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ELIN SOOMETS

Focal species in wetland restoration

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Focal species in wetland restoration

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Press

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LIST OF ORIGINAL PUBLICATIONS

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

I **Soomets, E.**, Rannap, R. & Lõhmus, A. 2016. Patterns of assemblage structure indicate a broader conservation potential of focal amphibians for pond management. PLoS ONE 11: e0160012.
(Available from: http://doi.org/10.1371/journal.pone.0160012).

II Rannap, R., Kaart, T., Pehlak, H., Kana, S., **Soomets, E.** & Lanno, K. 2017. Coastal meadow management for threatened waders has a strong supporting impact on meadow plants and amphibians. Journal for Nature Conservation 35: 77–91.
(Available from: https://doi.org/10.1016/j.jnc.2016.12.004).

III **Soomets, E**., Lõhmus, A. & Rannap, R. 2017. Brushwood removal from ditch banks attracts breeding frogs in drained forests. Forest Ecology and Management 384: 1–5.
(Available from: https://doi.org/10.1016/j.foreco.2016.10.023).

IV **Soomets, E.**, Rannap, R. & Lõhmus, A. 2019. Restoring drained forested peatlands by combining ditch-blocking and partial cutting: impact on breeding amphibians. (submitted manuscript).

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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
CBD – Convention on Biological Diversity
EEA – European Environment Agency
EU – European Union
GLM – general linear model
IUCN – International Union for Conservation of Nature
HELCOM – Helsinki Commission; The Baltic Marine Environment Protection Commission
NODF – nestedness metric based on overlap and decreasing fill
OECD – Organisation for Economic Cooperation and Development
SER – Society for Ecological Restoration International Science

1. INTRODUCTION

1.1 Wetland habitat degradation and loss

Freshwater ecosystems are under severe anthropogenic transformation and over-exploitation worldwide (Dudgeon et al., 2006; Strayer & Dudgeon, 2010; Geist, 2011). The main causes of their deterioration are: exploitation of water and peat resources; wetland conversion to other land use – notably afforestation, agriculture and urban development (Joosten & Clarke 2002; Silva et al., 2007; Vörösmarty et al., 2010); external impacts of intensified forestry and agriculture (Williams et al., 2004; Feld et al., 2016; Arntzen et al., 2017; Vilmi et al., 2017); and fish stock management, drainage and abandonment of cattle ponds (Curado et al., 2011; Lemmens et al., 2013).

The rates of wetland loss have accelerated since the 20th century (Davidson, 2014), and natural wetland area has declined by more than 50% during this period (OECD, 1996; Zedler & Kercher, 2005; Davidson, 2014). Conversion to agricultural land has been the dominant driver. Asia stands out with the largest area of wetlands remaining, but also the largest area lost (Davidson, 2014; Davidson et al., 2018). Another region with a large historical wetland loss is North America, although the process has somewhat slowed down since the 1980s (Davidson, 2014). Europe has the largest number, but smallest area, of wetland sites among continents; it lost more than half of its natural wetland area before 1990 and the loss has slowed down slightly since then (Acreman et al., 2007; EEA, 2010; Xu et al., 2019).

In Eastern Europe, including the Baltic countries, wetland loss has been mainly due to draining for agricultural purposes (Hartig et al., 1997). Nowadays vast areas of historical temperate wetlands have shrunk to fragments in pasture areas and agricultural landscapes, losing their functionality as wetland ecosystems (Brinson & Malvárez, 2002). In the Baltic States, Fennoscandia and Russia another major form of wetland exploitation has been artificial drainage for forestry. By the early 1990s, more than 13.5 million hectares of wetlands had been drained for forestry in these regions (Paavilainen & Päivänen, 1995). In addition to inland wetland drainage, formerly grazed wet meadows have decreased on the coasts of the Baltic Sea, e.g. from 29 000 ha to 8000 ha in Estonia; these have turned into scrublands and reed-beds mainly due to disappearance of small farms and cessation of grazing (Luhamaa et al., 2001).

Freshwater ecosystems are long acknowledged to have rich and unique biodiversity to be sustained (Strayer & Dudgeon, 2010; Moreno-Mateos et al., 2012; Ramsar, 2018). This is supported by wetland habitat heterogeneity and, often, by relatively high net primary productivity (Tiner, 1984). The human-caused habitat degradation and loss have also led to reduction of wetlands' biodiversity (Dudgeon et al., 2006; Strayer & Dudgeon, 2010; Geist, 2011). Well known is, for example, the decline of amphibians (Semlitsch, 2002; Stuart et al., 2004; Ficetola et al., 2015; Arntzen et al., 2017) and wetland birds (Wilson et al., 2004; Wetlands

International, 2012; Pearce-Higgins et al., 2017), that are also in the focus of the current doctoral thesis. To reverse these trends, it is critically important to reduce wetland exploitation and restore damaged wetland ecosystems.

1.2 Ecological restoration of wetlands

When disturbance has disrupted ecosystem structure or function beyond an ecological threshold, the ecosystem may no longer be able to recover its former state of functioning. This causes also permanent loss of habitats and biodiversity, which can only be restored through specific habitat restoration activities. Such activities are now recognized as a global priority (Aronson & Alexander, 2013). Notably, the 2010 Aichi Targets set an internationally accepted political goal of restoring at least 15% of degraded ecosystems by 2020 (CBD, 2010).

The primary aim of restoration activities is to assist "the recovery of an ecosystem that has been degraded, damaged or destroyed" (SER Primer, 2004). In the scientific literature, multiple terms and definitions are related to such aim, often interchangeably (e.g. Li, 2006; Lima et al., 2016). For example, van Andel and Aronson (2012) distinguish four main opportunities to restore ecosystems and their constituent habitats, depending on starting conditions and the goal: **near-natural restoration** (almost non-assisted natural recovery); **true ecological restoration** (reconstruction of a previous-like state or self-sustaining target) in response to crossed biotic barriers; **ecological rehabilitation** (improvement of ecosystem functions) in response to crossed abiotic barriers; and **reclamation** to re-establish productive conditions in heavily degraded lands. **Mitigation** is a distinct restoration approach to provide compensation where the impact of disturbance is inevitable (Perrow & Davy, 2002). Another set of terms refers to "creation", "rehabilitation" and "enhancement", which are similar to restoration, but differ in some way from the process of renewing natural self-regulating ecosystem (Gwin et al., 1999).

In this thesis I refer to different aspects of habitat restoration as follows: (re)**creating** new ponds (i.e., replacement habitats) in paper **I**; **rehabilitation** via grazing and mowing on historical coastal meadows in paper **II**; and **enhancement** via forest partial cutting (**III**) combined with **true ecological restoration** of former water regime via ditch blocking (**IV**) in forested peatlands.

Wetland restoration is a relatively new concept in the history of conservation (Wheeler et al., 1995; Shackelford, 2013), although there has been international attention on conservation and sustainable use of wetlands since the Ramsar Convention (1971). Extensive wetland habitat restoration projects have been carried out in North America (mainly coastal areas), Europe and Asia (Li et al., 2019; Xu et al., 2019). For example, during the last 30–40 years, more than 10 mln ha of North-American wetlands have been restored with variable success (Nadakavukaren, 2011; Copeland, 2017). In Europe, Germany, United Kingdom and France have historically lost large wetland areas (Silva et al., 2007) and now stand out with the largest number of wetland restoration projects (Coops & van

Geest, 2007). In different parts of Europe, there are many successful examples of restoring river floodplain functioning and rewetting polders (Verhoeven, 2014; EU, 2007), restoring peatlands (e.g. Andersen et al., 2017; Brown et al., 2016; Menberu et al., 2016), wet grasslands (EU, 2007; Joyce, 2014) and ponds (Rannap et al., 2009b). Mainly in Asia, a significant share of all wetlands is artificial – created by converting natural wetlands into rice paddies (Leadley et al., 2014). Due to agricultural intensification, these wetlands are losing their values as compensating areas for ecosystem functions and biodiversity (Katayama et al., 2015; Giuliano & Bogliani, 2019). Restoration of wetland ecosystems can provide various important services, including a major role in carbon accumulation; water quality, storage and regulation; nutrient cycling; habitat provisioning for aquatic and semi-aquatic biodiversity; cultural heritage and recreation for people (Frolking et al., 2006; Kimmel & Mander, 2010; Lamers et al., 2015).

Despite long term restoration efforts, there are many obstacles to sufficient conservation of wetlands, particularly in densely populated areas of Asia (Kentula, 2000; Moreno-Mateos et al., 2012; Prigent et al., 2012; Choi, 2004). The obstacles include: a lack of scientific understanding of wetlands complexity and causal pathways to modify their ecosystems and assemblages; unclear objectives and criteria of restoration success; and multiple social, economic, and political constraints. An important principle of successful restoration is that each ecosystem is approached individually and contextually (Kovalenko et al., 2012; Tokeshi & Arakaki, 2012). However, specifically for the purpose of preserving biodiversity, it is difficult and laborious to detect, monitor or manage every aspect of species and habitat. Thus, shortcuts are sought to reasonably simplify the management and speed up knowledge acquisition. Among such shortcuts, monitoring and managing for a few carefully selected species (termed, e.g., focal species, umbrella species, flagship species, target species) has long been one of the key issues in conservation biology (Simberloff, 1998; Caro & O'Doherty, 1999; Caro, 2010).

1.3 The focal species approach

This dissertation addresses the concept of restoring and managing habitats and ecosystems according to selected specialized 'focal' taxa. According to Lambeck (1997) **focal species** are defined as the most sensitive species to individual threats in a changing environment, representing four main categories: area-, resource-, process- and dispersal-limited species. So far, the practical use of focal species approach (often included as set of umbrella species that indirectly protect many other species; Roberge & Angelstam, 2004) has been mainly confined to a (virtual) selection of strict protected areas (Rodrigues & Brooks, 2007; Seddon & Leech, 2008; Caro, 2010). However, its application to habitat management, (e.g. Simberloff, 1998; Caro & O'Doherty, 1999; Carignan & Villard, 2002; Roberge & Angelstam, 2004) and restoration (e.g., Petranka & Holbrook, 2006; Kumar et al., 2018) has been also debated worldwide.

Birds and environmentally sensitive aquatic animals are among the most attractive groups of focal species, since they are relatively easy to sample and possess unique habitat requirements. Specifically, for wetland conservation, they are intimately connected with the hydrologic conditions of ecosystems (Suter et al., 2002; Balcombe et al., 2005; Caro, 2010).

Although selected bird species may not be the most appropriate indicators of species richness of other taxon groups (Lund & Rahbek, 2002; Xu et al., 2008), they can effectively indicate full avian biodiversity of conservation interest (Suter et al., 2002; Senzaki & Yamura, 2016). Due to birds' sensitivity to anthropogenic perturbations (Brawn et al., 2001), they have practical value for prioritization of larger areas for conservation planning (Roberge & Angelstam, 2004; Alexander et al., 2017) and for habitat management (Paillisson et al., 2002). Also, birds can indicate certain habitat qualities (Rempel et al., 2016; Vallecillo et al., 2016) and aspects of restoration success (Crozier & Gaulik, 2003).

The evidence of amphibians as focal species in freshwater ecosystems is contradictory. Across landscapes that contain both terrestrial and aquatic habitat, amphibians are probably poor cross-taxon indicators (Beazley & Cardinal, 2004; Xu et al., 2008; Ruhi et al., 2014; Vehkaoja & Nummi, 2015). However, because of limited dispersal abilities (Smith & Green, 2005; Kovar et al., 2009) and high site fidelity (e.g. Loman, 1994; Bucciarelli et al., 2016), amphibians may have indicator value for conservation purposes on a more local scale. Amphibians might also indicate the success of ecosystem restoration (e.g. Waddle, 2006; Welsh & Hodgson, 2013; Diaz-Garcia, 2017), specifically in aquatic habitat restoration (Price et al., 2007). For example, in Italy, *Rana italica* has been proposed as a bioindicator for water quality condition in small headwater streams (Lebboroni et al., 2006). Welsh and Ollivier (1998) showed amphibian suitability as indicators of stream ecosystem dysfunction after road construction and fine sediment pollution into pristine streams. Creation and restoration of temporary waterbodies have also been assessed based on amphibians' response, in comparison with natural and restored/created water bodies (Kolozsvary & Holgerson, 2016; Rothenberger et al., 2019).

In this dissertation, I used meadow birds and pond-breeding amphibians to examine the effects of habitat management in three different wetland systems. Among birds, I selected Baltic dunlin (*Calidris alpina schinzii*) to study the habitat change and overall assemblage richness along with management intensity (mowing, grazing) of restored coastal meadows (**II**). Among amphibians, I explored great crested newt (*Triturus cristatus*) and common spadefoot toad (*Pelobates fuscus*) in relation to pond creation (comparing natural, man-made and specifically constructed ponds) and suitability for broader amphibian and macroinvertebrate assemblages (**I**). I also used more widely distributed brown frogs – moor frog (*Rana arvalis*) and common frog (*R. temporaria*) – to evaluate habitat changes in the aquatic habitats of degraded peatland forest ecosystems after their ecological restoration for a protected bird, western capercaillie (*Tetrao urogallus*) (**III**, **IV**).

1.4 Aims and motivation

The general aim of my studies was to explore wetland management and restoration effectiveness, notably for threatened wetland assemblages, as guided by habitat-sensitive focal species. The dissertation consists of four case studies in different wetland realms in Estonia: ponds (**I**), managed wet grasslands (**II**), and peatlands drained for forestry (**III, IV**).

I use focal taxa to address three broader knowledge gaps in the management of wetland habitats through focal species. First, the *relationship between focal taxa and assemblage structure* (**I**). I studied small water bodies within terrestrial habitat mosaics, which have been degraded due to intensive agriculture, forestry drainage and abandonment of traditionally managed lands (Céréghino et al., 2008; Curado et al., 2011). As a restoration opportunity, threatened and widespread pond-breeding amphibians readily inhabit newly created or reconstructed ponds (Rannap et al., 2009b; Magnus & Rannap, 2019) but it is not known whether the assemblages are linked enough to use the amphibian targets also for other co-occurring (semi) aquatic taxa in such restoration. Formally, then, confirming assemblage nestedness might be an effective step in focal species selection (Beazley & Cardinal, 2004).

Secondly, *relationships between the abundance of waders and broader diversity of coastal grasslands* (**II**). Managed wet coastal grasslands are known to support diverse plant communities, provide breeding grounds for amphibians and threatened birds (Paal, 1998; Kuresoo et al., 2004; Rannap et al., 2007). After being abandoned as traditional agricultural areas, the diversity declines, often despite using modern approaches to conservation management. This is probably due to insufficient knowledge of exact habitat characteristics that have historically supported viable populations of coastal-meadow species.

Thirdly, *frog breeding in drained forested peatlands as an indicator* for habitat management and restoration options. The drainage ditches, which substitute natural depressions in these ecosystems, are considered to be attractive (Remm et al., 2015) but low-quality breeding sites for amphibians (Suislepp et al., 2011). I studied the impact of forest partial cut (**III**) and ditch blocking manipulations (**IV**) on brown frogs breeding habitat, and the most preferred target conditions.

I address the following study questions:

i. Does habitat management for threatened species create quality habitats also for other species of conservation concern (as compared to non-managed areas), i.e., is increased abundance of focal species accompanied by a generally higher diversity of wetland-dependent species (**I**, **II**)?
ii. Are the key factors that shape assemblages similar in all three wetland study systems (**I–IV**)? Which habitat characteristics are most important for the nesting of threatened focal species on coastal meadows (**II**)?
iii. To what extent do reduced shade and changed water regime mitigate the drainage effects in forest areas where only ditches have remained as breeding sites for amphibians? Does ditch blocking favour the formation

of other types of small water bodies? How rapidly do frogs colonize the improved breeding habitats (**I**, **III–IV**)?

iv. What are the opportunities of using selected wader and amphibian species as focal species for conservation management and restoration (**I–IV**)? Is nestedness analysis a useful tool for the practical task of selecting focal species for habitat conservation (**I**)?

2. MATERIAL AND METHODS

2.1 Study area and design

The research was carried out in the mainland and in the western archipelago of Estonia. Estonia is situated in the hemiboreal vegetation zone in Europe. It has a humid temperate climate, where the mean January and July temperatures are –6 °C and +17 °C, respectively, and the average precipitation is 600–700 mm/yr. In order to preserve the diversity of nature and to ensure favourable status of threatened species and habitats, 19% of terrestrial and 28% of the total water area (marine and freshwater pooled) are protected in Estonia. More than 300,000 ha have been designated as Wetlands of International Importance (Kimmel et al., 2010).

There were three study systems, representing coastal meadows (wet grasslands), forested peatlands, and small ponds in various landscapes, respectively (Fig 1). The first study system (**I**) was established in six protected areas in northern, eastern and southern Estonia where large-scale pond restoration and construction has been carried out specifically for the great crested newt and/or common spadefoot toad. In total, 231 small ponds (mean area 0.5 ha), including natural pools, specially constructed ponds for these amphibians, and man-made ponds, were studied.

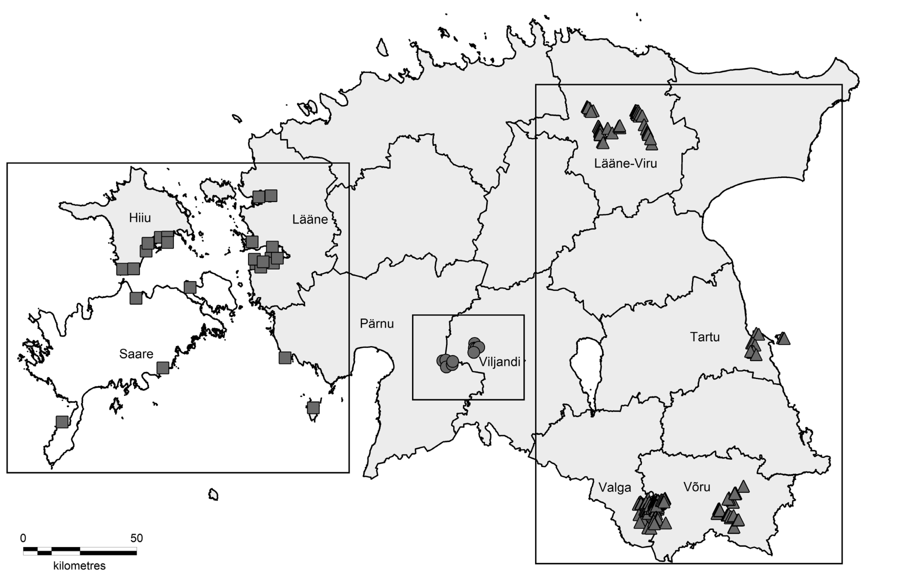

Figure 1. Locations of the study areas of the three study systems (boxes) and sites in Estonia. Triangles are the ponds (**I**), squares represent the coastal meadows (**II**) and circles are ditched forested peatlands (**III–IV**).

The second study system (**II**) included West-Estonian coastal meadows (Fig. 1), which are a priority (threatened) habitat type as listed in Annex I of the EU Habitats Directive (92/43/EEC). Of 24 coastal meadows studied (mean area 99 ha), 11 had natural hydrology and 13 were ditched. The meadows were selected in cooperation with conservationists and local land owners, because administrative and local support is critical for preserving coastal meadows (Gonzalo-Turpin et al., 2008). All these meadows had been used as pastures for at least five consecutive years before the beginning of this study.

In the third study system (**III–IV**), I assessed whether bog-forest restoration for a focal bird, western capercaillie, also affects amphibians in two adjacent drained bog landscapes in south western Estonia (Fig. 1). These studies were based on a before–after–control–impact (BACI) experimental design, which combined partial forest cut (also brushwood removal from ditch banks and maintaining the access-roads to restoration areas) and ditch blocking. For paper **III**, I selected a total of 32 overgrown 100-m ditch sections (half of these controls) comprising the ditch canal and partly decomposed and overgrown ditch spoil. In paper **IV**, a broader set of 151 ditch sections was explored; of these, 52 transects were subjected to ditch blocking (42 transects also to partial cutting of the surrounding forest), 34 transects to partial cutting only, and 65 were control transects.

2.2 Study species

The studies focused on protected vertebrate species whose populations are targeted by habitat management and restoration in different wetland types in Estonia (Table 1). The amphibians considered included great crested newt, common spadefoot toad and brown frogs. In Estonia, great crested newt and common spadefoot toad prefer to breed in relatively *small water bodies*, such as ponds and karst lakes. An optimal breeding pond for great crested newt has diverse submerged vegetation and is surrounded by mosaic landscape of forest and open habitats (Rannap et al., 2009a). The common spadefoot toad selects breeding sites on sandy soils and with open surroundings (Rannap et al., 2013, 2015). In the *forested peatland* study system, I selected the most characteristic and well detectable amphibian species – common frog and moor frog ('brown frogs'; Table 1; Pikulik et al., 2001). Brown frogs may also breed in artificial ditches if suitable small water bodies are not available (Remm et al., 2018).

The birds of interest were four species of coastal waders (Table 1) whose *coastal meadow* habitats have deteriorated due to overgrowth by tall vegetation, expansion of trees and bushes. Therefore, in paper **II** threatened waders were selected as focal species to reflect meadow habitat quality also for less demanding species (e.g. frogs, some vascular plants).

Table 1. Studied focal species, their conservation status, habitats and expected results of habitat restoration.

Species	IUCN Red List category with population trend (Europe) and [reference]	Wetland type	Habitat restoration/ management measure	Expected impact	Study
Great crested newt (*Triturus cristatus*)	Least Concern* Decreasing [1]	small water bodies (ponds)	pond construction	higher abundance of threatened species	**I**
Common spadefoot toad (*Pelobates fuscus*)	Least Concern* Decreasing [1]				
Moor frog (*Rana arvalis*)	Least Concern* Stable [1]	ponds, coastal meadows, forested peatland	pond construction; peatland restoration; grazing and/or mowing	higher abundance; increase of breeding habitat availability	**I–IV**
Common frog (*Rana temporaria*)	Least Concern Stable [1]				
Baltic dunlin (*Calidris alpina schinzii*)	Least Concern** [2,3]	coastal meadows	grazing and/or mowing	higher abundance of nesting birds	**II**
Common redshank (*Tringa totanus*)	Least Concern [2]				
Northern lapwing (*Vanellus vanellus*)	Vulnerable [2]				
Black-tailed godwit (*Limosa limosa*)	Vulnerable [2]				

* species of EU Habitats Directive (Annex II and/or IV)
** species of EU Birds Directive (Annex I) and HELCOM Red List Category: Endangered
References: [1] IUCN, 2020 [2] BirdLife International, 2015 [3] HELCOM, 2013

2.3 Data collection

2.3.1 Surveying species

The main method to collect amphibian data was visual counting of adults and spawn clumps (**II–IV**) and dip netting of larvae (**I–IV**). Spawn clumps, specimens and larvae were identified in the field and the latter two where thereafter released into their natal water bodies. In study **I,** both amphibian larvae and aquatic macro-invertebrates were collected in June in 2010, 2011 or 2013. During 45 minutes of active dip netting the vegetation and detritus material were searched through using the same standard dip net (40 × 40 cm frame hand dip-net) for both taxon groups. Collected data included abundance of all amphibians, and larvae of dragonflies (Anisoptera) and damselflies (Zygoptera), with a focus on species protected by the EU Habitats Directive, and adults and larvae of selected large water beetles (specifically, the globally vulnerable *Dytiscus latissimus* and *Graphoderus bilineatus*) (Foster, 1996a, 1996b).

In study **II**, the fieldwork was conducted in 2012 (spring with above-average precipitation) and 2013 (average spring) on 24 coastal meadows. Brown frogs were surveyed twice in each year: (i) in late April-early May, all water bodies present (artificial ditches, depressions, floods, pools) were sampled for spawn clumps; large flooded areas were searched on 3-m wide transects; (ii) in the first half of June, all water bodies and flooded areas were dip-netted for the presence of larvae.

In ditches and large floods, 10 dip-net sweeps were made per 50 m of transect. In water-filled depressions, pools and other types of smaller wetlands, 10–30 dip-net sweeps were made depending on the size of the water body, covering all aquatic microhabitats.

On the same meadows, breeding territories of four wader species (Table 1) were mapped based on nests, territorial birds, pairs or birds with breeding behaviour (**II**). The first census was carried out between 10–31 May and the second between 1–20 June (at least 10 days between the subsequent visits). Territorial pairs recorded in the same area during both counts were interpreted as the same pair. The abundance of vascular plant species was described in randomly located 25 × 25 m plots once in July and August 2012 or 2013 using the Braun-Blanquet (1964) scale (**II**: Appendix B).

Studies **III–IV** were also based on annual visual census of amphibian spawn clumps in late April (in 2014–2018) and – for assessing amphibian breeding success – on dip netting of larvae in June (20 dip net sweeps per each 100 m ditch section).

2.3.2 Measuring habitat characteristics

To assess the impact of environmental factors on focal species and assemblages, a set of expected key habitat characteristics were measured in the field. In study **I,** the area of water body, shade from the surrounding trees (% of the water table) and presence of fish were recorded. In studies **III–IV**, each ditch transect was characterized by average water depth (cm) and visually estimated proportion of water table shaded by woody canopies, brushwood or rank vegetation at every visit (April, June). In study **II** individual trees, bushes, wet areas with standing water (e.g. floods, depressions, pools) and the depth and width of ditches were measured in spring 2012 and 2013. Other landscape-variables in study **II**, such as area and width of meadows, area of wet features, distance to the nearest forest edge and bushes, length of ditches and coastline covered with reed-bed, were measured from the Estonian base map using MapInfo, ArcPad/ArcGIS or QGIS software. In addition, national soil map of Estonia was used in study **IV** to record ditch locations on sapric and hemic Histosols.

2.4 Data processing

Whenever supported by variable distributions, I used conventional parametric tests: t-test and ANOVA. Repeated-measures ANOVA was used for attributing between-year differences (repeated measure) in the focal species abundance or environmental parameter to manipulation (categorical factor; forest partial cutting and/or ditch blocking (**III, IV**). Alternatively, conventional non-parametric tests (Spearman rank correlation analysis, Wilcoxon rank-sum test, Friedman ANOVA) were used; e.g., to study the relationships between the measured coastal meadow characteristics, nesting waders, breeding amphibians and abundances of selected vascular plant species (**II**). Generalized Linear Models (GLM, based likelihood-ratio test) were a basic tool in many multifactor analyses, including: (i) relating the number of species to pond type and incidence of focal species (**I**); (ii) assessing between-year (a repeated measure) and manipulation-related changes in environmental parameters (shade and water depth), frog spawn clumps (=breeding habitat selection) and larvae (=success of breeding) in ditches (**III**); (iii) for assessing complex interaction effects between year, manipulation and soil type on the mean numbers of brown frogs' spawn clumps and larvae (**IV**). Univariate Poisson regressions were used for explaining the breeding of four wader species on coastal meadows via habitat characteristics (**II**).

Tests of focal species in study **I** were carried out. First, since the focal species approach relies in part on nested assemblage pattern (Lindenmayer et al., 2002), formal nestedness analyses were performed for each type of pond. At the assemblage-scale, Lomolino's (1996) "departures method" was used to estimate the impact of environmental factors and presence of fish to assemblage nestedness. To assess pre-selected focal species (great crested newt and spadefoot toad) as indicators for other amphibians and aquatic macro-invertebrates, the NODF metric (Nestedness based on Overlap and Decreasing Fill; Almeida-Neto et al., 2008) was used. This procedure individually tests species-pairs, i.e. the presence of each focal species vs. that of other amphibians and aquatic macro-invertebrates (details in paper **I**). Secondly, given that lack of threatened species' presence data and habitat suitability may be a problem of focal species selection (Lindenmayer et al., 2002), the abundance of the focal species was assessed in each type of pond. Thus, a combination of relatively uncommon occurrence (frequency < 25%; Honnay et al., 1999; Sætersdal et al., 2005) and its difference between specially constructed and other ponds were interpreted as habitat-sensitivity of the potential focal species (**I**).

In the coastal meadow assemblage analyses (**II**), multivariate patterns in coastal meadow characteristics, nesting waders, plants and breeding amphibians were established using the co-inertia analysis (Dolédec & Chessel, 1994). The overall concordance (correlation between tables of coastal meadow characteristics and wader or amphibian species) was estimated as the RV-coefficient, followed by permutation test for statistical significance (**II**).

3. RESULTS

3.1 Characteristics and conservation values of the studied wetland systems

In the study of 231 *ponds* (**I**), the water bodies constructed specially for amphibians had fewer fish than natural ponds ($\chi^2 = 21.42$; $p < 0.0001$) or man-made ponds ($\chi^2 = 45.39$; $p < 0.0001$). Constructed ponds also were the least shaded (most shaded were natural ponds) and smallest (Table 4 in **I**). We found four species of amphibians and four macro-invertebrates protected by the EU Habitats Directive in this system. In 69% of studied ponds, at least one such protected species was found (in 92% of constructed ponds, 77% of natural ponds and 48% of man-made ponds). Yellow-spotted whiteface (*Leucorrhinia pectoralis),* great crested newt and common spadefoot toad were the most frequent protected species found, while *Dytiscus latissimus* was the rarest.

The study system of 24 *coastal meadows* (**II**) was also highly variable. The mean meadow width differed 8 times, and only 10 meadows were larger than 100 ha and wider than 200 m. Larger meadows were relatively wetter than smaller meadows in both springs (in 2012: $r = 0.66$, $p < 0.001$; in 2013: $r = 0.74$, $p < 0.001$), and were further away from bushes and/or forest edge ($r = 0.44$, $p = 0.030$). Almost half of studied meadows were extensively managed (having > 50% of the area with vegetation ≤ 10 cm high, the rest with vegetation > 10–30 cm high), while 17% had low management intensity (> 50% of the meadow area unmanaged, the rest having vegetation > 30 cm high). Wider extensively managed meadows had significantly fewer single trees than narrower meadows with moderate or low management intensity ($r = -0.43$, $p = 0.035$; $r = -0.50$, $p = 0.014$, respectively).

Among studied waders, northern lapwing and common redshank nested in every meadow; Baltic dunlin inhabited 56% and black-tailed godwit 20% of the meadows. Breeding ruffs (*Philomachus pugnax*) were found only in 2012 in a single meadow. The most area-sensitive plants were 'weak competitors' – species of managed coastal meadows inhabiting higher and drier parts of the supra-saline zone (see study **I**, Appendix B); these were more abundant on wider meadows ($r = 0.49$, $p = 0.015$). Both brown frog species were frequent and bred in meadows with relatively longer ditch networks; their breeding success depended on extensive meadow management, amount of water in spring and ditches.

The *forested peatland* study system lacked any natural water bodies (natural depressions; flooded areas) before habitat restoration but the ditches were inhabited by five species of amphibians, among which the moor frog and common frog were the most frequent (**IV**). The mean water levels in ditches in April were rather similar among landscapes and soil types. However, habitat restoration by ditch blocking dramatically affected subsequent water conditions (Fig. 2). The 15 ditches that had been left partly open retained > 50% of ditch length with open deep water in channels (ca. 70 cm), and 36 ditch sections also developed flooded areas with shallow water (ca. 20–30 cm deep in spring) between or around the deep-water ditch sections. The April water levels in these two types of partly open ditches increased almost four-fold by 2017–2018: by 41 ± 19 (SD) cm and 44 ± 19 (SD) cm.

Partial cutting of trees had little effect on water levels (Fig. 3A in **IV**), but halved the mean shade above existing ditches (**III**). Given also minor additional effects caused by uncontrolled brushwood removal from ditch banks by foresters or at ditch blocking, the whole landscape became more open by the end of the study (**IV**).

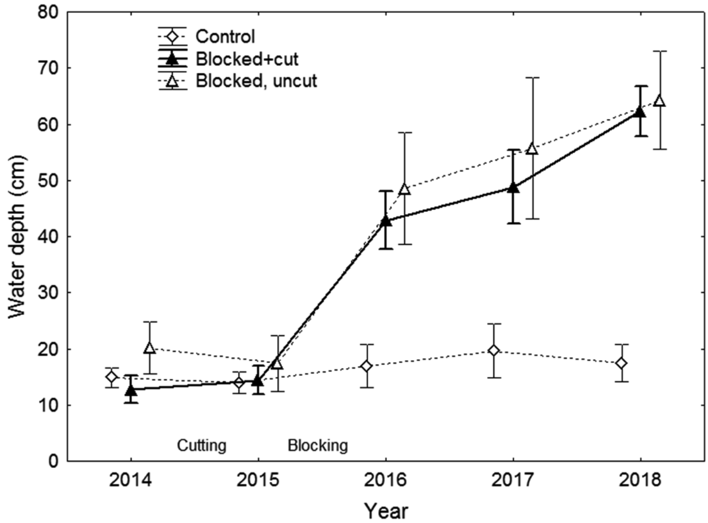

Figure 2. Mean (± 95 CI) April water depth by manipulation type in repeatedly surveyed ditches (**IV**). 26 blocked ditches with partial cuttings in the surroundings vs. 7 without cuttings. GLM: Year, $F = 54.1$, $p < 0.001$; Cutting, $F = 1.6$, $p = 0.219$; Year × Cutting, $F = 0.2$, $p = 0.954$. Control ditches ($n = 48$) are only shown for scaling.

3.2 Assessment of focal taxa

Among the eight EU-level protected species in the *pond* study, only the great crested newt fitted in a nested assemblage structure in every pond type, at $\alpha = 0.05$ (Table 1 in **I**). Thus, the ponds constructed for either this species or the spadefoot toad hosted most accompanying protected species. Additionally, presence of this newt had an independent effect to the number of other amphibian and insect species considered ($\chi^2 = 32.9$, $p < 0.01$); this effect was negative in natural and man-made ponds, but not in the constructed ponds (see Fig. 2 in **I**).

In *coastal meadows* Baltic dunlin (a potential focal species) and black-tailed godwit nested at higher densities in larger meadows (dunlin 2012: $r = 0.61$, $p = 0.002$; 2013: $r = 0.77$, $p < 0.001$; godwit 2012: $r = 0.41$, $p = 0.044$; 2013: $r = 0.49$, $p = 0.014$; **II**). Northern lapwing and common redshank had high densities also on smaller meadows (although the abundances were proportionately smaller) (see Fig. 2 and appendix D in paper **II**). The width of inhabited meadows was rather consistent among wader species but, again, the dunlin had higher nesting densities on wider meadows (2012: $r = 0.44$, $p = 0.031$; 2013: $r = 0.66$, $p < 0.001$). The dunlin also nested more frequently in meadows hosting 'weak competitor' plants and, additionally, species of the supra-saline zone ($r = 0.42$, $p = 0.041$; $r = 0.43$, $p = 0.037$, respectively). In the wet year (2012), the abundance of spawn clumps of common frog associated positively with the occurrence of 'weak competitor' plants ($r = 0.47$, $p = 0.021$).

In the *forested peatland* study, brown frogs (the proposed focal species group) were the most frequent amphibians (**III–IV**). The multi-year mean reproduction index in moor frog (EU protected species) was much higher (1.3 ± 0.8) than in common frog (0.4 ± 0.2); such contrast in relative breeding success appeared in every year (**IV**). Spawn clumps of brown frogs were never found at 29% studied ditch sections, and only three ditches (2%) had breeding activity in every year studied (**IV**).

3.3 Impact of wetland restoration and management on biota

Constructed *ponds* had the highest number of recorded amphibian and aquatic macro-invertebrate species among pond types (Fig. 2 in **I**). The factors influencing community structure (including nestedness; Table 4 in **I**) were: fish presence, pond size, shade, and age of pond (only tested in constructed ponds). In constructed ponds, the assemblages were significantly more structured in the absence of fish (NODF = 51.86, $p < 0.01$, $n = 60$) than in their presence (NODF = 13.14, $p = 0.93$, $n = 5$). An opposite pattern was found in natural and man-made ponds: those without fish (natural ponds: NODF = 26.14, $p < 0.01$, $n = 32$; man-made ponds: NODF = 28.1, $p < 0.01$, $n = 35$) had less structured pattern compared to ponds with fish (natural ponds: NODF = 34.75, $p < 0.01$, $n = 57$; man-made ponds: NODF = 42.04, $p < 0.01$, $n = 55$). Pond size was a significant factor of nestedness for man-made ponds only, while shade (and not size) affected natural and constructed ponds (**I**).

Among *coastal meadows*, larger and wider meadows with extensive management, without trees, and with large areas of wet features were generally favoured as breeding sites by all studied wader species. These features were also related to yearly variation in habitat quality: in 2012 (wet year), half of the studied meadows qualified as optimal nesting sites, while in 2013 (average year) only 38%. A large area of wet features was preferred by redshank (both years), Baltic dunlin (2012) and lapwing (2013). The black-tailed godwit preferred a combination of extensively managed area and a large area of wet features (2012), while ditched extensively managed meadows were preferred in 2013 by Baltic dunlin and godwit. Moderately managed meadows with long ditch networks had positive effect on lapwing (**II**).

For brown frogs in *ditches in peatland forests*, restoration techniques varied in their impacts both on the abundance of spawn clumps (year × manipulation type: F = 6.9, p = 0.014) and on tadpoles (F = 4.3, p = 0.047) (**IV**). The abundance of spawn clumps increased immediately in 2015, after partial cleaning of ditch banks (Fig. 3B; also Table 1 in **III**); this effect was due to reduced shade and also affected tadpole abundance (Fig. 3C). In later years, there were no further changes in spawn clump abundances in repeatedly surveyed transects in partially cut sites (Friedman ANOVA: $\chi^2 = 4.4$, p = 0.112).

In the next spring after ditch blocking, frogs' breeding activity declined (Fig. 4B), most drastically in the common frog (only four spawn clumps in two blocked transects were found in 2016 compared with 113 clumps on five transects in 2015). In moor frog the clump numbers declined from 147 to 102, but the number of breeding transects only from 13 to 11. However, in the following years, the breeding activity recovered and exceeded the levels prior to ditch blocking, most notably in the treatment combining ditch blocking and partial cutting (Fig. 4A). The manipulation effects on tadpoles were as follows: (i) blocked, but uncut, sites produced 1%–3% of all tadpoles in 2014–2016, but > 10% in 2017–2018 (an overall increase 3–4 times); (ii) tadpole numbers increased from 2014 to 2015 by 36% in control sites, but by 129% in partially cut sites; and (iii) a decline in tadpole numbers from 2015–2016 was restricted to ditch filling sites (63% reduction), while control sites had stable tadpole numbers (**IV**).

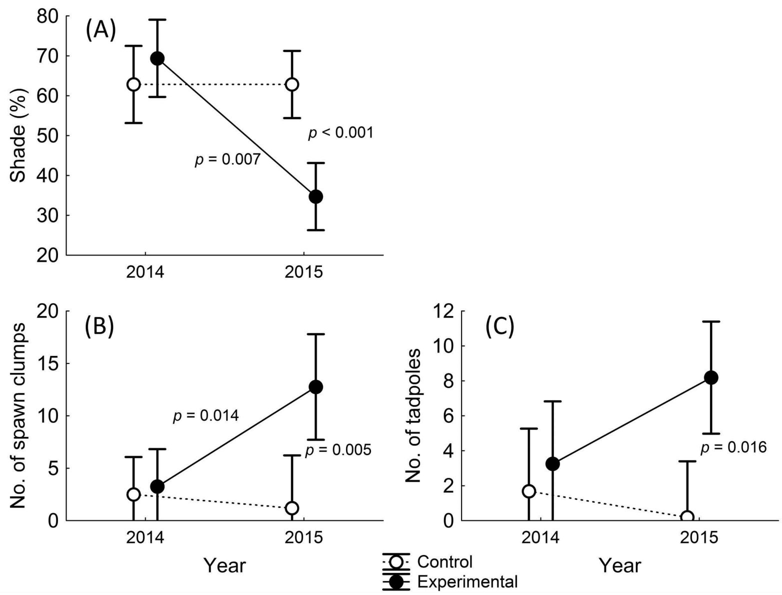

Figure 3. Changes in mean shade (A), the number of spawn clumps (B) and tadpoles (C) of brown frogs in 16 brushwood-removal and 16 control sites, 2014–2015 (**III**). Each 'site' constituted a 100 m section of a drainage ditch. The p-values of significant post-hoc comparisons (Tukey test: p < 0.05) are shown (on lines are the between-year differences). Vertical bars denote 95% confidence intervals.

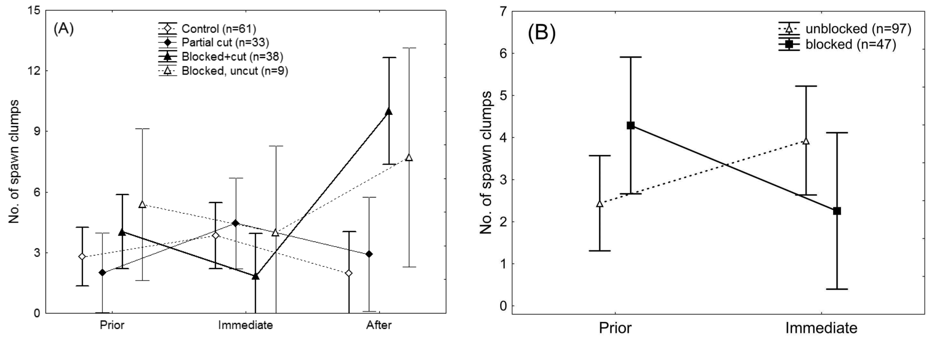

Figure 4. Mean (± 95% CI) no. of spawn clumps of brown frogs in repeatedly surveyed ditches (**IV**). (**A**) All four manipulation types in springs prior to (2014–2015), immediately following (2016), and after the ditch blocking (2017–2018) (n =141 repeatedly surveyed transects). GLM: Year, F = 4.1, p = 0.018; Manipulation, F = 2.3, p = 0.076; Year × Manipulation, F = 7.5, p < 0.001. (**B**) The contrast between the periods prior to and immediately following ditch blocking, cutting manipulations pooled (n = 144 transects). GLM: Year, F = 0.2, p = 0.641; Manipulation, F < 0.1, p = 0.922; Year × Manipulation, F = 9.2, p = 0.003.

4. DISCUSSION

4.1 Focal species for habitat restoration and management

It has been debated how often restoration of degraded habitats achieves expected results and, more generally, how to measure such restoration success (Suding, 2011; Zhao et al., 2016; Remm et al., 2019). To meet these challenges, lists of key attributes of successful restoration have been elaborated (SER Primer, 2004; Ruiz-Jaen & Aide, 2005; van Andel & Aronson 2012; Wortley et al., 2013). Ecologically, the SER (2004) attributes reflect: species composition, ecosystem function, ecosystem stability and landscape context (Shackelford et al., 2013). Similarly, there is no consensus on how to assess wetland restoration (Ruiz-Jaen & Aide 2005), but water and soil quality and assemblage composition are widely used as indicators (Zhao et al., 2016). The latter typically focuses on vegetation structure and succession (Ruiz-Jaen & Aide 2005; Matthews & Endress, 2008; Poulin et al., 2013) while animals, particularly vertebrates, have been neglected (Kentula, 2000; Brudvig, 2011).

In my thesis I showed that certain amphibians (**I, III–IV**) and waders (**II**) respond to conservation management and also reflect wider conservation values. They thus acted as potential focal species to assess restoration and management success in various wetland habitats. Specifically, ponds constructed for the protected great crested newt hosted higher diversity of amphibians than natural water-bodies or man-made ponds (**I**). This was despite a small negative influence of this species (if present), which may be related to its predation impacts on other species (Griffiths et al., 1994). Large, wide, and extensively grazed coastal meadows provided optimal nesting sites not only for the Baltic dunlin but also supported higher overall biodiversity of plants, amphibians and waders (**II**). Similar results have been obtained in other types of grasslands, where management which reduces plant competition generates complex and heterogeneous habitat mosaics (Palmer et al., 2010; Rosenthal et al., 2012) that favour higher species diversity of amphibians and plants (Bennett et al., 2006; Thiere et al., 2009; Gaujour et al., 2012). In drained forested wetlands ditch-blocking and partial cutting strongly supported the breeding of brown frogs (**III–IV**), which is consistent with other results from managed forests (Dibner et al., 2014). The key factors – increase in sun exposure and reduction of leaf litter – may also reshape macroinvertebrate communities and structure of understory plants (Batzer et al., 2000; Haapala et al., 2003; Melody & Richardson, 2004; Bartemucci et al., 2006) that needs further studying.

Criteria for the selection of focal species include time- and cost-effectiveness and context-dependence (Caro, 2010). My field methods for detecting focal species were mostly visual counting of amphibian spawn, dip-netting of larvae, and territory mapping of birds (**I–IV**). The advantages of such observational techniques are small impacts on study animals and small demands on equipment and observer training. Of specific analytical methods, I used nestedness analysis (**I**).

While conventional approach for managing biodiversity is location based (Bestelmeyer et al., 2003), it is not obvious how location-specific focal species should be. At least, each wetland type should probably have its own set of focal species. There are also regional considerations. For example, great crested newt was an appropriate focal species within its distribution range (**I**), which did not reach to my study systems **II–IV** (see study **I** Fig. 1). Also coastal waders (**II**) can be used as focal species in limited coastal areas. Although brown frogs were widespread in each system studied, they appeared management sensitive only in the drained-forest system (**III–IV**).

4.2 Assemblage dynamics after restoration actions

In general, ecological wetland restoration enhances overall biodiversity by providing diverse habitat complexes and various successional stages for assemblages (e.g. Balcombe et al., 2005; Klimkowska et al., 2007; Rey Benayas, 2009; Brand et al., 2014; Meli et al., 2014). However, the full impact of habitat restoration only becomes evident during prolonged time periods. For example, plant succession is relatively slow in water bodies (Moreno-Mateos et al., 2012); while vegetation cover secondarily affects general species richness, particularly of plant-dependent (semi-) aquatic species such as dragonflies (Remsburg & Turner, 2009; Cunningham-Minnick et al., 2019) and amphibians (Lehtinen & Galatowitsch, 2001; Pechmann et al., 2001). Study (**I**) indeed confirmed different assemblages in natural and specially constructed ponds (age 3–9 years, sometimes without macrophyte cover), which may result from the succession. The lack of a dense shady stand and scrub may be a cause of greater species richness and formation of species assemblage patterns (**I**). In overgrown meadow systems (**II**) more than 10 years of re-introduced habitat management may be required to achieve breeding habitat for waders (Thorup, 1998) or up to decade to obtain some recovery of threatened plant species (Moora et al., 2007; Schrautzer et al., 2011). Additionally, a diverse habitat management regime may be necessary (Kose et al., 2019) to support viable populations of threatened species.

Change of wetland's canopy cover and water regime directly affect amphibian breeding habitat conditions after habitat restoration. I found immediate improvement after clearing of ditch banks: the newly open ditch sections became preferred breeding sites of brown frogs (**III**). It is likely, however, that such cutting has to be repeated to maintain water area sun-exposed in the long term. An opposite (negative) response was found in the next spring after ditch blocking, although this also opened up the surroundings. The likely reason is that the construction work killed hibernating frogs in ditches and ditch banks (**IV**; see also Pechmann et al., 2001, Hartel et al., 2011). In later years, the breeding population of brown frogs increased to higher than pre-restoration levels, however. One likely factor is that ditch blocking favored the formation of other types of small water bodies, which were quickly colonized by brown frogs that may have used the ditch networks as migration corridors (Mazerolle, 2005). A longer perspective on these restoration-created flooded areas and ponds is not available yet. However, further plant succession is likely to offer suitable breeding and hibernation sites for other semiaquatic species that require large, sun-exposed permanent water bodies, such as green frogs (*Pelophylax sp*.), newts and dragonflies (Griffiths, 1997; Kadoya et al., 2004; Vehkaoja & Nummi, 2015; Cunningham-Minnick et al., 2019).

4.3 Key factors for wetland restoration

The key factors that shaped assemblages in all three wetland study systems were rather similar: habitat area (**II**), exposure to sun (**I–IV**), and presence of shallow-water areas (**II–IV**). For example, large *coastal meadow*s with short grass and sun-exposed wet features were optimal both for waders (see also Thorup, 1998; Ausden et al., 2001; Leyrer et al., 2018; Kaasiku et al., 2019), brown frogs and a plant assemblage with weak competitive abilities (**II**). Importantly, large coastal meadows were also more likely to have open shallow-water areas with varied micro-topography. Thus different key factors act in concert; e.g., water-logging suppresses vegetation growth (Thorup, 1998; Ausden et al., 2003) and reduces the risk of predation on coastal waders (Laidlaw et al., 2019).

Similarly, Stumpel (2004) have argued that large *ponds* are more heterogeneous providing opportunities for greater number of amphibian species. For example, the relatively small constructed ponds may not be large enough for threatened diving beetles as *Dytiscus latissimus* and *Graphoderus bilineatus* (**I**). In terms of assemblage nestedness, however, pond size was a significant factor in man-made ponds only (**I**). It is not clear what was the mechanism, since man-made ponds were larger, but they had several low-quality features for amphibians (frequent presence of fish; more shaded). Instead, sun-exposure played an important role in forming strong community composition patterns (nestedness) in natural and constructed ponds. The latter were most exposed and also most species rich, including threatened species, such as great crested newt or common spadefoot toad. Sunlight warms up water, which accelerates tadpole development (Skelly et al., 2002) and the establishment of macrophyte cover (Bornette & Puijalon, 2011) that is vital for hiding from predators (Martin et al., 2005). Scheffer et al. (2006) have also found that water bodies with smaller surface area, but greater vegetation cover, can have more species than large lakes.

More than a half of the coastal meadows (**II**) and the *peatland forest* system studied (**III–IV**) had their water regimes disturbed by artificial drainage. It is known that ditch network reduces the number, area and longevity of depressions and natural shallow water bodies both on coastal meadows (Eglington et al., 2008) and commercial forests (Suislepp et al., 2011), especially in years with lower precipitation. While old ditches with shelving margins, resembling foot-drains or rills are used as feeding habitats by waders (Milsom et al., 2002), deep ditches with steep banks are usually avoided (Żmihorski et al., 2018). My study (**II**) also confirmed that ditches can be used as foraging grounds for waders, especially in years with average precipitation (2013), when the availability of wet patches is limited. In commercial forests, ditches are often the only wet features available (also in study **IV**), but due to their lower quality ditches can be less often used as amphibian breeding sites compared to natural or novel water bodies (Suislepp et al., 2011). When blocking ditches to improve the situation, however, the timing is important to not disturb hibernating amphibians. In the Netherlands, the recommended time for water body cleaning is in early October – after amphibian reproduction and before hibernation (Stumpel, 2004).

5. CONCLUSIONS

1. This thesis explored habitat management and restoration of various wetlands as guided by the most habitat-sensitive focal species among amphibians and waders. My main conclusion is that this approach can indeed support a higher diversity of wetland species (**I, II**); however, my studies did not compare alternative approaches in terms of efficiency.
2. Key factors for the presence of focal species in different wetland systems are similar: the area of open habitat (either sun exposed water table or non-fragmented meadow area), with large wet patches (**I–IV**). Extensively grazed large (≥ 100 ha) wide (mean width ≥ 200 m) and wet coastal grasslands without woody vegetation provide breeding conditions for threatened waders (in particular Baltic dunlin, Black-tailed godwit and Common redshank), larger brown frogs' populations (common frog and moor frog), and more diverse vascular plant communities (**II**). Some of these conditions can be rapidly restored, such as the removal of brushwood (**III**) or blocking of ditches (**IV**). However, it is likely that maintaining these features, especially in semi-natural settings (such as coastal meadows or around constructed ponds) may need sustained grazing or mowing to prevent future overgrowth.
3. Restoring the heavily engineered ecosystem of ditched forested wetlands toward more natural states by partial forest cutting (keeping ditches exposed to the sun) and ditch blocking (restore more natural water regime) may mitigate some afforestation-related negative drainage impact on (semi-)aquatic species. The removal of brushwood from ditch banks and thereby 30% reduction of shade immediately transformed former heavily shaded water bodies into breeding habitat for brown frogs (**III**). A similar effect was found after blocking of ditches – formation of sun-exposed floods and ponds provided high quality breeding sites for amphibians in a very short time (**IV**). In my study, such restoration rapidly increased the populations of brown frogs typical of natural wetlands (**III–IV**).
4. Amphibians and waders can be used as focal species for restoration of degraded wetlands (**I–II**). Combining bird and amphibian species as focal taxa for different habitat components in the same ecosystem may be useful, as exemplified by adding brown frogs to the western capercaillie when restoring drained forested wetlands (**III–IV**). In addition, my study confirms nestedness method as an effective step in focal species selection (**I**).

KOKKUVÕTE

Suunisliigid märgalakoosluste taastamisel

Inimtegevusest tingitud elupaikade vaesumine ja hävimine on bioloogilise mitmekesisuse vähenemise peamine põhjus. Märgalad on väga liigirikkad ja eripärased ökosüsteemid, mida tuleb säilitada loodusliku mitmekesisuse hoidmise eesmärgil. Neid kahjustavad kõige sagedamini kuivendamine ning intensiivsest põllumajandusest lähtuv täiendav toitainekoormus ja mürgid. Poollooduslikke märgalakooslusi ohustavad aga ka traditsioonilisest kasutusest (nt karjamaadena) kõrvalejäämisega kaasnev võsastumine. Viimase sajandiga on kogu maailmast kadunud enam kui 50% märgaladest, mis on viinud paljude märgalasid asustavate liikide drastilise arvukuse languseni. Ohustatud liikide seas on suurepindalalistest päikesele avatud märgaladest sõltuvad kahepaiksed ja kahlajad, kellel on nende ökosüsteemide toitumisvõrgustikes oluline roll.

Elupaikade taastamine elurikkuse kadumise pidurdamiseks on looduskaitse ajaloos suhteliselt uus suund. Taastamisökoloogia mõiste ulatub tagasi 1930. aastate keskpaika, mil tehti esmakordselt katsetusi hävinud preeria taastamisega põllumaadele (Jordan III jt, 1987). Rahvusvahelist tähelepanu märgalakoosluste säilitamisele ja nende jätkusuutlikule kasutamisele hakati pöörama seoses Ramsari konventsiooniga (1971), kuid alles 20. sajandi lõpus muutus märgalade taastamine üldtunnustatud praktikaks ja arenes asjakohane uuringusuund. Tänapäeval on märgalakoosluste kujundamise ja taastamise laiemaks eesmärgiks nii olemasolevate elupaikade säilitamine, kahjustatud elupaikade ennistamine (ökosüsteemina), sihttaastamine (konkreetsetele organismirühmadele) ning uute elupaiga-paigakomplekside loomine. Lihtsustatult on elupaikade ökoloogilise taastamise eesmärgiks rikutud tasakaaluga elupaikade rohkemal või vähemal määral tagasipööramine inimhäiringu eelsesse seisu.

Käesolevas doktoritöös käsitletakse elupaikade ja ökosüsteemide taastamise võttestikku, mis lähtub elupaigatundlikest suunisliikidest *(*ingl. *focal species*). Suunisliigid on liigid, millest igaüks on konkreetse keskkonnamuutuse suhtes väga tundlik, nii et esindusliku liigikomplekti kasutamisel saaks mitmekülgselt, aja- ja kuluefektiivselt jälgida ja suunata ökosüsteemide seisundit. Sealhulgas on maismaa- ja veelinde, aga ka keskkonnatundlikku vee-elustikku peetud praktilisteks suunisliikide rühmadeks nende suhteliselt lihtsa jälgitavuse tõttu. Teoreetilises plaanis peetakse linde sobivaiks suunisliikideks pigem suuremas (maastiku) mastaabis ja väiksema liikuvusega loomi lokaalsemate otsuste tegemiseks (Caro, 2010). Ühe lähenemisviisina kasutatakse doktoritöös liigimustrite uurimiseks hõlmatuse (*nestedness)* kontseptsiooni, mille kohaselt ennustavad koosluse kõige tundlikumad liigid teiste liikide esinemist, kuid kõige vähem tundlikud (generalist-) liigid on ebatõenäolised teiste liikide esinemise ennustajad.

Käesolev doktoritöö tegeleb kolme teadmiste lüngaga suunisliikidest lähtuval märgalakoosluste taastamisel ja kaitsel. Esiteks, kuivendussüsteemide rajamise ning põllu- ja metsamajanduse intensiivistumise tõttu on kahepaiksetele sobiv mosaiikne maastik märgalade ja väikeveekogudega Eestis suuresti kadunud.

Kuigi viimastel aastakümnetel on ohustatud kahepaikseliikidele edukalt taastatud või rajatud sadu väikeveekogusid (Rannap jt, 2009b), on teadmata nende terviklike koosluste struktuur. Teiseks, suured hooldatud rannaniidud tagavad mitmekesise taimestiku ning pakuvad kvaliteetset sigimispaika nii kahepaiksetele kui ka kahlajatele. Traditsiooniliste maahooldusvõtete kadumise järgselt pole looduskaitseliselt planeeritud maahooldus suutnud tundlike liikide arvukuse tõusu Eesti rannaniitudel tagada (Rannap jt, 2007; Elts jt, 2013). Seega on võtmetegurid ohustatud liikide arvukuse tõusu soodustamiseks ilmselt teadmata ja taastamistegevuses rakendamata. Kolmandaks otsiti vastust küsimusele, kas metsastamise eesmärgil kuivendatud märgalal on võimalik looduslikku veerežiimi taastada, kuidas see mõjutab kahepaiksete sigimiskoha valikut ning kas kahepaikseid saab kasutada elupaikade taastamise indikaatoritena.

Nendele küsimustele vastamiseks uuriti doktoritöös kolme ökosüsteemi: 1) eri tüüpi väikeveekogusid ava- ja metsamaastikul Põhja-, Ida- ja Lõuna-Eestis (**I**) ; 2) erineva veerežiimi ja suurusega hooldatud rannaniidualasid Lääne-Eesti rannikul ja saartel (**II**) ja 3) tugevasti kuivendatud metsaalasid Soomaa rahvuspargis ja Kikepera hoiualal (**III–IV**).

Ohustatud kahepaiksete uuring väikeveekogude biomitmekesisuse suunisliikidena (**I**) põhines kahe Eestis ja Euroopas ohustatud kahepaikseliigi – harivesiliku (*Triturus cristatus*) ja hariliku mudakonna (*Pelobates fuscus*) – varasemal edukal suure-skaalalisel sigimisveekogude taastamise ja rajamise projektil. Mõlemad liigid on levila ahenemise ja arvukuse languse tõttu arvatud rangelt kaitstavate liikidena Euroopa Liidu Loodusdirektiivi II ja/või IV lisasse. Samas on spetsiaalsete veekogude rajamine üsna kulukas. Uuringus võrreldi kahepaiksete ja vee-suurselgrootute (kiilid ja veemardikad) koosluste struktuuri ja koosesinemise mustreid spetsiaalselt rajatud veekogudes looduslike ja teiste inimtekkeliste väikeveekogude omaga (kokku 231 veekogu). Kõigis kolmes veekogutüübis leiti liikide vahelised hõlmatuse mustrid, mis aga varieerusid, olenevalt nt veekogude suurusest, varjulisusest, tekkeajast ja kalade esinemisest. Kõige liigirikkamad olid spetsiaalselt kahepaiksetele, peamiselt harivesilikule rajatud veekogud, s.t harivesiliku tarbeks väikeveekogude taastamine ja rajamine loob sobivaid elupaiku ka teistele (pool)veelistele liikidele. Kaitsealuste liikide ebaühtlane esinemine teistes veekogudes viitas aga sellele, et need ei vasta ohustatud liikide elupaiganõudlusele kas seetõttu, et nende rajamisel pole sellega arvestatud (inimtekkelised veekogud) või on (looduslikud veekogud) kuivenduse tagajärjel neile liikidele ebasobivaks muutunud.

Rannaniitude uuringusüsteemis (**II**) oli vaatluse all 13 kraavitatud ja 11 kraavitamata (loodusliku veerežiimiga) rannaniitu, mida oli vähemalt viiel viimasel järjestikusel aastal hooldatud (niidetud või karjatatud). Kirjeldati rannaniidu elupaiga omadusi, mis mõjutavad ennekõike nelja kahlajaliigi – mustsaba-vigle (*Limosa limosa*), niidurüdi (*Calidris alpina schinzii*), punajalg-tildri (*Tringa totanus*) ja kiivitaja (*Vanellus vanellus*) pesitsemist alal. Uuriti kas rannaniidu omadused, mis vastavad langeva arvukusega niidurüdi pesitsuspaiga nõudlusele, tagavad ka kvaliteetse kasvukoha või sigimispaiga rannaniidule omastele soontaimeliikidele ning rabakonnale (*Rana arvalis*) ja rohukonnale (*R. temporaria*).

Selgus, et ohustatud kahlajaliikidele on sobivaimaks pesitsuspaigaks suured (≥ 100 ha) ja laiad (keskmise laiusega ≥ 200 m) karjatatavad rannaniidud, kus puuduvad (ka üksikud) puud ning leidub ajutisi madalaveelisi lompe. Niisugustel rannaniitudel olid mitmekesisemad elupaigad, mistõttu sobivaid pesitsuskohti leidus nii madalmuruseid alasid eelistavatele kui ka kõrgemat taimestikku ja puhmaid vajavatele liikidele, samuti oli neil niitudel arvukamalt kahepaikseid ja mitmekesisem soontaimestik. Kuna leiti, et samasuguste omadustega olid ka niidurüdi pesitsusalad, võiks seda liiki kasutada suunisliigina rannaniitude taastamisel ja hooldamisel.

Kuivendatud siirdesoometsade uuringusüsteemis (**III–IV**) taastati metsise (*Tetrao urogallus*) elupaikade veerežiimi kuivenduskraavide osalise või täieliku sulgemise ning eri tüüpi harvendusraietega. Küsimus oli, kas nende alade veerežiimi taastumise jälgimiseks võiks kasutada kahepaikseid – rabakonna ja rohukonna. Manipulatsioonide eelselt kaardistati pruunide konnade sigimispaigad, milleks olid kuivenduse pikaajalisest mõjust tingituna jäänud vaid kraavid. Kirjeldati järgnenud manipulatsioonide (raie ja kraavide sulgemine) mõjusid ning koosmõjusid hinnati pruunide konnade kudemisele ja sigivusele. Taastamisalade kraavides kasvas pruunide konnade sigimisaktiivsus drastiliselt pärast 30% väljaraiest tingitud varjulisuse vähenemist. Veerežiimi muutuse tagajärjel tekkisid osaliselt üleujutatud alad ja lombid, mis järgnevatel aastatel muutusid pruunide konnade eelistatud sigimispaikadeks. Seda kinnitas nii kudupallide keskmise tiheduse kahekordistumine kui ka kulleste arvu 3–4 kordne kasv pindala kohta, seda eriti kraavide osalist sulgemist ja raieid kombineerivatel kraavilõikudel. Seega saab kuivendatud ja metsastatud märgaladel kombineeritud taastamismeetodeid kasutades toetada looduslikele märgaladele tüüpiliste kahepaiksete populatsioone. Pruunid konnad sobivad Eestis suunisliikideks soometsade valgus- ja veerežiimi kujundamisel.

Suunisliikide kasutamise kohta märgalakoosluste taastamisel võib seega kokkuvõtvalt öelda, et elupaikade kujundamine nende eriomastele ohustatud liikidele tagab ka paljude teiste märgaladest ja vee-elupaikadest sõltuvate liikide suurema liigirikkuse.

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***

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PUBLICATIONS

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Scientific publications:

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Rannap, R., Kaart, T., Pehlak, H., Kana, S., **Soomets, E.** & Lanno, K. 2017. Coastal meadow management for threatened waders has a strong supporting impact on meadow plants and amphibians. Journal for Nature Conservation 35: 77–91.

Soomets, E., Lõhmus, A. & Rannap, R. 2017. Brushwood removal from ditch banks attracts breeding frogs in drained forests. Forest Ecology and Management 384: 1–5.

Soomets, E., Rannap, R & Lõhmus, A. 2019. Restoring drained forested peatlands by combining ditch-blocking and partial cutting: impact on breeding amphibians. *Manuscript*

Conference presentations:

The 27th International Congress for Conservation Biology and the 4th European Congress for Conservation Biology (ICCB-ECCB), 02–06.08.2015, Montpellier, France; oral presentation: Species patterns in small freshwater bodies guides towards focal species approach in aquatic habitat restoration (co-author: R. Rannap).

19th SEH European Congress of Herpetology, 18–23.09.2017, Salzburg, Austria; oral presentation: Brushwood removal from ditch banks attracts breeding frogs in drained forests (co-authors: A. Lõhmus, R. Rannap).

Dissertations supervised:

Linda Puusalu, Master's Degree, 2017. The structure and reproductive behaviour of the natterjack toad *Bufo Calamita* in a population of its northern range edge at Veskijärve, University of Tartu.

Riin Magnus, Master’s Degree, 2017. Natural ponds and ponds specially constructed for amphibians: their properties and importance for spadefoot toad (*Pelobates fuscus*), great crested newt (*Triturus cristatus)* and for amphibian species richness), University of Tartu.

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Teaduspublikatsioonid:

Soomets, E., Rannap, R. & Lõhmus, A. 2016. Patterns of assemblage structure indicate a broader conservation potential of focal amphibians for pond management. PLoS ONE 11: e0160012.

Rannap, R., Kaart, T., Pehlak, H., Kana, S., **Soomets, E.** & Lanno, K. 2017. Coastal meadow management for threatened waders has a strong supporting impact on meadow plants and amphibians. Journal for Nature Conservation 35: 77–91.

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Soomets, E., Rannap, R & Lõhmus, A. 2019. Restoring drained forested peatlands by combining ditch-blocking and partial cutting: impact on breeding amphibians. *Käsikiri*

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19th SEH European Congress of Herpetology, 18–23.09.2017, Salzburg, Austria; suuline ettekanne

Juhendatud väitekirjad:

Linda Puusalu, magistrikraad, 2017. Kõre (*Bufo calamita*) populatsiooni struktuur ja sigimiskäitumine levila põhjapiiril, Veskijärve asurkonna näitel, Tartu Ülikool.

Riin Magnus, magistrikraad, 2017. Looduslikud ja kahepaiksetele spetsiaalselt rajatud väikeveekogud: nende omadused ja olulisus mudakonnale (*Pelobates fuscus*), harivesilikule (*Triturus cristatus*) ning kahepaiksete liigirikkusele, Tartu Ülikool.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
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