxa, with on average 132 species and 32 higher taxa annually. The mean diversity per sample varied between 11 and 18 taxa. The proportion of collected species compared to the total number of species recorded in Estonia varied between 11 and 100%; constituting overall about one third (31%) of the total Estonian freshwater fauna (among taxon groups identified mostly to species; Table 2). Among all collected macroinvertebrates (**I**, **IV**), insects dominated with 272 taxa and 102 279 individuals most of which belonged to the orders Diptera, Coleoptera, and Ephemereoptera. Most abundant taxa were water louse *Asellus aquaticus* (33 648 individuals; 457 observations) and Chironomidae (33 286 individuals; 565 observations), both contributing about 21% to the total number of individuals.

Table 2. The number of taxa recorded per taxon group compared to the total number of (semi-)aquatic species in this group recorded in Estonia among the taxon groups identified mostly to species level.

Taxon group	No. of species found	No. of species in Estonia	Proportion (%)
Bivalvia: Sphaeridae	8	40 [a]	20
Crustacea: Amphipoda, Isopoda	3	6 [a]	50
Gastropoda	25	33 [a]	76
Hirudinea	9	19 [b]	47
Hydracarina	18	161[c]	11
Oligochaeta	18	95 [b]	19
Coleoptera	103	193 [de]	53
Ephemeroptera	14	43 [a]	33
Lepidoptera	5	5 [af]	100
Odonata	23	57 [g]	40
Plecoptera	3	21 [a]	14
Trichoptera	37	190 [h]	19
Total	**266**	**863**	**31**

[a] Timm, 2015; [b] Timm, 1999; [c] Smit et al., 2010; [d] Silfverberg, 2004; [e] Roosileht, 2015; [f] Jürivete & Õunap, 2008; [g] Martin, 2013; [h] Viidalepp et al., 2011;

Those two were also most widespread – Chironomidae were found in 88% of observations (total N = 641) and *A. aquaticus* in 71% of observations. Comparison of dominant taxa between landscape and mitigation study revealed that this were relatively similar between waterbody and management types, though slight differences in the specific order occurred (Appendix). We recorded two nationally red listed (Estonian Red List of Threatened Species, 2008) and protected species, listed also in the EU Habitats Directive (92/43/EEC): *Hirudo medicinalis* from one ditch (**I**), one pre-DNM ditch and one remnant pool (**IV**); and *Graphoderus bilineatus*, from one natural pool (**I**), one ditch enlargement and one natural pool (**IV**).

3.1.2. The effect of forest drainage and comparison of waterbody types

In landscape region study (**I**) neither mean richness per waterbody (Fig. 3 in **I**), or assemblages differed significantly and uniformly between waterbody types within landscape regions. Assemblages of ditches (MRPP: $p < 0.030$) and natural pools ($p < 0.048$) did differ between regions with the exception of remnant pool assemblages ($p > 0.066$). NMS ordinations showed a strong overlap between the assemblages in different waterbody types and high dispersion, suggesting very varied assemblages (Fig. 5 in **I**). We did not find any characteristic species for ditches, wheel rut pools, or natural and remnant pools. Total taxon richness pooled over landscape regions was relatively similar between natural pools, while remnant pools had noticeably lower richness than all the other waterbody types (Fig. 3).

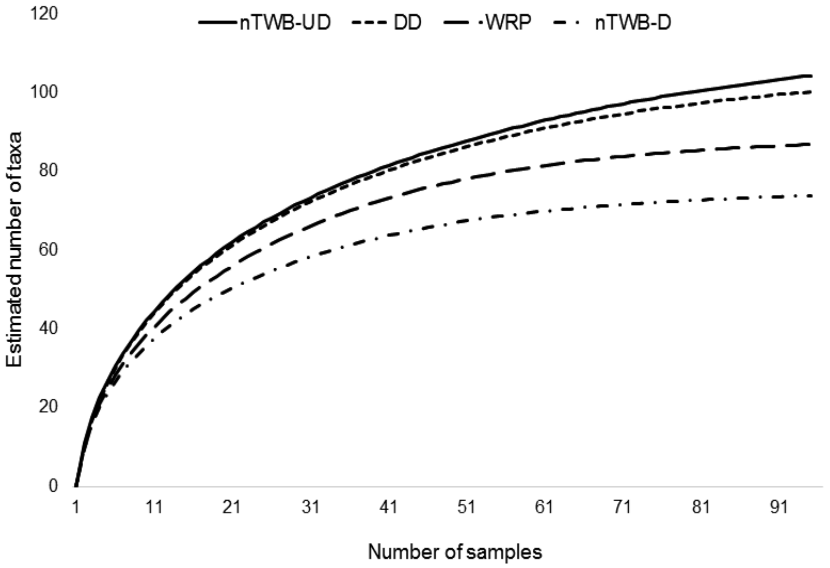

Figure 3. Accumulation curves for aquatic invertebrate taxa (mostly at genus level) from the four waterbody types. nTWB-UD – natural pools; DD – ditches; WRP – wheel rut pools; nTWB-D – remnant pools. Figure reproduced from paper **I.**

Mitigation study (**IV**) also revealed that in terms of mean diversity indices pre-DNM ditches and pools did not differ, though ditches had greater number of higher taxa per sample compared to remnant or natural pools (Tukey HSD test: $p = 0.003$). Assemblages, however, differed (PerMANOVA: $F = 4.01$; $p < 0.001$): Trichoptera were more common in natural pools whereas Bivalvia, Ephemeroptera, Gastropoda, Hirudinida, Isopoda (= *Asellus aquaticus*) and Plecoptera (= *Nemoura cinerea* and *N. dubitans*) prevailed in ditches (Appendix 3 in **IV**). Remnant pools had very few indicator species, only a midge *Chaoborus flavicans* and beetles *Helophorus strigifrons* and *Hydroporus* spp. (Appendix 4 in **IV**).

3.1.3. Functional communities

The biomass, abundance and taxa richness varied among feeding groups (Fig. 4; Appendix in **II**). We observed two distribution patterns resulting in large total biomass of a feeding group. (i) Very large individuals abundant only in a few and absent from majority of waterbodies. These were scrapers in ditches and with only a few species, mainly gastropods *Planorbis planorbis*, *Aplexa hypnorum* and *Lymnaea stagnalis*. (ii) Individuals with medium biomass numerous in majority of the waterbodies – shredders in ditches, including generalistic species such as waterlouse *Asellus aquaticus* and stonefly *Nemoura cinerea*; and caddisflies *Limnephilus stigma* and *Trichostegia minor*. Similarly abundant and ubiquitous were filterers, though their biomass was only high in ditches, where 70% of their individuals constituted of bivalves (mostly *Pisidium* spp.). In pools, 66% of individuals belonged to small-bodied Nematocera (e.g., *Aedes, Culex, Culiseta* and *Dixella* sp). Predators and gatherers had highest taxa richness but were moderately abundant and with lowest total biomass.

Functional group composition differed between ditches and remnant pools in regards of biomass (PerMANOVA: $F = 7.8–2.5$; $p < 0.006$) and abundance ($F = 7.6–2.6$; $p < 0.004$). Scrapers occurrence, abundance, and biomass was significantly higher in ditches (Table 2 in **II**; Fig. 4). The frequency of scrapers was best explained by pH and shade. In case of abundance, pH lost its significance (in first step $p = 0.001$) in relation to waterbody type, which suggests that it is probably one of the reasons for greater scraper abundance in ditches. Ditches had also higher abundance and biomass of shredders and biomass of filterers (Table 2 in **II**; Fig. 4). Gatherers' biomass was higher in remnant pools. However, leaf- and graminoid litter explained the biomass of gatherers even better than waterbody type (Table 2 in **II**). Neither abundance nor biomass of predators differed between waterbody types (Table 2 in **II**; Fig. 4).

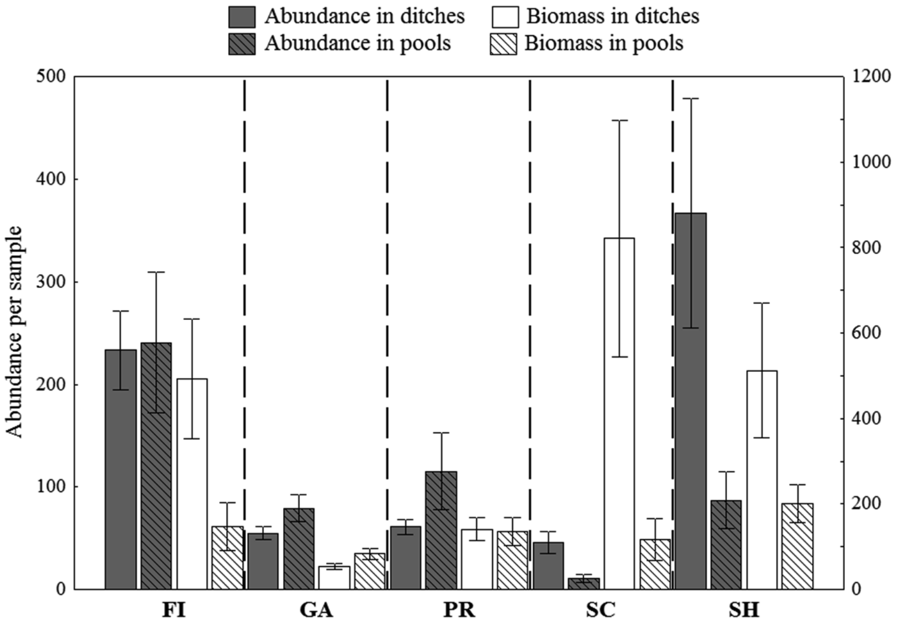

Figure 4. Mean abundance (number of individuals) and biomass with standard errors of functional feeding groups per sample collected during 20 sec from 4 m^2 in each waterbody. FI – filterers; GA – gatherers; PR – predators; SC – scrapers; SH – shredders. Figure reproduced from paper **II**.

3.1.4. The effect of DNM

Remnant pools were heavily affected by DNM – about 65% (average over the plots and all post-DNM years compared to first sampling) were destroyed or dry after DNM at the time of sampling (**IV**). Pools closer to ditches tended to have higher probability to dry out or be destroyed by machinery though this correlation was relatively weak (Spearman $R = –0.37$; $p = 0.043$). A significant decline in the mean number of taxa ($F = 10.5$; $p = 0.003$), higher taxa ($F = 11.3$; $p = 0.002$) and Shannon index ($F = 9.5$; $p = 0.004$; Fig. 5) was observed after DNM. This was mostly due to the drying of the pools, as the exclusion of dried waterbodies rendered these differences insignificant. The total number of taxa decreased by 60% and abundance by 69% (Table 2 in **IV**).

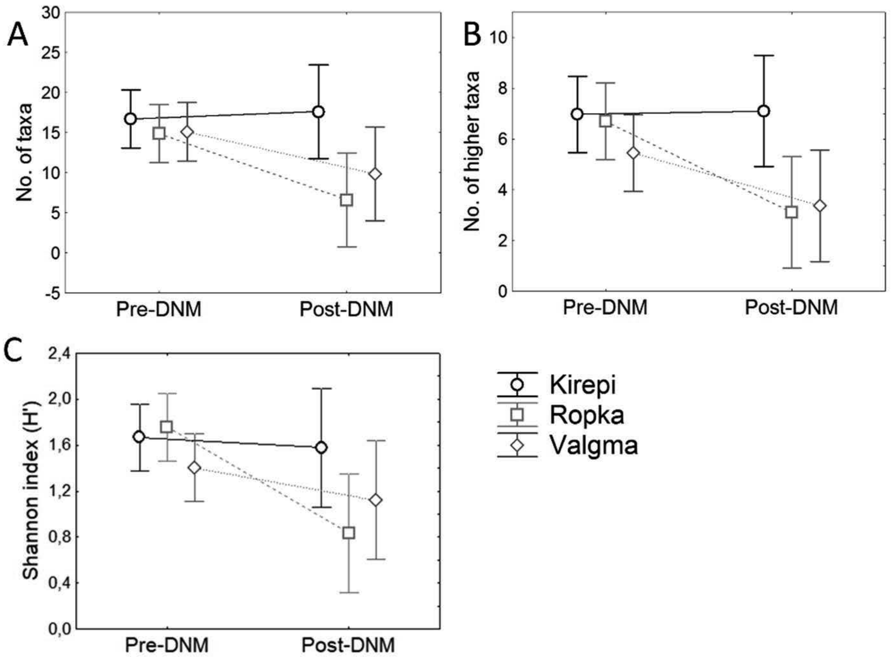

Figure 5. Mean number of taxa (A), higher taxa (B) and Shannon index (C) with 95% confidence intervals in pre- and post-DNM remnant pools in three drained plots. Dried out waterbodies are included. Figure reproduced from paper **IV**.

In ditches the effect of DNM was evident in assemblage composition, but short-lived for diversity indices (**IV**). Mean number of taxa (GLM: $F = 10.7$; $p < 0.001$), higher taxa ($F = 10.2$; $p < 0.001$) and Shannon index ($F = 4.4$; $p = 0.002$) dropped immediately after DNM. However, the number of taxa recovered to pre-maintenance levels in less than two years and the higher taxa in less than three years (Fig. 5 in **IV**). Shannon index increased compared to pre-DNM state (Fig. 6). The recovery of the number of taxa was best explained by the increase in the cover of (semi-)aquatic plants (Appendix 5 in **IV**). Assemblage shift also took place right after DNM (GLM: $F = 8.01$; $p < 0.001$), but stayed distinct after four years (Tukey HSD Test: before vs 4th year: $p = 0.023$; Fig. 6). Plot-scale taxon richness was 8% and abundance 26% lower in ditches after DNM (2^{nd}–4^{th} year; Table 2 in **IV**). Many previously numerous taxa, such as caddisflies *Limnephilus stigma*, *Phacopteryx brevipennis* and *Trichostegia minor*; mayflies *Siphlonurus aestivalis* and *S.lacustris*; and flies from genera *Mochlonyx* and *Aedes*, were affected (Appendix 1 in **IV**). At the same time, the total abundance of dominant taxa (Chironomidae and *Lumbriculus variegatus*) more than doubled (2.8 and 2.5 times respectively). Over all waterbodies (excluding mitigation pools), a total of 93 taxa out of 228 were not re-detected after DNM (Appendix 1 in **IV**). Among the more numerous disappeared taxa were *Cyphon* sp., *Glyphotaelius pellucidus* and *Plectrocnemia conspersa*. Also, 17 taxa previously present in the area only colonized mitigation pools after DNM (**IV**).

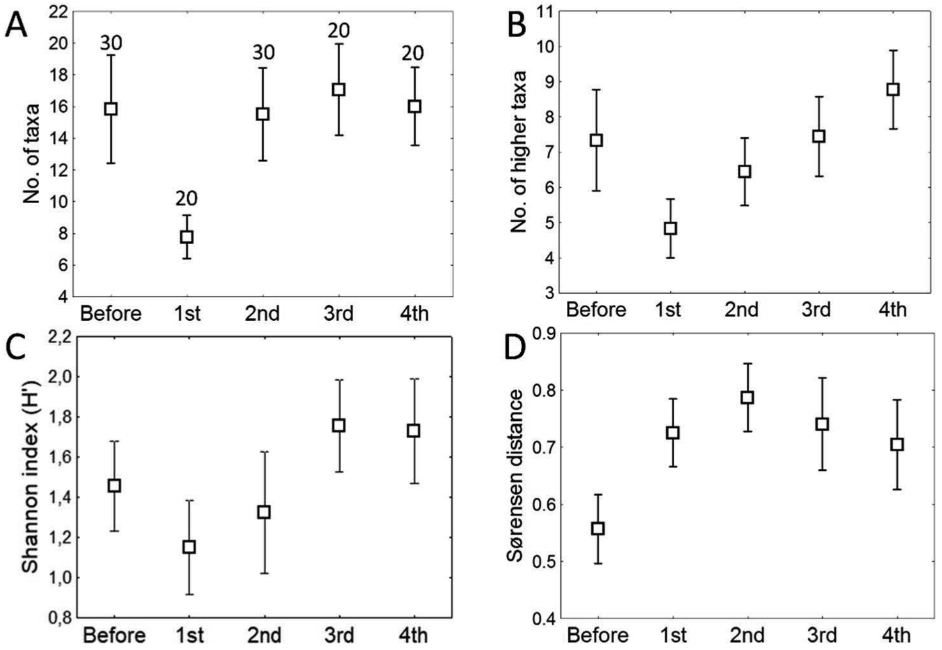

Figure 6. Shift and recovery of mean number of taxa (A), higher taxa (B), Shannon index (C) and assemblages (D) after DNM in ditches with 95% confidence intervals. The before values per ditch were calculated as the average value for all the 'before' observations, and for graph D, the average assemblage difference between 'before' years. The values for 1.–4. years after DNM in graph D were found by calculating the average difference between the assemblages in that year and the 'before' years in each ditch. Sample size for all diversity indices is shown in graph A. Figure reproduced from paper **IV**.

3.1.5. Mitigation pools

Mitigation pools had distinctly different assemblages compared to natural pools (Appendix 2 in **IV**). According to the indicator species analysis, Amphipoda (= *Gammarus lacustris*), Coleoptera, Diptera, Gastropoda, Oligochaeta, Platyhelminthes, Trichoptera, and Trombidiformes were more characteristic to natural pools, whereas Ephemeroptera, Hemiptera, and Odonata were more common in mitigation pools (Appendix 3 in **IV**). The differences in assemblage composition correlated with greater water depth in mitigation pools and larger amount of vegetation, graminoid and leaf litter, and shade in natural pools (Appendix 2 in **IV**). The greater abundance and occurrence of Ephemeroptera in mitigation pools was mainly due to *Cloeon dipterum* (98.7% of individuals). Other common mayflies *Siphlonurus aestivalis* and *S. lacustris* did not inhabit mitigation pools. Three species of Odonata (*Sympetrum danae*, *Coenagrion hastulatum* and *Cordulia aenea*) were only found in mitigation pools (Appendix 1 in **IV**).

Compared to cleaned ditches, only Hemiptera were more common in mitigation pools, namely in ponds (Appendix 3 in **IV**). Ditches in this comparison supported more Bivalvia, Gastropoda, Isopoda (= *Asellus aquaticus*), Oligochaeta and Plecoptera (= *Nemoura cinerea; N. dubitans*) (Appendix 3 in **IV**). In fact, out of 188 taxa recorded from post-DNM ditches and remnant pools, 63 did not colonize mitigation pools. Among those were molluscs such as *Planorbis planorbis*, *Aplexa hypnorum*, *Planorbarius corneus*, *Lymnaea stagnalis*, *Pisidium subtruncatum* and *P. milium*; a fly *Culiseta morsitans*; mayflies *Siphlonurus aestivalis* and *S.lacustris*, and watermite *Parathyas palustris*. Ditch assemblages were associated with larger amount of vegetation, while those in mitigation pools with deeper water (Appendix 2 in **IV**).

3.2. Amphibians

3.2.1. Amphibians in commercial forests and the effect of DNM

Before maintenance the tadpoles were caught in less acidic ditches with higher amounts of vegetation. Although brushwood was removed a year before ditch cleaning in Valgma and Ropka, the tadpole occupancy increased only after DNM, suggesting that the adults did not have enough time to react to the brushwood removal while choosing sites for spawning or the abundant sediments and deep water were an additional limitation for breeding. After DNM, tadpoles were present in greater number of ditches than before, but in smaller number of pools as shown by the interaction of maintenance and waterbody type (Table 3). The habitat characteristics causing the maintenance effect in the ditches were the cover of (semi-)aquatic plants, water depth, and pH. Maintenance lowered the average depth of water, increased the pH and the cover of (semi-)aquatic plants, though the macrophytes were mostly replaced by algae (Table 3 in **III**). Only pH partially explained the effect of maintenance (Table 3).

Despite a major loss of natural pools during ditch maintenance, the remaining pools still contributed considerably to breeding opportunities as shown by landscape-scale spawn clump observations. Most of the spawn clumps of brown frogs were found in clear-cut pools and ditches across all three sites. The proportion of moor frog spawn and tadpoles was higher in natural and mitigation pools compared to ditches, but this trend was not confirmed by a follow-up survey (Table 4 in **III**; Vaikre et al., 2019). Our data indicates that remnant pools and ditches may dry out during the summer months in some years, while mitigation pools most likely will not (**III**; Vaikre et al., 2019).

Brown frogs seemed to occupy mitigation pools in plots, where natural pools were unavailable (Table 4 in **III**; pers. obs.). The best model describing the tadpole occurrence in mitigation pools included the presence of shallow littoral zone and pool type (Table 3). The tadpoles were caught more frequently in pools with shallow littoral zone, but the difference between separate pools and ditch enlargements was negligible. Seven out of 11 enlargements with no spawn clumps in April had tadpoles in June or July. In addition to late breeders, this may be explained by the aggregation of tadpoles from ditches to enlargements (**III**). We also detected the larvae of other amphibian species, but only in mitigation pools and ditches: *Pelophylax lessonae* (in one ditch and one mitigation pool), *Lissotriton vulgaris* (in four ditches and 10 mitigation pools), *Triturus cristatus* (in one ditch and two mitigation pools), and *Bufo bufo* (in four pre-DNM ditches).

3.2.2. Brown frogs in drainage-affected protected areas

We only found moor frog (*R. arvalis*) spawn clumps in five out of eight undrained protected sites. Contrary, no spawn clumps were found in drained reference sites. Canopy cover, significantly denser in drained sites (Table 1 in **III**; $t = 6.37$, $p < 0.001$), was probably one of the main factors hindering breeding (Table 3). Sites with ditches dammed by beavers provided breeding habitat for brown frogs (both moor frog and common frog) more often than sites without beavers (Table 3). However, tree stand was only slightly sparser in beaver sites (Table 1 in **III**; paired t-test: $t = 1.54$, $p = 0.150$) and did not explain the occurrence of spawn clumps (Table 3).

Table 3. Logistic regression models explaining the occurrence of brown frog spawn and tadpoles. The models for commercial forests included the year and site as random factors. Table reproduced from paper **III**.

Model and factors		**df (residuals)**	**OR (CI)**	**z**	**p**
A)	Spawn in fens	14			
	canopy cover (%)	1	0.91 (0.85, 0.98)	–2.17	0.03
B)	Spawn in laggs	24			
	canopy cover (%)	1	1.00 (0.96, 1.05)	0.341	0.733
C)	Tadpoles in commercial forests	294			
	ditch maintenance		3.95 (1.86, 8.38)	–0.81	0.419
	type (pool vs ditch)		0.72 (0.32, 1.60)	3.58	< 0.001
	maintenance × type		0.04 (0.01, 0.21)	–3.79	< 0.001
D1)	Tadpoles in ditches in commercial forests	144			
	pH	1	1.95 (1.21, 3.14)	2.73	0.006
	water depth (cm)	1	1.03 (0.99, 1.07)	1.68	0.094
	cover of (semi-)aquatic plants	1	1.02 (1.00, 1.03)	3.01	0.003
D2)	…maintenance factor added	143			
	pH		1.38 (0.80, 2.38)	1.15	0.25
	water depth (cm)		1.06 (1.01, 1.11)	2.58	0.01
	cover of (semi-)aquatic plants (%)		1.02 (1.00, 1.03)	2.57	0.01
	maintenance		4.66 (1.31, 16.6)	2.38	0.017
E)	Tadpoles in mitigation pools	68			
	type (pond vs. ditch enlargement)		1.77 (0.39, 7.98)	0.74	0.459
	water depth (cm)		1.00 (0.97, 1.02)	–0.29	0.769
	presence of shallow littoral zone		3.68 (0.83, 16.7)	1.72	0.084

4. DISCUSSION

4.1. Macroinvertebrate fauna

Small, temporary waterbodies in Estonian forest and fen landscapes hold considerable macroinvertebrates diversity and are therefore a major contributor to regional species pool as demonstrated also elsewhere (e.g. Hall et al., 2004; Nicolet et al., 2004; Della Bella et al., 2005; Bilton et al., 2009; Florencio et al., 2009; Armitage et al., 2012). In addition, the variability of macroinvertebrate functional communities, reflected in functional feeding groups, including the difference between the networks of ditches and remnant pools, is remarkable in drained forests (**II**). The surveyed pools and ditches hosted specialists, occurring primarily in temporary waterbodies, e.g. mosquitos; opportunistic organisms with a range of habitat preferences; and even some taxa usually inhabiting more permanent waterbodies. Although the overall taxonomic richness was high, a handful of taxa dominated numerically, which could be expected in habitats that impose environmental restrictions to its inhabitants, such as re-occurring dry phase, that inhibits predation and competition (Schneider & Frost, 1996). These were common, widespread species that could be described as habitat generalists and with less-demanding ecological requirements (e.g. *A. aquaticus*) but also species with special adaptions for surviving drought (e.g. *Aedes sp.*). The high species turnover between waterbodies indicates a system of aquatic habitats with various conditions along hydrological gradient (Armitage et al., 2003; Penaluna et al., 2017). Therefore, conservation or management practices aimed to preserve the biodiversity of temporary waterbodies should take their spatial and hydrological diversity into consideration and operate at landscape-scale.

4.2. Overgrown ditches as habitats for macroinvertebrates and amphibians

Vegetated uncleaned ditches are a major stronghold for aquatic macroinvertebrates in drained forests (**I, IV**). This concurs with previous studies from other ecosystems: ditches can serve as substitutes for aquatic or semi-aquatic species whose natural habitats have been lost or deteriorated (often because of the same ditches), and/or support uncommon taxa (Chester & Robson, 2013; Biggs et al., 2017). However, most comparative studies do not consider waterbodies that ditches have replaced or they compare communities only after the fact (but see Simon & Travis, 2011), since such studies were rarely conducted at the time of first-time drainage. There is also a possibility that some sensitive taxa do not inhabit ditches (or dredged streams) or have been lost due to ditching. Williams et al. (2004) found that in Southern England (mostly) seasonal agricultural ditches supported nationally uncommon and rare species, although their communities were less diverse when compared to ponds, streams, and rivers. We found that ditches had a unique combination of species relative to natural or remnant pools (**IV**). In landscape study (**I**), though, we did not detect any indicator species for ditches nor other types of waterbodies which could be attributed to a large habitat variation within both ditches and pools. Ditches appeared to provide habitat for taxa requiring (semi-)permanent waters, e.g. groups without terrestrial stages and/or weak dispersers. This indicates that ditch assemblages might be shaped by longer hydroperiod or by the connectivity within the drainage network (consisting of small field ditches and larger collector ditches), thus facilitating the colonization of species after local drought events (Simon & Travis, 2011; Rosset et al., 2017; Rolke et al., 2018).

On the other hand, unmanaged shaded ditches do not support viable brown frog populations in drained protected forests (**III**). Even though secondary succession e.g. leaving ditches to overgrow in drained peatlands incorporated into reserves may seem to offer a low-cost approach for wetland recovery, these areas are generally unfavorable habitats for most wetland specialist species (Lõhmus et al., 2015). In some landscapes though, e.g. protected wooded pastures, ditches can support amphibian biodiversity (Hartel et al., 2011) and in commercial forests brown frogs were found in less acidic macrophyte rich ditches (**III**). Most likely explanation, why this is not so in drained peatlands, is the increased canopy cover and overgrowth of ditches with Sphagnum mosses. Brushwood removal from ditch banks generates immediate response from brown frogs (Soomets et al., 2017). Likewise, beavers greatly improve the breeding conditions for brown frogs in ditched protected sites (**III**). Similar results have been shown in other studies about both the Eurasian and North American beaver (*Castor canadensis*) in streams (e.g. Dalbeck et al., 2007; Stevens et al., 2007; Hossack et al., 2015) and ponds (Vehkaoja & Nummi, 2015). Notably, brown frogs bred in relatively shady beaver sites. This could be explained by the nutrient rich sediments in beaver floods, which favor periphyton, i.e. the food for tadpoles (Coleman & Dahm, 1990; Naiman et al., 1994; Skelly et al., 2002). Beavers may provide only temporary mitigation though, when considering territory shifts and the continuous hunting pressure in Estonia (Nummi & Kuuluvainen, 2013; Veeroja & Männil, 2019).

In addition to distinct communities, ditches were also functionally different from remnant pools – feeding groups that rely on autochthonously produced recourses (scrapers, filterers, and less contrastingly shredders) were aggregated to ditches, whilst gatherers were more common in pools (**II**). This result suggests that the production of periphyton and algae is most likely greater in ditches compared to remnant pools because of the inherent properties of ditches. The main driver of functional community composition in our study was water pH, specifically causing higher scraper frequency in ditches. As gastropods formed more than 99% of scraper quantity, their preference for higher pH and calcium rich water at least partly explains high scraper abundance in ditches. In Estonia, ditches tend to be on average less acidic compared to small forest pools (Remm et al., 2015b), which is probably caused by the exposure to mineral calcium-rich subsoil during ditch digging; and have mostly longer hydroperiod than pools (Suislepp et al., 2011; Remm et al., 2015b). More permanent nature of ditches allow for richer autochthonous food base (Boven et al., 2008). Interestingly, comparison between natural, restored, and channelized streams has found that dominant feeding groups in latter were also filter feeders and scrapers while detritivores dominated in former (Muotka et al., 2002). This was suggested to derive from the lower retention capacity in channelized streams (Haapala & Muotka, 1998; Muotka et al., 2002), though this might not be the cause in uncleaned ditches of study **II** with generally slow flow velocity. Other factors that can shift macroinvertebrate community dominance from species that process coarse organic matter (i.e. shredders) to species that feed primarily on phytoplankton (i.e. gatherers, filterers and scrapers) in lotic waterbodies are nutrient enrichment (Sharpley & Menzel, 1987; Hershey et al., 1988; Correll, 1998) and increased sun exposure due to forest harvesting (Webster et al., 1992). Those factors were probably less important distinguishing ditches and pools in study **II** considering the relatively similar shading and electrical conductivity rates. It is reasonable to conclude that habitat factors select feeding groups directly through food resources, but also because of the environmental filter on the other biological traits of the organisms.

4.3. Drainage and DNM impoverishes the assemblages in remnant pools

We did not find any substantial or uniform effect of past forest drainage on macroinvertebrates' mean taxon richness in pools (Figure 3. in **I**, Table 2. in **IV**). The deterioration of ditches may have partially impaired their functioning and raised the groundwater level (Sikström & Hökkä, 2016) allowing the recolonization of taxa that initially disappeared. Presumably, first time drainage has a strong initial effect on pool macroinvertebrates, because even DNM substantially decreased the abundance and the total number of taxa in remnant pools (whereas pool-scale diversity was affected only when the loss of pools was considered; **IV**). Also, it is difficult to decouple drainage effect from the habitat value of ditches as drainage does not necessarily change the total abundance of available waterbodies in the landscape (Remm et al., 2015b). Ditches will certainly add some new species (**IV**) and could facilitate colonization to remaining pools. Additionally, our study design, allowing for a large variation in landscape properties, could complicate the detection of differences in assemblages between waterbody types as local conditions seem to play an important role in the formation of macroinvertebrate communities (**I**).

In contrast, comparing pre-DNM waterbodies in experimental study sites revealed assemblage differences (**IV**). This suggests that drainage causes permanent replacement of invertebrate taxa, shown also for other drainage-sensitive organisms (Laine et al., 1995; Remm, 2015), even if it does not necessarily affect waterbody-scale taxa richness at least decades after drainage. Species richness at waterbody-scale may not be an adequate metric to evaluate drainage effect or other habitat modifications on macroinvertebrates. Large numbers of studies in aquatic environments have shown no effect of various anthropogenic modifications to species richness (e.g. Williams et al., 2002; Heino et al., 2009; Ilmonen et al., 2012), but the modifications such as drainage can affect specialist red-listed species (Ilmonen et al., 2012). A meta-analysis of terrestrial animals suggests that community-level measures (such as species richness) are indeed poor indicators for disturbance because of compensatory mechanism that maintain community-level properties, e.g. extinction can be offset by colonization (Supp & Ernest, 2014). One shortcoming of our case-studies was the lack of species-level identifications for some macroinvertebrate groups, though some studies have shown that genus or family level data can reflect the same amount of variation in assemblages as species data (Heino & Soininen, 2007; Bowman & Bailey, 2011). Species level identifications are definitely important for detecting threatened and vulnerable species and the lack of species-specific scientific knowledge about macroinvertebrates certainly is a problem in freshwater conservation (Strayer, 2006), as it hinders the implementation of informed conservation actions and the use of focal species approach (*sensu* Lambeck, 1997) in these systems.

Ditching and DNM substantially decreased the total number and abundance of taxa in remnant pools (**IV**). This gives merit to the assumption that the main effect of forest drainage is the homogenization of pool assemblages. Drainage-affected pools in study **I** supported altogether fewer invertebrate taxa than unaffected ones, though this result is not supported by a statistical test. The fact that the assemblages of remnant pools did not differ between landscape regions contrary to ditches and natural pools (**I**) reinforces this result. The hydroperiod of forest waterbodies, which drainage has shown to shorten (Suislepp et al., 2011; Remm et al., 2015b), affects their biodiversity and functioning (Colburn, 2004). Drainage induced homogenization of assemblages and replacement of specialist taxa with generalists has occurred also in agricultural landscapes (Blann et al., 2009) and in peatlands (Laine et al., 1995). The replacement of ecological specialist due to ecosystem degradation with widespread broadly adapted generalist is a general problem and will ultimately results in more simplified ecosystems that are less resilient to disturbances and state changes (McKinney & Lockwood, 1999; Howarth et al., 2014).

4.4. DNM impoverishes macroinvertebrate fauna but attracts amphibians to ditches

DNM is a major but in some respect short-term disturbance for ditch-dwelling invertebrates (**IV**). Macroinvertebrates have been shown to colonize new habitats relatively quickly (Williams et al., 2008; Jeffries, 2010), and indeed, promptly arriving pioneer species composed novel and distinct assemblages. Even so, the shift in assemblages could cause a decrease in landscape-scale diversity considering that the future prospect is to clean ditches in every 5–7 years, thus, disrupting the development of late-successional communities (Estonian Forestry Development Plan, 2018). For some species (e.g. with low dispersal ability and specific habitat requirements) a full-scale rotational DNM, directly removing benthic invertebrates, could result in local extinction. Cleaning ditches from organic material can also limit certain taxa or functional groups, as it leads to decreased availability of microhabitats, changes in food base (primary production) and affects physical ditch parameters (Painter & Friday, 1995) including water depth and hydroperiod (**IV**). For example, the structural complexity of macrophytes is a key factor supporting invertebrate diversity and overall density in ditches and other waterbodies (Bazzanti et al., 2009; Hinojosa-Garro et al., 2010; Kovalenko et al., 2010; Lucena-Moya and Duggan, 2011; Whatley et al., 2014; Bazzanti, 2015). In our study, some characteristics of macroinvertebrate communities covaried with macrophytes: the quantities of shredders, which were greater in ditches, correlated positively inter alia with graminoids and macrophyte cover (**II**) and the recovery of vegetation partially explained the increase of the number of macroinvertebrate taxa in ditches, probably reflecting the rise in habitat complexity (**IV**). Considering the interdependence of terrestrial and aquatic food webs, changes in hydrology and land use may eco in adjacent ecosystems (Stenroth et al., 2015; Lafage et al., 2019) therefore the repercussion of DNM could be far-reaching.

The impact of DNM on amphibians is multiplex. On one hand, the removal of brushwood (Soomets et al., 2017) and cleaning ditches from emergent vegetation (**III**) attracts amphibians, though the high colonization rates are probably caused by an assembly of shifted habitat features. On the other hand, cleaned ditches and remnant pools may act as ecological traps in drained forests as they are likely to dry out before tadpole metamorphosis (DiMauro & Hunter, 2002; Suislepp et al., 2011). Our results show that water depth is further decreased by ditch cleaning (**III**), an achieved goal in management perspective, increasing the probability of desiccation, especially in years with low precipitations. Clear-cutting, often practiced after DNM, can provide variety of sun-exposed waterbodies that have become main breeding sites for amphibians in commercial forests (**III**; Dibner et al., 2014; Remm et al., 2015b), probably because of warmer water temperatures. Hence, regular rotational clear-cutting can provide additional opportunities to sustain brown frog populations and partly mitigate the loss of naturally (semi-)open wetlands in commercial forest. Extensive clear-cuts, though, would decrease the quality of habitat complex as brown frogs prefer mature stands during their terrestrial life period (Lõhmus, 2006). However, in combination with DNM, waterbodies in clear-cuts may also dry out before metamorphosis of tadpoles, as shown by a follow-up study in the same sites (Vaikre et al., 2019) and thus become ecological traps. Therefore, brown frog populations in commercial forest may not be sustainable in the long run without implementing some mitigation measures.

4.5. Mitigation pools as a part of sustainable forest management

Mitigation measures have to balance economic goals with biodiversity gains and therefore should target multiple species in most effective sites (Remm, 2015). We proposed mitigation pools that could be excavated in conjunction with DNM, to minimize the cost and mitigate the loss of natural waterbodies. We argue that, alongside retention trees (Gustafsson et al., 2012) or meadow patches (Jonason et al., 2016), mitigation pools should be considered as future normality in sustainable forest management. Our mitigation pools were colonized by all the amphibian species present in these forest areas (**III**) and previously uncommon macroinvertebrates (Ephemeroptera and Odonata; **IV**) that are globally in decline (Sánchez-Bayo & Wyckhuys, 2019). Similarly, ponds initially designed for brown frogs in Western-Estonian drainage impoverished landscapes, provided habitat for uncommon macroinvertebrates, including Odonata (Remm et al., 2015a). Mitigation pools may not represent a truly "no net loss" solution for macroinvertebrates though, as their communities are distinct from naturally occurring waterbodies, probably due to deeper water and less shade, whilst communities in natural pools were influenced by more abundant vegetation, graminoid and leaf litter (**IV**). Achieving a right water balance in constructed wetlands to meet the needs of some target species has proven to be rather difficult (Denton & Richter, 2013; Kolozsvary & Holgerson, 2016) and the ability of created pools to mimic the physical conditions and ecological functions of natural pools, especially temporary ones, is questionable. The solution would be first of all, to indorse forestry management that facilitates the protection of already existing waterbodies (incl. vegetated ditches) and in addition, a creation of an array of different pools that would benefit numerous taxa simultaneously.

Creating mitigation pools is especially important for maintaining a source populations of amphibians in commercial forests after DNM, but these waterbodies are colonized only when specific habitat requirements, e.g. shallow littoral zone, are met (**III**; Porej & Hetherington, 2005). Mitigating the loss of amphibian breeding sites by constructing artificial wetlands can be highly successful (Brown et al., 2012) and is practiced in Estonia to count for the loss of natural wetlands, specifically for threatened species (e.g. *Triturus cristatus*, *Pelobates fuscus*: Magnus & Rannap, 2019). Hydrologically stable mitigation pools with longer hydroperiod would support species that breed later in the season (Pechmann et al., 2001); or species that prefer more permanent waterbodies with well-established aquatic vegetation (Miaud, 1995; Gustafson et al., 2006; Rannap et al., 2012). As many species prefer woodland habitats in their terrestrial phase (Lõhmus, 2006; Vuorio et al., 2015), variety of pools specifically in forest are important to ensure the availability of breeding sites (Vági et al., 2013). Though, it might be necessary to remove brushwood and abundant emergent plants regularly to keep pools sun-exposed. However, the ecological needs and preferences of target species must be considered to maximize the potential for successful colonization and long-term persistence (Brown et al., 2012). Further, the maintenance of habitat connectivity in addition to habitat quality is also important for the viability of amphibian populations (Semlitsch & Bodie, 1988). In managed forests, connectivity is reduced by extensive forest management and shorter logging rotation (Vuorio et al., 2016).

Leaving some ditch sections uncleaned should be tested as an additional mitigation measure in respect of biodiversity response and drainage sufficiency. Our results (**IV**) indicate that such solution could support macroinvertebrate recolonization to newly cleaned sections. As shown by Painter (1998), this method (alternating short cleaned and uncleaned sections) could preserve already existing communities. Uncleaned sections also protect the quality of downstream waters by slowing the velocity of runoff, preventing bank erosion and retaining eroded solids in the ditch network (Finér et al., 2018). These may be even more effective in that regard than sedimentation traps and do not hinder stand development (Haahti et al., 2018). Overall, DNM strategies should move from whole-system-based approaches to ditch-based and try to simulate natural dynamics by ensuring a mosaic of connected habitats of different succession levels.

5. CONCLUSIONS

In present thesis, I examined the effect of forest drainage and DNM on small waterbodies and their associated fauna, focusing on the conservation value of these habitats and ways to mitigate the loss of biodiversity in drained forest landscapes. Conclusions are as follows:

(i) Small forest waterbodies are species rich, diverse and dynamic habitats, thus playing an important role in sustaining regional freshwater diversity and supporting various ecosystem function providers in drained forests. The trophic organization in ditches and remnant pools is different due to habitat factors selecting feeding groups directly through food resources and environmental filters on other biological traits. Ditches create habitat for taxa that require (semi-)permanent waters, e.g. groups without terrestrial stages and/or weak dispersers. High regional richness and species turnover indicates that conservation or management practices aimed to preserve the biodiversity of temporary waterbodies should take their spatial and hydrological diversity into consideration and operate at landscape-scale.

(ii) The effect of drainage (and DNM) on macroinvertebrates manifests through habitat loss and subsequent shift and homogenization of assemblages as ditching and DNM substantially decreased the total number and abundance of taxa in remnant pools and changed ditch communities. The replacement of ecological specialist with broadly adapted generalist is a concerning global trend that forest drainage contributes to. Site-scale taxa richness does not indicate any change caused by drainage, suggesting that waterbody-scale species richness may not be an adequate metric to evaluate drainage effect on macroinvertebrates.

(iii) Overgrown ditches in protected peatlands do not substitute natural floods as breeding habitats for brown frogs presumably because of dense canopy cover and concurrent lower water temperatures. Beaver sites can provide high quality reproduction sites for moor frog, even when relatively shady. The habitat value of drained protected peatlands relies on restoration agent such as beavers. Therefore leaving these sites for natural succession in areas without beavers is not a feasible measure for supporting amphibian populations.

(iv) Ditch maintenance in commercial forests leads to desiccation of natural pools, while simultaneously attracting brown frogs into cleaned ditches. Remnant pools, which were preferred by brown frogs, and newly cleaned ditches, have higher desiccation risk; therefore, brown frog populations in commercial forest may not be sustainable in the long run without implementing mitigation measures.

(v) Special measures are essential to mitigate the effect of DNM to macroinvertebrates and amphibians in managed and drained forests. Since DNM causes a major loss of remnant pools and decreases the diversity and abundance of macroinvertebrates, its necessity and economic profitability in given situation must be carefully considered. If possible, certain ditch sections should be left uncleaned to aid biodiversity recolonization to cleaned sections. Construction of mitigation pools cannot be used as a “no net loss” measure, but rather as a mean to supplement the species pool with species not common in drained forests. Nevertheless, creating mitigation pools alongside DNM seems to be feasible and also cost-effective method to increase the diversity and number of available waterbodies in drained forest and thus support biodiversity. For amphibians, these pools should be designed with a shallow littoral zone to provide regions of warm water.

KOKKUVÕTE

Metsakuivenduse mõju vee-suurselgrootutele ja kahepaiksetele ning võimalused säästlikuks metsamajandamiseks

Väikeveekogud, mida iseloomustavad väike pindala ja/või ajutine kuivamine võivad olla paljudes maastikes väga arvukad ning nende hulk ja paiknemine sõltub enamasti kohalikust kliimast, topograafiast ja hüdroloogilisest režiimist. Väikeveekogude paiknemine maastikus on ajas järjepidev, sest hoolimata ajutisest kuivamisest koguneb vesi samadesse lohkudesse uuesti. Ajutine kuivamine takistab orgaanilise aine akumulatsiooni ning lohu täitumist setetega. Väikese valgala ning suure kaldajoone ja pindala suhte tõttu on väikeveekogud väga mitmekesised elupaigad, mis omadustelt suuresti varieeruvad. Sellistel veekogudel on suur ökoloogiline väärtus: nad pakuvad elupaika paljudele unikaalsetele liikidele, kes püsiveekogusid erinevatel põhjustel ei asusta ning tänu kõrgele beeta-mitmekesisusele panustavad oluliselt regionaalsesse mitmekesisusse. Väikeveekogud on kõrvalolevate maismaaökosüsteemidega ka tugevas vastastikuses seoses. Näiteks veeputukate maismaalised arengujärgud kannavad toitaineid väljapoole veeökosüsteeme ning võivad moodustad ligi 50% putuktoiduliste maismaaloomade toidust mõjutades viimaste arvukust, kooslusi, kasvu ning käitumist. Näiteks pääsukeste pesakonna elulemus sõltub just veeselgrootute rohkusest pesitsusperioodil. Seetõttu on väikeveekogud (metsa)-ökosüsteemide funktsioneerimise olulised komponendid.

Väikeveekogude arv ja levimus maastikus sõltub suuresti inimtegevusest. Üks oluline märgalade, sh väikeveekogude vähenemist ja kadu põhjustav tegur – eriti just parasvöötme sega- ja okasmetsavööndi arenenud metsamajandusega maades – on metsakuivendus. Ligi 30% Euroopa märgalade degradeerumise põhjuseks peetakse metsakuivendust eesmärgiga suurendada puidutootlikkust liigniisketes metsades ning siirde- ja madalsoodes. Eestis moodustab kuivendatud metsamaa hetkel 25% metsade kogupindalast. Kohe pärast kraavivõrgu rajamist alaneb põhjaveetase, väheneb üleujutuste kestus ning suureneb vee äravool, kuna liigne vesi juhitakse kraavide abil alalt välja. Paranevad mulla õhustatus ning orgaanilise aine lagunemistingimused, mistõttu hoogustub puude kasv. Ka puistul endal on märkimisväärne mõju ala veerežiimile. Tänu transpiratsioonile kaob vesi pinnasest kiiremini ning suurenenud võrade liituvuse tõttu jõuab allesjäänud veekogudesse vähem sademeid. Kuivenduse mõju ökosüsteemidele on pikaajaline ning suuresti pöördumatu – eduka kuivendamise korral muutub eelnevalt turvast tootnud (ava)kooslus metsaökosüsteemiks, milles suurem osa primaarproduktsioonist akumuleerub puiduna. Kraavivõrgustiku rajamine võib kuivendatud metsas veekogude koguarvu isegi suurendada, kuna looduslikud veekogud asenduvad kraavide ja teiste inimtekkeliste veekogudega. Samas väheneb nii looduslike veekogude hulk kui ka nende mitmekesisus ning säilinud veekogude veetase ja kvaliteet langeb, seda nii kalade kui kahepaiksete elu- ja sigimispaigana.

Ulatusliku metsakuivenduse tulemusena moodustavad kuivenduskraavide võrgustikud paljudes maastikes märkimisväärse vee-elupaiga. Näiteks Eestis ületab kraavide kogupikkus jõgede ja ojade pikkuse ligi 3,5 korda. Võrreldes looduslike vooluveekogudega on kraavid ühetaolisema põhjastruktuuri ja vooluga ning vähenenud voolutakistuste hulgaga sängis. Samas pakuvad kraavid (asendus)elupaiku vee-elustikule ning on olulised juhtudel, kui kuivenduse tagajärjel on muud looduslikud vee-elupaigad hävinud. Kraavi väärtus vee-elustiku seisukohast sõltub tema omadustest, nt taimestiku rohkusest, hüdroperioodi (aeg, mil veekogu sisaldab vett) pikkusest, asukohast maastikul ning teiste veekogude olemasolust. Kraavides esinevad kooslused on sageli palju varieeruvamad võrreldes püsiveekogude kooslustega. Kui kahepaiksed kasutavad kraave nii sigimiseks kui elupaigalaikude vahel liikumiseks, siis kalastiku poolest on kraavid ojadega võrreldes tunduvalt vaesemad. Kuna kraavid kipuvad turba tihenemise ja kinnikasvamise tõttu oma kuivendusfunktsiooni kaotama, toimub jätkuvalt olemasolevate kraavide hooldus ja rekonstrueerimine. Metsakuivenduse ja kraavide rekonstrueerimise elustikumõjude seisukohast on kõige põhjalikumalt uuritud soontaimed ja puud ning uuritud on ka korrashoiutööde mõju kuivendussüsteemist allavoolu jäävate veekogude elustikule. Üllatuslikult on vähem tähelepanu pälvinud kuivendussüsteeme (v.a põllumajandusmaastikul) ning muid väiksemaid metsaveekogusid asustav elustik.

Doktoritöö keskendub väikeveekogude suurselgrootutele kahes ruumilises mõõtmes: maastiku mastaap (**I**) ja kuivendusobjekti mastaap (**II–IV**), kasutades võrdlevaid meetodeid ja osalist BACI (*before-after control-impact*) disaini. Maastiku mastaabis uurisin metsakuivenduse mõju väikeveekogude suurselgrootutele juhutransektidel üle Eesti. Kuivendusobjekti mastaabis uurisin (1) funktsionaalsete toitumisrühmade (filtreerijad, kraapijad, kiskjad, kogujad ja peenestajad) erinevust kraavides ja kuivendatud ala lompides; (2) kraavide rekonstrueerimise mõju vee-suurselgrootutele ning kahepaiksetele ülepinnalise kudupalliandmestiku ning kulleste põhjal; ning (3) spetsiaalselt kaevatud leevendusveekogude asustamist nende kahe rühma poolt. Eksperimentaalalad hõlmasid kolme kraavitatud riigimetsa ala, kus seirati vee-suurselgrootuid ja kahepaikseid nii enne kui pärast kraavide rekonstrueerimist ning leevendusveekogude (eraldiseisvad tiigid ning kraavilaiendid) rajamist. Võrdluseks koguti proove ka kolmelt ligikaudu sama pindalaga kuivendamata metsaalalt. Uuritavate liigirühmade valikul lähtuti nende senisest vähesest uuristusest metsakuivenduse kontekstis ja arvatavast kuivendustundlikkusest. Kahepaiksete kõrval on täheldatud ka vee-selgroogsete liigirikkuse ja arvukuse vähenemist, kusjuures peamiseks põhjuseks on elupaikade, sh märgalade hävimine ja kvaliteedi langus. Samas on mõlemal rühmal oluline roll toitainete ringluses ja lagundamisel.

Uuringute käigus tuvastatud vee-suurselgrootute liigirikkus oli märkimisväärne. Maastikutransektidelt (**I**) leiti 139 liiki ja 52 kõrgemat taksonit ning 6-aastase eksperimentaaluuringu käigus (**IV**) 312 liiki ning 68 kõrgemat taksonit, kusjuures aastane liigirikkus oli keskmiselt 132 liiki ning 32 kõrgemat taksonit. Peamiselt liigini määratud rühmade seas moodustas leitud liikide arv ligi ühe kolmandiku antud rühmade koguliigirikkusest Eestis. Kõiki andmeid (**I**, **IV**) arvestades osutusid kõige arvukamaks rühmaks putukad, eriti arvukad olid kahetiivalised, mardikad ning ühepäevikulised. Kõige arvukamateks taksoniteks olid aga vesikakand (*Asellus aquaticus*) ja surusääsed (*Chironomidae*), mõlemad moodustasid ligi 21% isendite koguarvukusest. Mõlemad taksonid olid ka kõige levinumad: *Chironomidae* leidus 88% vaatlustes ning *A. aquaticus* 71% vaatlustes. Leiti ka kaks Eesti Punasesse nimestikku kuuluvat liiki: apteegikaan (*Hirudo medicinalis*) ja lai-tõmmuujur (*Graphoderus bilineatus*). Selgrootukooslusi iseloomustas suur veekogude vaheline varieeruvus.

Taimestikurikkad rekonstrueerimata kraavid on vee-suurselgrootutele oluliseks elupaigaks kuivendatud metsades (**I, IV**), kahepaiksete sigimist piirab aga peamiselt varjulisus (**III**). Looduslike ning jäänuklompidega (säilinud lombid kuivendatud aladel) võrreldes olid kraavide selgrootukooslused erinevad (**IV**), kraavid loovad elupaiku liikidele, kes vajavad pigem püsivamaid veekogusid. Võimalik, et kraavide kooslusi mõjutab ka nende ühendatus nii omavahel kui eesvooludega, sest see võimaldab liikidel, kellel maismaalise eluviisiga staadiumid puuduvad, levida ning pääseda kuivamisest. Ka funktsionaalsete toitumisrühmade koosseis rekonstrueerimata kraavides (**II**) viitab sellele, et nad on pikemat aega veega täitunud. Kraapijate biomass, arvukus ja esinemissagedus oli kõrgem kraavides ja see oli arvatavasti põhjustatud kraavivee kõrgemast pH-st – elupaigaomadusest, mida eelistavad teod, kes moodustasid suure osa kraapijatest. Samuti oli kraavides kõrgem peenestajate arvukus ja biomass ning filtreerijate biomass. Kogujate biomass oli kõrgem lompides, mis tulenes arvatavasti kõrreliste ja lehevarise rohkusest neis veekogudes. Kahepaiksete puhul ei ole kraavitatud kaitsealade looduslikule suktsessioonile jätmine jätkusuutlik, kuna liitunud võrade all kulgevad kraavid väärtuslikke sigimispaiku ei paku (**III**). Kobraste tegevus lõi aga sigimispaiku ka kuivendatud kaitsealadel, olenemata varjulisusest (**III**).

Maastikeüleses uuringus (**I**) ei erinenud vee-suurselgrootute mitmekesisus ega ka koosluste kooseis veekogutüüpide vahel. Samad veekogutüübid maastikurajoonide võrdluses aga erinesid (v.a jäänuklombid). Suur looduslik varieeruvus maastikurajoonide vahel võis raskendada kuivenduse mõju tuvastamist. Vee-suurselgrootute kogumitmekesisus oli sarnane kraavides ja looduslikes lompides, kuid madalam jäänuklompides. See viitab, et kuivendamine põhjustab veeselgrootute koosluste ühetaolisemaks muutumist allesjäänud lompides. Ka eksperimentaaluuringus (**IV**) ei erinenud vee-selgrootute keskmine taksonirikkus, seltside mitmekesisus ja Shannoni erisusindeks veekogutüüpides statistiliselt oluliselt rekonstrueerimiseelses olukorras. Küll aga erinesid veekogutüübid koosluste poolest. Kuivendamata ala lompe iseloomustasid suurematest rühmadest ehmestiivalised, kraave aga karbid, teod, ühepäevikulised, kaanid ja kakandid ehk rühmad, kes eelistavad pigem püsivamat vett.

Rekonstrueerimisel oli märkimisväärne mõju lompide ja kraavide elustikule (**IV**). Suur osa (65%) lompidest kadus või hävitati. Rekonstrueerimise tagajärjel vähenes suurselgrootute kogutaksonirikkus jäänuklompides 60% ning arvukus 69%. Keskmised elustikunäitajad vähenesid oluliselt aga vaid siis, kui kuivanud veekogud olid mudelisse kaasatud. Lompide täielik või kiirem kuivamine rekonstrueerimise tagajärjel on murettekitav ka kahepaikseid silmas pidades, kuna raba- ja rohukonnad eelistasid lisaks kraavidele sigida just raiesmikulompides (**III**). Kraavides kahanes taksonite ning seltside mitmekesisus kohe pärast rekonstrueerimist märgatavalt (**IV**). Pioneerliigid jõudsid aga kiiresti kohale ning juba teiseks-kolmandaks aastaks olid keskmised elustikunäitajad taastunud, arvatavasti tänu veesisese taimestiku taastumisele. Kooslused ei muutunud nelja vaatlusaasta jooksul rekonstrueerimis-eelsete sarnasteks. Ka kogumitmekesisus vähenes rekonstrueerimisjärgselt 8% ning arvukus 26%. Oluliselt vähenesid ka enne rekonstrueerimist laialt levinud taksonite koguarvukused, samas kui ennegi väga arvukate ning hästi reostust taluvate elupaigageneralistide, nagu surusääsed ja rabeliimukas (*Lumbriculus variegatus*), koguarvukused suurenesid vastavalt 2,8 ja 2,5 korda. Kraavide rekonstrueerimine, mis vähendas nende varjulisust ja suurendas vee pH-d, tõstis oluliselt kulleste esinemise tõenäosust kraavides, samas kui lompides kulleste kohtamise tõenäosus nende kuivamise tõttu langes (**III**).

Leevendusveekogude kooslused erinevad oluliselt looduslike lompide omadest (**IV**). Leevendusveekogude rajamine loob lisaelupaiku peamiselt kiilidele, ühepäevikulistele ja lutikalistele, keda looduslikes veekogudes leidub vähem (**IV**). Leevendusveekogud pakkuvad sigimispaika ka kahepaiksetele, juhul kui neil esineb madalaveelist lauget kaldaala (**III**). Lisaks pruunidele konnadele leiti leevendusveekogudes ka kõiki teisi piirkonnas esinenud kahepaikseid. Kraavilaiendid võimaldavad kullestel kraavide kuivamise korral ellu jääda ja moonde läbida – tõenäoliselt liikusid kullesed kuivavatest kraavidest laienditesse, sest suvel leiduskulleseid ka laiendites, kuhu kevadel ei koetud (**III**).

Väikeveekogud on unikaalsed ja mitmekesised elupaigad (**I–II, IV**), mis ei ole aga piisavalt looduskaitselist tähelepanu pälvinud, eriti majandusmetsades. Käesolev töö näitas, et kuivenduse mõju väikeveekogude elustikule toimub läbi elupaikade kao ning sellega kaasneva koosluste teisenemise ja homogeniseerumise (**I, IV**). Väikeveekogudega seotud liikide toetamiseks on vaja taastada kuivendatud märgalad või mitte takistada neis kobraste tegevust (**III**), säilitada juba olemasolevaid veekogusid majandatavatel metsamaastikel (**IV**) ning ohustatud liikide elupaiganõudlusi silmas pidades rajada erinevaid leevendusveekogusid populatsioonide järjepidevuse säilitamiseks ja toetamiseks (**III–IV**).

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***

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APPENDIX

Mean abundance per sample of dominant taxa in comparison of two studies (**I, IV**). Number of samples over the years for different waterbody types are given. Note that abundance values are not strictly comparable between two studies, since sampling procedures differed.

		Landscape study (I)		**Mitigation study (IV)**			
Taxonomic unit		**Natural plots (74)**	**Drained plots (107)**	**Natural plots (49)**	**Pre-DNM plots (158)**	**Post-DNM plots (133)**	**Mitigation pools (130)**
Bivalvia	*Musculium lacustre*	0.24				2.04	
	Pisidium sp.	30.93	13.51				
	Pisidium casertanum			6.84	3.42	4.66	3.60
	Pisidium globulare			2.37	9.47		
	Pisidium obtusale			4.45	13.98	2.48	1.22
	Pisidium personatum						0.58
Crustacea	*Asellus aquaticus*	41.85	57.86	59.63	88.93	41.92	15.27
	Gammarus sp.		2.2				
	Gammarus lacustris			0.96	0.52	0.05	0.03
	Gammarus pulex				0.07		
Gastropoda	*Anisus ssp.*		1.76				
	Anisus spirorbis	0.59					
	Aplexa hypnorum	1.49		2.61	3.09		
	Batylomphalus contortus		0.71				
	Gyraulus rossmaessleri	0.42					
	Planorbis planorbis		1.46		2.42	2.44	
	Radix balthica			1.9	1.70		2.32
	Stagnicola corvus			1.59		6.2	0.51
	Stagnicola palustris					1.74	0.52

		Landscape study (I)		Mitigation study (IV)			
Taxonomic unit		Natural plots (74)	Drained plots (107)	Natural plots (49)	Pre-DNM plots (158)	Post-DNM plots (133)	Mitigation pools (130)
Hirudinea	*Erpobdella lineata*	0.05		0.22		0.14	0.02
	Erpobdella octoculata		0.03			0.13	0.02
	Glossiphonia complanata	0.03		0.04	0.08		0.01
	Haemopis sanguisuga		0.05	0.04	0.18		0.01
	Helobdella stagnalis	0.04	0.04		0.1	0.06	0.01
Hydracarina	*Euthyas truncata*		0.12	0.31			0.01
	Hydrachna leegei	0.16	0.26	0.43	0.35	0.11	0.02
	Hydryphantes ruber	0.11	0.33	3.29	2.16	0.36	0.01
	Parathyas palustris			0.31	0.84	0.1	
	Thyas rivalis	0.24					
Oligochaeta	*Aulodrilus limnobius*				0.09	0.94	0.07
	Bratislavia palmeni					0.45	
	Limnodrilus hoffmeisteri	0.31	0.04				
	Lumbriculus variegatus	4.91	6.3	7.61	4.65	13.89	2.61
	Nais communis						0.23
	Stylodrilus heringianus			0.22			
	Tubifex tubifex	0.74	1.05	0.71	0.82		
Coleoptera	*Acilius sulcatus*						1.35
	Anacaena lutescens	1.93	1.59	7.43	7.42	5.12	3.22
	Cyphon sp.	2.77					
	Haliplus sp.						1.42
	Hydrobius fuscipes			1.27			
	Hydroporus ssp.				1.44		
	Ilybius sp.		0.39			2.48	
	Microcara testacea	7.59	6.88	16.24	9.16	2.41	

		Landscape study (I)		Mitigation study (IV)			
Taxonomic unit		**Natural plots (74)**	**Drained plots (107)**	**Natural plots (49)**	**Pre-DNM plots (158)**	**Post-DNM plots (133)**	**Mitigation pools (130)**
Diptera	*Culicidae*	115	69.04				
	Aedes sp.			45.96	54.86	6.2	
	Chaoborus crystallinus					3.03	11.25
	Mochlonyx velutinus			22.22	9.91		
	Chironomidae	26.91	27.95	39.71	25.72	88.25	81.86
	Dixidae	11.32					
	Dixella sp.						5.49
	Simuliidae		4.72				
Ephemeroptera	*Baetis rhodani*					0.04	
	Caenis horaria						0.18
	Cloeon dipterum	2.36	1.33	4.35	4.00	7.00	27.87
	Heptagenia fuscogrisea	0.22					
	Leptophlebia marginata	0.81	0.23				
	Siphlonurus sp.		0.32				
	Siphlonurus aestivalis				1.01		
	Siphlonurus lacustris				0.6		
Hemiptera	*Corixa sp.*	0.04	0.01				
	Corixa dentipes				0.19		
	Gerris sp. (larvae)			0.18	0.16	0.13	1.06
	Gerris lacustris	0.12	0.13	0.24	0.44	0.47	
	Micronecta sp.	0.12					
	Notonecta sp.						2.2
	Sigara sp.		0.07	0.71	0.16	0.2	2.15

Taxonomic unit		Landscape study (I)		Mitigation study (IV)			
		Natural plots (74)	Drained plots (107)	Natural plots (49)	Pre-DNM plots (158)	Post-DNM plots (133)	Mitigation pools (130)
Lepidoptera	*Acentria ephemerella*	0.04	0.04				
	Cataclysta lemnata	0.01	0.06	0.9	0.08	0.02	
	Elophila nymphaeata				0.03	0.04	
	Nymphula stagnata	0.19	0.03	0.02	0.08	0.07	0.02
Odonata	*Aeshna cyanea*			0.27	0.17		1.11
	Coenagrion sp.		0.14			0.26	
	Coenagrion armatum					0.33	1.46
	Coenagrion lunulatum					0.55	
	Cordulia aenea	0.2					
	Enallagma cyathigerum				0.06		
	Lestes sp.	0.16					
	Lestes dryas				0.32		
	Libellulidae			0.61			
	Libellula quadrimaculata						0.75
	Orthetrum sp.	0.16	0.13				
	Somatochlora sp.		0.07				
	Somatochlora flavomaculata			0.04			
Plecoptera	*Nemoura cinerea*	2.04	10.04	0.12	3.05	10.86	0.38
	Nemoura ssp.		0.19		0.18		
	Leuctra sp.	0.07					
Trichoptera	*Limnephilus sp.*	1.08	0.94				0.08
	Limnephilus auricula					0.26	0.03
	Limnephilus flavicornis	0.45					
	Limnephilus stigma		1	5.33	3.13	0.57	0.22
	Phacopteryx brevipennis		0.45	0.45	1.39	0.41	
	Trichostegia minor	1.80	0.69	1.84	1.22		

PUBLICATIONS

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Vaikre, M., Remm, L., Rannap, R., Voode, M. 2018. Functional assemblages of macroinvertebrates in pools and ditches in drained forest landscape. *Wetlands* 38: 957–964.

Remm, L., **Vaikre, M.**, Rannap, R., Kohv, M. 2018. Amphibians in drained forest landscapes: Conservation opportunities for commercial forests and protected sites. *Forest Ecology and Management* 428: 87–92.

Lõhmus, A., Kont, R., Runnel, K., **Vaikre, M.**, Remm, L. 2020. Habitat models of focal species can link ecology and decision-making in sustainable forest management. *Forests* 11: 721; https://doi.org/10.3390/f11070721.

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Conference presentations:

The 2nd Conference of Doctoral School of Earth Sciences and Ecology: Down to Earth, 16–17.05.2013, Tallinn, Estonia; oral presentation: Impact of artificial forest drainage on macroinvertebrates of small water-bodies (co-authors: L. Remm, R. Rannap).

The 9th European Wetlands Congress, Wetlands Biodiversity and Services: Tools for Socio-Ecological Development, 14–18.09.2014, Huesca, Spain; oral presentation: Macroinvertebrate diversity and community structure in woodland pools and ditches and their response to artificial drainage (co-authors: L. Remm, R. Rannap).

The 27th International Congress of Conservation Biology and the 4th European Congress for Conservation Biology (ICCB-ECCB), Mission Biodiversity: Choosing new paths for conservation, 02–06.08.2015, Montpellier, France; poster presentation: Macroinvertebrates in woodland pools and ditches and their response to artificial drainage in Estonia (co-authors: L. Remm, R. Rannap).

Dissertations supervised:

Triin Väisanen, Bachelor's Degree, 2016. "Koprad kui ökosüsteemi kujundajad looduskaitses" (Beavers as ecosystem engineers in nature conservation). University of Tartu, Institute of Ecology and Earth Sciences, Department of Zoology.

Kaisa Tihkan, Bachelor's Degree, 2016. "Funktsionaalsete toitumisrühmade seos väikeveekogude hüdroperioodiga" (The effect of hydroperiod on functional feeding groups). University of Tartu, Institute of Ecology and Earth Sciences, Department of Zoology.

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Vaikre, M., Remm, L., Rannap, R., Voode, M., 2018. Functional assemblages of macroinvertebrates in pools and ditches in drained forest landscape. *Wetlands* 38: 957–964.

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Konverentsiettekanded:

Maateaduste ja ökoloogia erialade doktorantide konverents “Down to Earth”, 16–17.05.2013, Tallinn, Eesti; suuline ettekanne.

The 9th European Wetlands Congress, Wetlands Biodiversity and Services: Tools for Socio-Ecological Development, 14–18.09.2014, Huesca, Hispaania; suuline ettekanne.

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Kaisa Tihkan, bakalaureusekraad, 2016. “Funktsionaalsete toitumisrühmade seos väikeveekogude hüdroperioodiga”. Tartu Ülikool, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

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