

JAAK-ALBERT METSOJA

Vegetation dynamics in floodplain
meadows: influence of mowing and
sediment application



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LIST OF ORIGINAL PAPERS

This thesis is based on the following papers which are referred to in the text by their Roman numerals.

- I** Metsoja J.-A., Neuenkamp L., Pihu S., Vellak K., Kalwij J. M., and Zobel M. 2012. Restoration of flooded meadows in Estonia – vegetation changes and management indicators. *Applied Vegetation Science* 15: 231–244.
- II** Neuenkamp L., Metsoja J.-A., Zobel M., and Hölzel N. 2013. Impact of Management on Biodiversity-Biomass Relations in Estonian Flooded Meadows. *Plant Ecology* 214: 845–56.
- III** Metsoja J.-A., Neuenkamp L., and Zobel M. 2014. Seed Bank and Its Restoration Potential in Estonian Flooded Meadows. *Applied Vegetation Science* 17: 262–73.
- IV** Metsoja J.-A., Luuk O., and Zobel M. Community assembly during early stages of floodplain meadow succession. Manuscript

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Author's contribution to the papers (* denotes a contribution equal to the amount of <25%, ** denotes a contribution to the amount of 25%–75%, *** denotes the contribution to the amount of >75%).

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

1. INTRODUCTION

The conservation value of semi-natural grasslands is acknowledged throughout Europe (Pärtel et al. 2005; van Diggelen et al. 2006). Among these grasslands, floodplain meadows are considered highly threatened throughout their decreasing distribution range (van Diggelen et al. 2006). These meadows are temporarily wet grasslands located on river floodplains. They are subjected to seasonal flooding after either a snow melt or periods of heavy rainfall. Floodplain soils are often fertile because of high nutrient content in alluvial sediments that are carried in by running water (Paal 1997; van Diggelen et al. 2006; Mant et al. 2012). The area of semi-natural grasslands has decreased in Europe during the 20th century, due largely to abandonment (Milberg 1995; Touzard et al. 2002; Joyce 2014) or conversion into intensive agricultural land (Krause et al. 2011). On abandoned floodplain meadows, the natural succession leads first towards dominance of tall grasses and sedges and later to shrubs (Klimkowska et al. 2010; Török et al. 2011) causing changes in grassland community species composition and a decrease in species diversity (Liira et al. 2009). When floodplain meadows are converted to arable fields, even more drastic changes occur. In many cases, the floodplain's hydrological regime is altered, resulting in the drying of soils and artificial hydroperiods, and in disconnectivity between the river channel and its floodplain (Doering et al. 2012; Mant et al. 2012). The fertilizing of soils (Donath et al. 2003) and replacement of meadow species by hay or crops (Krause et al. 2011) leads to deterioration or total loss of natural grassland vegetation in agriculturally intensively used areas.

In order to preserve semi-natural grasslands, numerous ecological restoration projects have been initiated and continue to be carried out (Hölzel and Otte 2003; Kiehl et al. 2010; Török et al. 2011), including restoration of floodplain and fen meadows (Grootjans et al. 2002; Klimkowska et al. 2007, 2010). Successful restoration of floodplain meadows and other wet habitats in most of Europe strongly depends on effective rehabilitation of the hydrological regime and the removal of excess nutrients (Grootjans et al. 2002; Klimkowska et al. 2010), combined with the reintroduction of diaspores of target species (Hölzel and Otte 2003; Poschlod and Biewer 2005; Donath et al. 2007; Klimkowska et al. 2007), as their absence greatly curtails restoration efforts (Donath et al. 2003; Rosenthal 2006; Bischoff et al. 2009). The restoration of European floodplain grasslands is very laborious and expensive, because of high costs involved both in re-meandering the rivers that are disconnected from their floodplains (Mant et al. 2012), and also in the topsoil translocation to remove soil nutrients and to further improve the hydrological conditions of the meadows (Hölzel and Otte 2003; Kiehl et al. 2010).

To maintain the high conservation value of floodplain meadows, it is of crucial importance that restoration activities are followed by continuous extensive management of the grasslands, either by grazing or mowing. Mowing and hay removal can influence directly both productivity and nutrient content by

removing biomass, hence reducing nutrient levels in the ecosystem. At the same time, local plant species richness is affected by productivity, which in turn is dependent on nutrient pools in the soil (Berendse et al. 1992; Wahlman and Milberg 2002). Therefore, when assessing the effect of meadow management on plant species diversity, it is essential to examine management in terms of its impact on all three components – species richness, productivity and nutrient status of the ecosystem.

Hay removal is known to remove nutrients from the ecosystem and thus reduce long-term biomass production (e.g. Olde Venterink et al. 2001). Many studies have shown that nitrogen (N) and phosphorus (P) are the most important growth-limiting nutrients in European herbaceous grass- and wetland vegetation (Verhoeven et al. 1996; Olde Venterink et al. 2003). The relative importance of soil N and P in explaining patterns of plant species richness has not been completely disentangled yet. N is frequently considered as the key nutrient limiting terrestrial production (Bobbink et al. 1998; Stevens et al. 2004), but recent studies found N and P co-limitation to be equally important (Elser et al. 2007) or P limitation being even relatively more important (Wassen et al. 2005; Klaus et al. 2011).

Productivity affects species richness in grasslands via competition for light in conditions of an increased amount of aboveground living biomass (Hautier et al. 2009). Compared with competition for soil resources, competition for light is more asymmetric and thus more likely to drive inferior species to extinction (Grime 2002). Mowing and grazing remove disproportionately more tall plants, thus reducing asymmetry in competition (Grime et al. 1987; Lepš 1999). When management ceases, tall-growing species can exhibit their competitive potential and outcompete short-growing species (Jensen and Schrautzer 1999). Similarly, seedling recruitment is strongly hampered by raised biomass levels (Tilman 1997; Foster and Gross 1998; Lepš 1999; Foster et al. 2004). Under high productive conditions, as in the floodplain meadows, regular extensive management – mowing and hay removal – is mandatory in order to enable short plant species, otherwise suffering from asymmetric light competition, to persist (Lepš 1999; Hautier et al. 2009; Poptcheva et al. 2009). However, as shown by Socher et al. (2012), management can modulate biodiversity-productivity relations in various directions, depending on regional environmental settings.

In addition to the amount of living biomass, litter is also an important factor influencing plant community structure and processes (Xiong et al. 2003; Lamb 2008; Patrick et al. 2008; Loydi et al. 2013). Plant litter can alter germination cues (Facelli and Pickett 1991; Weltzin et al. 2005), cause direct physical interference (Facelli 1994), provide a cover for seeds and seed predators (Crawley and Long 1995; Donath and Eckstein 2012), and encourage pathogens (Xiong and Nilsson 1999). In particular, a thick litter layer may inhibit seed germination and seedling establishment, and thus reduce local plant species richness (Jensen and Gutkunst 2003; Eckstein and Donath 2005; Lamb 2008).

Besides unsuitable nutrient concentrations in the soil, the restoration of semi-natural plant communities is often limited due to the lack of diaspores. Several

studies suggest various techniques of propagule addition (Vecrin et al. 2002; Donath et al. 2007; Jõgar and Moora 2008; Nordbakken et al. 2010; Schmiede et al. 2012). In addition to diaspore introduction, the possibilities of using a viable soil seed bank of target areas as a possible source of diaspores for meadow restoration have been discussed as well (e.g. Robertson and James 2007; Bossuyt and Honnay 2008). Some studies have reported greater species diversity in the soil seed bank of wet habitats compared to dry habitats (Bekker et al. 2000; Valkó et al. 2011), thus one may expect that the significance of the seed bank as a diaspore source during restoration may be higher in floodplain meadows, compared to other types of grasslands. Bekker et al. (1998) found that groundwater level can affect seed survival in soil, but the effect was species specific, with higher water levels favouring wet grassland plants. Also, Jutila (2001) reported that many plant species of coastal grasslands benefit from flooding. The same study recorded a rather high number of seeds in the soil seed bank of coastal grasslands (average 84 000 seeds m⁻²), and Gerard et al. (2008) have found even higher numbers (> 300 000 seeds m⁻²) on flooded meadows – compared to 13 500 as an average for various European plant communities in an overview by Bossuyt and Honnay (2008).

The studies in abandoned grasslands have reported impoverishment of the soil seed bank during overgrowth by shrubs and trees and conclude that the potential role of the seed bank with respect to vegetation restoration may be small (Kalamees and Zobel 1998; Bisteau and Mahy 2005; Bossuyt and Honnay 2008; Rosef 2008; Jacquemyn et al. 2011; Valkó et al. 2011). The observed changes in seed banks may follow directly from changes in aboveground vegetation: the diversity and the share of meadow species decreases with the expansion of shrubby and woody vegetation (Mitlacher et al. 2002; Jacquemyn et al. 2011). Several studies, however, have demonstrated that the decrease in diversity of the soil seed bank may be less drastic (Milberg 1995; Dutoit and Alard 1995; Maccherini and De Dominicis 2003) and, at least in some semi-natural grasslands, overgrown areas can act as important sources of seeds of target species (Kalamees et al. 2012). It has been argued that due to increasing dissimilarity between the soil seed bank and aboveground vegetation in time, only the seed bank of more recently abandoned areas could play a practical role in restoration (Wagner et al. 2003). On the other hand, recent studies of dry meadows by Auffret and Cousins (2011) and Kalamees et al. (2012) have shown that the share of meadow species in the soil seed bank can remain as high as 70% or more, even in areas abandoned for 50 years. Such abandoned areas with a viable seed bank may thus have a high potential for ecological restoration.

In floodplains and other riparian systems, the river water – especially during flooding events – has been shown to be a very important vector for plant dispersal (Boedeltje et al. 2003, 2004; Moggridge et al. 2009; Fraaije et al. 2015). Due to the floods, a large number of both vegetative and generative propagules (e.g. > 100 000 vascular plant specimens developed from a sampled water volume of 17 850 m³; Boedeltje et al. 2003) can be carried as far as

hundreds of kilometres (Danvind and Nilsson 1997). On the other hand, studies on floodplain meadows (Bischoff 2002; Bissels et al. 2004) have demonstrated that – at least for some target species of restoration – the flooding does not improve the dispersal. Yet, many such floodplain meadows may have impoverished species pools due to intensive agriculture. In addition, highly altered hydrological regimes and landscape fragmentation can hamper species dispersal (Bissels et al. 2004).

In Estonia, the historical area of floodplain meadows has reached up to 100 000 ha by the beginning of 20th century (Kukk and Sammul 2006) and has since then decreased to a contemporary area of *ca.* 16 000 ha (Poollooduslike..., 2016). Floodplain meadows are distributed all over Estonia, majority of them being located at the bigger rivers (e.g. Emajõgi, Kasari, Pärnu, Narva, Põltsamaa and Pedja; Paal 1997). Although floodplain meadows in Estonia have largely escaped agricultural conversion compared to other meadow types (Wagner et al. 2003), abandonment and subsequent overgrowth by bushes and trees pose a major threat to most of the remaining floodplain meadows (Truus and Tõnisson 1998). Along with changes in plant community composition and decreasing diversity in abandoned meadows (Liira et al. 2009), this overgrowth also results in the decline of habitats for many bird species, such as the Great snipe (*Gallinago media*; van Turnhout et al. 2012).

In comparison to Central Europe, the restoration strategies in Estonia have been less demanding as overall land-use intensity is relatively low. Although there are examples of channelled rivers in Estonia (e.g. the straightened lower stream of the river Kasari influencing the largest floodplain meadow complex in Estonia; Matsalu..., 2015), the number of rivers running in naturally meandering beds is relatively large in Estonia compared to many other European regions. In addition, the main threat to floodplain meadows in Estonia has been (at least since 1970s) abandonment rather than agricultural intensification (Paal 2007). Therefore the abiotic conditions of floodplain meadows are relatively unchanged and the local species pool is intact (Sammul et al. 2000), allowing efforts to focus on restoring meadow management (Liira et al. 2009) and – in one single reported case – the reintroduction of locally extinct rare plant species (Jõgar and Moora 2008).

In addition to their natural hydrology and a well-preserved species pool, Estonian floodplain meadows are a very important study object in respect to the whole Northern Boreal alluvial meadows habitat type (Natura 2000 type 6450). According to different sources (Eriksson 2008; Habitats assessment..., 2014) the area of Estonian floodplain meadows (*ca.* 16 000 ha; Kukk and Sammul 2006) comprises up to 50% of the total habitat type area in Europe. Almost half of Estonian floodplain meadows (7 000 ha) are managed under agri-environmental schemes and the national semi-natural communities management plan recommends an increase in the managed area up to 12 000 ha by 2020 (Poollooduslike..., 2016). In contrast to some other semi-natural habitat types, the percentage of the already managed area in relation to a set target is relatively large. Also in the European-wide assessment (Habitats assessment..., 2014), the

status of the habitat in terms of surface area is considered favourable in Estonia. Yet the same report (Habitats assessment..., 2014) admits the quality of the management to be insufficient. This arises the need for a scientific evaluation of the effects of management on the floodplain meadows diversity and conservation value.

The above-mentioned numerous studies published about the restoration of European floodplain grasslands have often focused on restoring the grasslands in agriculturally intensively used areas: on ex-arable fields (Vecrin et al. 2002; Hölzel and Otte 2003; Donath et al. 2007) or hydrologically altered floodplain systems (Bissels et al. 2004; see also a review of different restoration techniques in Klimkowska et al 2007). In addition, also the abandoned grasslands have been addressed both in Central and Northern Europe (e.g. Jensen and Schrautzer 1999; Bischoff et al. 2009; Truus and Puusild 2009; Huhta and Rautio 2014; Joyce 2014). From a review on abandoned wet grasslands by Joyce (2014) it is evident that there are several shortcomings in studies on vegetation recovery in wet grasslands: only a few studies address a restoration time scale of ten or more years, the role of soil seed banks is hardly ever addressed (but see Wagner et al. 2003), and studies often lack mechanistic understanding of the processes governing vegetation dynamics in grassland restoration. We therefore aimed at a complex of studies addressing not only the changes in vegetation, but also in the soil seed banks, and also disentangling the possible mechanisms that mediate the management effect on floodplain plant communities. We could address a relatively long period – ten years – of restoration and maintenance management.

The current thesis aims to:

- 1) Assess the effect of restoration management on plant diversity and community composition in floodplain meadows (**I**, **II**, **III**);
- 2) Determine which plant growth forms are favoured by management (**II**) and which species can serve as indicators of management status (**I**);
- 3) Find out if the positive effect of management on species diversity is mediated by nutrient removal (**II**) or by creating suitable microsites by removal of litter (**II**) or dense sward (**II**, **IV**);
- 4) Ascertain, whether restoration success is limited by missing propagules either in aboveground (**IV**) or in belowground sources (**III**);
- 5) Describe possible processes that govern the plant community assembly during early successional phases, specifically dispersal and competition (**IV**).

2. MATERIAL AND METHODS

2.1. Study area

All studies were conducted in the Alam-Pedja Nature Reserve (NR), Central Estonia (26° 14' E; 58° 28' N). The area of the NR is 342 km², elevation 32–47 m a.s.l, mean annual temperature +4.5 °C and mean annual precipitation 629 mm. The NR was founded in 1994 to protect forests and wetlands; 260 km² were declared as a wetland of international significance (Ramsar Site) in 1997. Since 2004 the total conservation area has been designated as a Natura 2000 site, including ca 3000 ha of Northern Boreal alluvial meadows (Natura 2000 habitat type 6450) along the banks of the rivers Suur-Emajõgi, Põltsamaa and Pedja. All three are unregulated lowland rivers and form natural meanders, or oxbows, some of which get filled with sediments over time and lose their connection to the river, eventually appearing on floodplains as terrestrialized parts of former riverbed. The prevalent soils on the studied floodplains are fluvisols with a humus layer of 30–60 cm, in some places up to 150 cm (Soil Map of Estonian Land Board, xgis.maaamet.ee, accessed 31.05.2016).

Flooding takes place on average between 28.03–2.05 at Pedja and 29.03–15.05 at Põltsamaa river floodplains (data from the Estonian Meteorological and Hydrological Institute from 2000–2011). The meadows at Suur-Emajõgi river are annually flooded with up to 1.5–2 m of water from the end of March to the end of May, in some years even to mid-July. The highest parts in the Pedja river floodplain are flooded in five years out of eleven (2000–2010) and at maximum level are covered with up to 25–60 cm of water; the lowest parts are annually flooded with up to more than two meters of water (J-A Metsoja personal observations).

The flora of NR contains 485 species. There are 30 nationally protected species of which *Dactylorhiza incarnata*, *Gladiolus imbricatus* and *Iris sibirica* occur on floodplain meadows. The majority of the NR is covered with bogs, mires and forests; grasslands cover ca 10% of the NR surface. Altogether, 21 Natura 2000 habitat types are present in the NR; eight are designated as priority habitats (Alam-Pedja..., 2015). The vegetation on the floodplain meadows of the NR is variable. Species poor and highly productive plant communities dominated by tall grasses (*Phalaris arundinacea*, *Phragmites australis*) occur near the banks of rivers rich in alluvial sediments. Sedge-dominated communities with *Carex acuta* and *C. elata* prevail on the lowest parts of the floodplains with the longest inundation period and a considerable amount of alluvial sediments (unpublished data of J-A Metsoja). Topographically, the floodplain of the river Suur-Emajõgi is very even (33–35 m a.s.l, Alam-Pedja... 2015), thus the tall grass and sedge communities form the majority of the floodplain vegetation there. At the rivers Pedja and Põltsamaa, where the topography is more varied, tall forb communities (dominated by *Filipendula ulmaria* or *Urtica dioica*) prevail on medium elevations, and the highest parts of the

floodplains are covered with the most species-rich plant communities (up to 24 species m⁻²; **I**), dominated by *Trifolium medium*.

2.2. Meadow management

Until the 1980s, the flooded meadow areas were mown regularly once a year for hay-making, with haystack removal mainly in winter. Management then ceased almost completely, causing many meadows to overgrow with willows (*Salix spp.*). In 2000 (or in 2005 at Põltsamaa study area), the restoration management started by removal of the shrub overgrowth by a tractor and a shredder (Lagarde SX 400). The same machinery was used until 2005 at Pedja and Emajõgi study areas and the shredded hay was left on ground. Since 2006, the sites at Pedja and Emajõgi have been managed by mowing with machinery, the hay is harvested, baled and removed from the meadows. At Põltsamaa, only shredding was used during the study period. The managed floodplain meadow area in the NR has increased up to 1100 ha by 2015. Annual mowing starts from the first decade of July and lasts till the beginning of September, following the historical timing of management. However, due to weather conditions (e.g. floods following heavy rainfall in summer) the regularity of management *in situ* varies considerably and the wettest parts of the meadows are subjected to mowing not in each year but approximately in six to seven years out of ten (J.-A. Metsoja, personal observations).

2.3. Study design

2.3.1. Management studies

The two field sites (Pedja I and Pedja II) of studies **I**, **II** and **III** are located near Kirna village next to the River Pedja. Two major meadow types can be distinguished at both sites according to the typology of Estonian grasslands (Krall et al. 1980): 1) sedge meadows (with *Caricetum acutae* community; on average 0.8 m above river surface, measured 24.07.2011) are present in old riverbeds with high and long lasting inundation; 2) topographically higher (1.7 m above river surface) and less frequently inundated parts of the floodplain relief are occupied by tall forb meadows (*Filipendulo-Geranium palustris* community). In study **I**, the same two meadow types were distinguished in a third site (Põltsamaa) at the River Põltsamaa: sedge and tall forb meadows, 1.0 and 1.5 m above river surface, respectively (for site locations in **I–III**, see Figure 1 in paper **I**). In study **I**, an additional meadow type 3) mesic meadow (*Deschampsieto-Festucetum rubrae* community) was distinguished at the highest parts of the floodplain (2.2 m above river surface) in sites Pedja I and Pedja II.

Studies **I–III** focused on the effects of management on species diversity, biomass, and related measures. To compare managed and unmanaged grasslands, each site had an unmown reference area (*ca.* 50 × 120 m in size) that was left unrestored by NR authorities for monitoring purposes. Both mown and unmown (abandoned for *ca.* 25 years) areas covered all the meadow types present at a given site. The meadow types were sampled in uniform areas of *ca.* 30 × 30 m (stands), avoiding the transitional vegetation patches between different communities. The unique combinations of these meadow types (two or three types per site), management regimes (mown vs. unmown), and study sites (Pedja I, Pedja II, Põltsamaa) were referred to as stands in study **I**, and form the basis for the factorial study design used in papers **I–III**. In addition to mown and unmown (abandoned for *ca.* 25 years) stands, in study **III** we included shrub-encroached stands on former meadows abandoned for *ca.* 50 years, to find out if relatively long-abandoned grasslands with unfertilized soils and unaltered hydrological conditions still harbour a viable grassland species seed bank.

2.3.2. Sediment deposition study

Study **IV** addressed plant community assembly and changes in functional diversity on ten sites with human-induced disturbance at the River Suur-Emajõgi before (2011) and after (2012–2014) the disturbance. In 2010–2011, within the framework of the LIFE project funded by the EU, hydrological connections between ten oxbows and the main river channel were re-opened. On each site, alluvial sediments were excavated from an oxbow end and deposited on adjacent floodplain meadow with a thickness of *ca.* 30–50 cm and area of *ca.* 20 × 50 m. These 20 × 50 m areas are analogues to *stands* in studies **I–III**. The vegetation before the sediment deposition on those ten sites was dominated by sedges (*Carex acuta* and *C. elata*) and reed canary grass (*Phalaris arundinacea*).

The differing times since meadow abandonment (0, 25, and 50 years; study **III**), and since sediment deposition (0=before, 1–4 years after; study **IV**) are hereafter commonly referred to as the successional stages.

2.4. Field sampling, sample processing

In all studies, the aboveground vegetation was sampled by estimating the projective cover in percentages of each vascular plant species in six to ten (depending on the study) randomly located 1 m² plots per stand (*ca.* 30 × 30 m) just before the annual mowing. In study **I**, the vegetation was sampled before the restoration management started in 2000, and was then re-surveyed in 2010. In studies **II** and **III**, sampling took place in June 2011, and in study **IV**, we sampled in August in 2011–2014.

In study **II**, the aboveground biomass and litter – lying and standing dead biomass – was sampled adjacent to the vegetation sampling plots. The biomass was cut with scissors 2–3 cm above the soil surface within an area of 0.1 m² and, immediately after harvesting, the samples were dried for 24 h at 75 °C, and weighed. All dried samples were ground to pass through a 0.5 mm screen. We measured the concentrations of the main plant nutrients: Carbon (C), Nitrogen (N), Phosphorus (P), Potassium (K), Magnesium (Mg) and Calcium (Ca) with near infrared reflectance spectroscopy (NIRS; Foley et al. 1998) using a Spectra Star 2400 (Unity Scientific, Columbia, MD, USA).

In study **III**, we sampled the soil seed bank after vegetation sampling within the same plots. The seed bank was sampled with 36 soil cores (10 cm in height, 4 cm in diameter) per each 1 m² plot. The samples were later washed on a 212 µm mesh sieve (the concentration method of TerHeerdt et al. 1996) and laid out as a layer of max. 5 mm on trays with growing substrate. After 90–120 days of growth, the emerged plant specimens were identified to the species level. The number of seedlings of each plant species in each plot was registered. To express the seed bank density per 1 m², the total number of seedlings in the sampled surface area per plot (452.4 cm²) was extrapolated to 1 m².

For the recorded species in study **IV**, traits related to water dispersal (buoyancy) and competitive ability (plant average height) were obtained from LEDA database (Kleyer et al. 2008). To assess the functional diversity of the studied communities, we used the functional species pool framework (de Bello et al. 2012), which, more effectively than a conventionally used null models approach, separates the biotic (including dispersal) effects from environmental filtering. According to the approach of de Bello et al. (2012), the functional trait convergence or divergence patterns within local, sampled communities are tested not against random communities, but against a set of trait values possessed by the species comprising a habitat type species pool (a set of species suitable for given habitat conditions). As the habitat type species pool, we used floodplain meadow inventories data from the whole River Suur-Emajõgi study area (including all ten study sites), provided by the Estonian Seminaturl Community Conservation Association. The data comprise vascular plant presence-absence data on 92 meadows. All of the meadows are semi-natural floodplain meadows (Natura 2000 habitat type 6450), so the species growing there are adapted to the same abiotic habitat conditions that occur on the ten study sites. Following the methodology of study **II**, we also sampled the soil seed bank on two sites of study **IV** (in 2011), to differentiate the propagules present locally in the sediments and those that dispersed to the sites.

2.5. Data analysis

As univariate response variables, we used species richness (**I–IV**); Shannon diversity (**I, II**); proportion of graminoids (**I**); cover value of different growth forms (tall forbs, small herbs, sedges, grasses, **II**); proportion of flooded

meadow species in the vegetation and in the soil seed bank (III); soil seed bank density and similarity to target vegetation (III). Nutrient concentrations, above-ground biomass and litter were used as dependent variables when assessing the effect of management in study III. In study IV, we used community-weighted mean trait values, and functional diversity (trait convergence or divergence) as dependent variables. As explanatory categorical variables we used management regime (I, II) or successional stage (III, IV); time of survey (in I, as the mown and unmown meadows did not differ in disturbance regime in 2000, before the restoration started, but did so in 2010); meadow type (=plant community, I–III); and site as a fixed factor (I–IV). Nutrient contents in plant aboveground tissues, litter and aboveground biomass were used as independent continuous variables when explaining species richness in study III. Litter and aboveground plant cover were used to explain species richness in the vegetation and the soil seed bank, and aboveground species richness to explain the species richness in the soil seed bank (II). In order to analyse the effect of single categorical predictors on the variance of studied dependent variables, we used one-way ANOVA (I) and t-tests (IV), or – in the case of non-normal distribution of residuals – Mann-Whitney (II) and Kruskal-Wallis (III, IV) non-parametric tests. When the categorical predictor had more than two levels, the Tukey HSD test or Kruskal-Wallis multiple comparisons tests were used to further differentiate between groups. When assessing the correlation of continuous variables, Pearson correlation (III) or Spearman rank correlation (II) coefficients were used.

When building more complex models with both categorical and continuous variables and possible interaction terms as explanatory variables, general linear models (GLM, I, III) and general additive models (GAM, II) were used. The best model selection was based on Akaike Information Criterion (II, III) and GAM framework (III).

To identify the species associated with particular combinations of meadow type and management regime in study I, we used Indicator Species Analysis (Dufrene and Legendre 1997).

In studies I and III, we used non-metric multidimensional scaling (NMDS) to visualize differences in species composition among the meadow types and successional stages. Permutational multivariate tests were used to test for the differences in species composition of 1) mown and unmown meadows (MRPP-test, study I), and 2) of different meadow types, successional stages (times since abandonment) and their interaction (PerMANOVA, study III).

3. RESULTS

3.1. The effect of restoration management on vegetation and soil seed bank diversity, and on plant community composition in flooded meadows

A total of 139 vascular plant species were found in the vegetation of the sites in studies **I–III** (excluding species identified only to a genus level; see Appendix, Table 1). Before restoration started in 2000, the 1 × 1m vegetation plots at Pedja and Põltsamaa contained on average 7.7 vascular plant species both in stands subjected to later management, and in those left unrestored as controls (**I**). By 2010, the average richness had increased to 8.9 species and the most significant change was on site Pedja I in the mesic meadow, where the mean richness had increased in mown (from 18.3 to 19.9) and decreased in unmown plots (from 17.7 to 15.2) (Figure 4 in **I**). Pedja I also had the highest number of species per site (85) as well as the highest maximum per plot (24). We recorded 70 species at Pedja II and 57 species at Põltsamaa. On average, the mesic meadow had a significantly higher mean number of species per plot (17.5) than the sedge (6.5) or tall forb meadow (6.2).

Meadow type as a main effect or an interaction term was a significant explanatory variable in all models explaining species diversity: GLM (Table 2 in **I**, Table 3 in **III**) and GAM (Table 2 in **II**). Mowing resulted in an increase of richness on relatively drier meadows: mesic in study **I** (Table 2, Figure 4), and tall forb in study **II** (Table 1, Figure 4).

In study **III**, the species richness in the aboveground vegetation (totalling 89 species) and in the soil seed bank (63 species) was the lowest in the stands abandoned for 25 years (the unrestored monitoring stands) of both meadow types (Table 2, Figure 3 in **III**). The soil seed bank richness was positively correlated to the aboveground species richness in the mown stands and in the tall forb meadow. Notably, the species richness per plot was higher in the soil seed bank than in vegetation (Table 2 in **III**).

In the vegetation and in the soil seed bank, the proportion of typical floodplain meadow species was the lowest in stands abandoned for 50 years. Still, the proportion of typical floodplain meadow species in the soil seed bank of stands abandoned for 50 years was on average 42% (sedge meadow) and 34% (tall forb meadow) (Table 2 in **III**).

In 2010 the vascular plant species composition of mown and unmown meadows was significantly different at Pedja in the mesic and tall forb meadows, but not in the sedge meadow. At Põltsamaa, unmown and mown stands of both sedge and tall forb meadows were significantly different in 2010 (Figures 8 and 9 in **I**).

According to PerMANOVA (**III**), the meadow type explained 48.3% of the variation in the species composition in aboveground vegetation. The three successional stages also differed in their species composition and accounted for

9.8% of the variation (Figure 1 in **III**). In the soil seed bank, both the meadow type and the successional stage as grouping variables revealed observable patterns on the ordination diagram (Figure 2 in **III**). According to PerMANOVA, the meadow type explained 18.0%, the successional stage 15.9% and their interaction 11.1% of the variation in species composition.

3.2. Management effects on plant functional types and growth form composition.

Indicator species of management

In study **I**, the proportion of graminoids was increased by mowing on mesic Pedja meadows, but reduced by mowing in tall forb meadows at Põltsamaa (Figure 6 in **I**).

Also in study **II**, the effect of management on growth form composition differed between the two meadow types. Unmown sedge meadows were dominated by sedges and grasses, which covered on average 57% and 30%, respectively. Mowing reduced grasses to only 10% and increased sedges to 75%. In the tall forb meadow, unmanaged plots were dominated by tall forbs (mostly *Filipendula ulmaria*) with their cover reaching more than 75%. Other growth forms exhibited low cover – for instance, small herbs covered on average 2.9% (Figure 4, Table 1 in **II**). Mowing did not significantly suppress the dominance of *F. ulmaria*, but nonetheless resulted in a significant fivefold increase in small herbs and sedges up to 10% and 4% of cover, respectively. Grasses were also facilitated by management, although the trend was only marginally significant (Table 1 in **II**).

Combining the indicators for all study sites in **I**, *Ranunculus auricomus* serves as the best management indicator in mesic and tall forb meadows. The best management indicators for sedge meadows differ in Pedja and Põltsamaa (*Glyceria maxima*, and *Galium palustre* or *Polygonum amphibium*, respectively). *Trifolium medium*, *Carex cespitosa*, and *Calamagrostis canescens* serve as abandonment indicators in mesic, tall forb and sedge meadows, respectively (Table 4 in **I**).

3.3. Effects of litter and nutrients on species richness

Management significantly reduced the amount of litter in both meadow types addressed in study **II**, with plot means decreasing from 358 to 121 g/m² in the sedge meadow, and from 541 to 343 g/m² in the tall forb meadow (Figure 2, Table 1 in **II**). Litter in turn was a highly significant explanatory variable in the GAM for species richness (Table 2 in **II**). Species richness increased to a maximum of between 200 and 300 g litter per m² and then decreased at higher litter values (Figure 3 in **II**).

Also N concentration and C:N-ratio in aboveground biomass were highly significant predictors of species richness in two separate models (Table 2 in **II**), but the explanatory power of nutrient-related GAMs was smaller than that of productivity-related GAM (35% vs 44% of variance explained). In the latter, litter, and not aboveground biomass was the best predictor of species richness.

Although aboveground species richness was negatively correlated with the cover of vascular plants and litter, these effects were not included in the best GLM in study **III** (Table 3).

3.4. Propagule availability below- and aboveground

In the seed bank study (**III**) a total of 40 704 seedlings were examined and 63 species were identified. The overall average soil seed bank density was $12\,497 \pm 805$ seeds per m^2 , and the mown plots contained fewer seeds than the plots in stands abandoned for 25 or 50 years (Figure 4 in **III**). The seed bank density was higher in the tall forb meadow compared to the sedge meadow (Table 2 in **III**). The best GLM explained 27.3% of the variation in the soil seed bank density and included successional stage and meadow type as main effects, and an interaction of meadow type:site (Table 3 in **III**).

In study **IV**, it was shown that creating open microsites for propagules increased the species richness in sediment deposit areas from 6 to 23 species per plot on average. The total number of species in the ten sites before sediment deposition was 35. In the first year after sediment deposition, 85 new species arrived to the sites, and the total number of species in all years (2011–2014) was 159.

3.5. Changes in the functional diversity and plant community assembly during early succession

The community-weighted mean proportion of plants with good water dispersal ability was significantly higher after disturbance than before (Figure 4 in **IV**). On the landscape scale, the functional diversity of the dispersal-related trait (buoyancy) was lower after sediment deposition, indicating functional convergence in early successional stages (Figure 5 in **IV**).

The community-weighted mean plant height was lowest (<0.5 m) in the first year after sediment deposition, and later increased to the same level as before the disturbance (*ca.* 1.0 m; Figure 7 in **IV**). The functional diversity of competition-related trait (plant height) showed a random pattern at the local scale (Figure 9 in **IV**).

4. DISCUSSION

4.1. The effect of restoration management on vegetation and soil seed bank diversity, and on plant community composition in floodplain meadows

Restoration management in Alam-Pedja started with re-creation of open landscapes without woody vegetation. Consecutive shredding, and later mowing with hay removal have accompanied several changes in plant community composition, although these changes are sometimes masked by small-scale variability of vegetation. Different floodplain meadow community types, in our study, mesic meadow, tall forb meadow and sedge meadow, form a complex pattern of vegetation in accordance with local topography, and vary considerably in their community composition and diversity.

As expected, restoration management increased species richness of floodplain meadows in Alam-Pedja NR (I–III), in accordance with findings in other wet meadows (Lepš 1999; Grootjans et al. 2002; van Diggelen et al. 2006; Klimkowska et al. 2007; Matthews et al. 2009). However, the extent of changes varied among communities, drier meadows (mesic in I and tall forb in II) being more responsive to management. Wet meadows have been found to be more vulnerable to abandonment and respond more slowly to restoration measures than dry ones in other studies (e.g. Galvánek and Lepš 2009) as well. In highly productive communities, competition for light has been found to be the most important factor determining species richness (e.g. Lepš 1999; Eek and Zobel 2001; Hautier et al. 2009). Mowing has a balancing effect on competition for light (Kull and Zobel 1991) – it increases the amount of light reaching lower growing plants and the soil surface (Jutila and Grace 2002). Although the reduction in biomass due to mowing was on comparable levels in both sedge and tall forb communities, it must be kept in mind that the tall forb meadow was dominated by *Filipendula ulmaria*, which, in comparison with sedges, more strongly reduces the amount of light reaching lower levels of the canopy. Kotowski and van Diggelen (2004) have shown that the availability of light acts as a major environmental factor in determining distribution of small species in wet meadows. Moreover, a sufficient amount of light needed for growth of smaller species may already exist in sedge communities at less than 20 cm above ground, while in tall forb communities, the corresponding height is more than 80 cm (Kotowski and van Diggelen 2004). This means that mowing can more effectively improve light conditions in tall forb meadows than in sedge meadows.

With regard to more pronounced changes in richness of mesic meadows, the species turnover (Bruun and Ejrnaes 2006) and rate of seedling establishment (Jõgar and Moora 2008) are found to be higher in grassland communities with low rather than high standing crop. Indeed, both tall forb and sedge meadows have a high standing crop (Zobel and Liira 1997; study II) and the vegetation

consists of long-living perennials, including tussock grasses and sedges. It may be unrealistic to expect many local extinction and establishment events within short time periods. Also, the relatively larger species pool of mesic meadows, compared to that of tall forb and sedge meadows, and the establishment of new seedlings in conditions of lower standing crop (cf. Foster et al. 2004) might facilitate the stronger response to mowing on mesic meadows.

The weak response to management in the sedge community may also reflect its relatively lower intensity of management; approximately once or twice every five years, the sedge meadow was left unmown during the study period because of inundation during the summer. In addition, some authors have shown (e.g. Huhta and Rautio 2014) that the response to management cessation can be very slow in plant communities that are very little above the mean water level in the floodplain system. This might mean that the low-elevated sedge communities are rather close to their stable state because of high water level, and meadow management would not induce many (rapid) changes.

The total species richness in the seed bank was lower than in the vegetation by a ratio of 0.71 (study **III**), which is close to an average (0.78) across different European plant community types reported by Bossuyt and Honnay (2008). However, it is remarkable that the mean species richness per 1×1 m sampling plot was two to five times higher in the seed bank, in comparison to the vegetation. This contradicts the findings in both dry (Kalamees et al. 2012) and wet (Gerard et al. 2008) grasslands. The study by Plue and Hermy (2012) has shown a clustered spatial structure in the soil seed banks of different plant communities, and this spatial turnover could contribute to higher small-scale richness in the seed bank.

The species richness of the seed bank was the lowest in the 25-yr abandoned tall forb meadow, which in part is also attributable to the lowest richness in the vegetation of the tall forb meadow (**II–III**). Many studies have reported low correspondence between soil seed bank and target vegetation, and lack of target meadow species in the seed bank, thereby concluding that community restoration cannot rely on the soil seed bank (reviewed by Bossuyt and Honnay 2008). However, the representation of typical floodplain meadow species in the seed bank remained remarkably high – in 25-yr abandoned stands, 63% and 67% of species recorded in the seed bank (for sedge and tall forb meadows, respectively) were typical floodplain meadow species (**III**). Our results are in line with studies (Auffret and Cousins 2011; Valkó et al. 2011; Kalamees et al. 2012), that reported as much as 70% of target meadow species present in the soil seed bank of abandoned areas.

The species composition of both the soil seed bank and the aboveground vegetation differed along successional stages – similar results have been published both for seed banks (Kalamees and Zobel 1998; Bekker et al. 2000; Bisteau and Mahy 2005; Bossuyt and Honnay 2008; Rosef 2008; Jacquemyn et al. 2011; Valkó et al. 2011), and for grassland vegetation (Mitlacher et al. 2002; Jacquemyn et al. 2011; study **I**). However, our results (ordination and PerMANOVA in **III**) show clearly that differences among successional stages

with different periods of abandonment were more pronounced in the seed bank than in the aboveground vegetation. To our best knowledge, such a difference has not been reported before. A possible explanation for this may be the persistence of particular plant species in vegetative stages as remnant populations (*sensu* Eriksson 1996) throughout succession, without providing further input into the soil seed bank. The specific mechanism behind this difference warrants further study.

Both soil seed bank and aboveground vegetation also differed between meadow types (**III**), characterised by different soil moisture conditions. This was expected with respect to aboveground vegetation, given the information we have on the vegetation of Estonian flooded meadows (Paal 1997), and is in accordance also with study **I**. In addition to the possible effect of the aboveground vegetation, the seed bank compositional differences in the two meadow types can also be directly attributable to their different elevation from the river surface. Although both meadow types are annually inundated, they differ in flood duration and depth. Bekker et al. (1998) found that ground water level can affect seed survival and higher water tables favour wetland plant species. Jutila (2001) has shown that flooding can act as a factor facilitating seed germination, possibly by breaking dormancy. Hence hydrological conditions may have a direct effect on the number and species composition of viable seeds in the soil.

4.2. Management effects on plant functional types and growth form composition.

Indicator species of management

Restoration activities in floodplain meadows aim to establish vital plant communities that maintain typical grassland species, including small-statured plants (Bissels et al. 2004). Mowing or grazing is a prerequisite for maintaining such species as they reduce the asymmetric light competition and thus prevent their competitive exclusion (Grime et al. 1987). Management resulted in a significantly higher cover of sedges (in both meadow types, i.e. in sedge and in tall forb meadows) and small herbs (only in the tall forb meadow) (**II**). Consequently, management leads to a shift not only in species composition, but also in growth form composition, with stronger changes in the relatively drier of the two meadow types, the tall forb meadow. This result is in accordance with findings of Kotowski and van Diggelen (2004) discussed above.

In contrast, in *Filipendula ulmaria*-dominated tall forb meadows at Põltsamaa, the proportion of graminoids unexpectedly decreased (**I**). At both Pedja sites, mowing did not suppress *F. ulmaria* but still increased the cover of small herbs, sedges and grasses (**II**). One possible explanation is the different management regime of the two areas – at Pedja, the hay has been harvested since 2006, but at Põltsamaa it has always been shredded (mulched) and left on the ground. Although mulching is referred to as a feasible meadow management practice in

conditions of limited resources for management (Kahmen et al. 2002; Maskova et al. 2009; Liira et al. 2009), community changes under mulching still differ from that under conditions in which hay is removed (Römermann et al. 2009), obviously due to inhibition of germination of particular species (Eckstein and Donath 2005) probably because of excessive litter (study II).

We were able to identify reliable indicators for managed and unmanaged communities that can be used for quick inspection of the community status. The species of the *Ranunculus* genus are associated with well-managed semi-natural grasslands or pastures in other studies (Lamoureaux and Bourdot 2007; Aavik et al. 2008) as well. *Galium boreale*, which we found as the second best indicator of management in mesic meadows, is mentioned as an indicator of successful restoration of flooded meadows in Germany (Bischoff et al. 2009). The frequent occurrence of *Carex cespitosa* on unmanaged or poorly managed meadows is noted by Brzosko (2001) and, being relatively easily discernible by tussocks, serves as a practical indicator of abandonment. The need for such indicators will increase in the future as the area of managed meadows continues to increase (Poollooduslike..., 2016).

4.3. Effects of litter and nutrients on species richness

Study II clearly demonstrated that litter mass was a relatively more important determinant of species richness and diversity than the aboveground living biomass. The amount of litter usually increases along with increasing productivity (Foster and Gross 1998) and results in suppression of seedling emergence (Twolan-Strutt and Keddy 1996). In other cases, like communities suffering from drought, litter may exert a positive impact on seedlings (Holmgren et al. 1997; Eckstein and Donath 2005). In study II the threshold value for litter beyond which negative effects on species richness and diversity outweigh those of facilitation seemed to be about 300 g/m². This value represents a moderate level of litter at the studied sites, where values ranged from almost 0 to 700 g/m². With respect to the effects of management, which reduced the amount of litter across communities in almost all plots to below 400 g/m², one can conclude that hay removal following mowing is crucial for maintaining suitable microsites for seed germination in the studied floodplain meadows. Although the reduction of litter was proportionally higher in sedge meadows, the amount of litter only reached threshold values in tall forb communities due to management, but was below this threshold in sedge meadows, irrespective of management. This can also explain the stronger influence of management on species richness seen in tall forb meadows in comparison to that in sedge meadows (cf. 4.1 and 4.2., above).

Soil nutrient availability is a further factor that is connected to the issue of microsite availability, since an increase in plant-available nutrients leads to an increase in aboveground biomass Olde Venterink et al. (2001). This in turn is closely linked to the mechanism of competitive exclusion, decreasing niche

availability for shade intolerant smaller species and, finally, species richness as described above. The content of N in the aboveground biomass, considered as a proxy of overall nutrient conditions, as well as C:N ratio, were important determinants of species richness (II). Again, these results are in accordance with the overview by Olde Venterink et al. (2001). The explanatory power of N content was, however, lower compared with that of aboveground biomass and in particular with that of litter mass.

4.4. Propagule availability below- and aboveground

The soil seed bank density reported in study III was the lowest in mown sites. This contradicts most studies of grassland seed banks that have reported decreasing soil seed bank density and richness along successional gradients when meadows are overgrown by shrubs (Bakker et al. 1996; Wagner et al. 2003; Kalamees et al. 2012). Still, some studies report either no difference among successional stages (Milberg 1995) or even an increase in density or diversity with succession (Dutoit and Alard 1995; Valkó et al. 2011; Stroh et al. 2012). In the case of Alam-Pedja NR floodplain meadows, mowing in July might reduce the seed input in the soil because flower heads are removed before releasing seeds. Another possible factor explaining higher seed densities in abandoned plots is the significantly higher cover of litter in the 25-yr abandoned sites of our study, as litter has been shown to act as a trap for grassland plants' seeds (Ruprecht and Szabó 2012). The overall mean density of the seed bank was relatively high compared to previous studies on grasslands (reviewed by Bossuyt and Honnay 2008).

Previous studies have reported higher seed density and also greater species diversity of the seed bank in wet habitats compared to drier habitats (Bekker et al. 2000; Gerard et al. 2008; Valkó et al. 2011). In our study system, on the contrary, the seed bank density was higher in the relatively drier tall forb meadow, compared to the more wet sedge meadow. At the same time, the 25-yr abandoned tall forb meadow was the least diverse with respect to both aboveground vegetation and soil seed bank, and was strongly dominated by a single species in the seed bank – *Veronica longifolia*.

The results of study IV demonstrated that there is plenty of propagule input and seedling recruitment to the studied sediment deposition sites. After only one vegetation period, the average vascular plant cover on the sites was *ca.* 60% and the average species richness per plot was four times higher in comparison to the vegetation before the sediment deposition. This is in contrast with findings of Bischoff (2002) and Bissels et al. (2004), who found no evidence that a natural flooding regime or closeness to remnant populations of target species could increase seedling recruitment in floodplain grasslands. Arguably in our system, the availability of a suitable microsite (un-vegetated soil in the sediment deposit areas) played an important role. We can conclude that in our study system, the species richness is not dispersal-limited, but rather microsite-limited.

Propagules that arrived to the sediment deposition sites were relatively good dispersers by water. Danvind and Nilsson (1997) did not find a relation between dispersal unit floating capacity and species distribution ranges in a northern Swedish river system. We detected that species' dispersal unit's floating capacity was positively related to its occurrence in early successional communities on sediment deposition sites (1–3 years after sediment deposition). Danvind and Nilsson (1997) argued that most of the hydrochorous dispersal in their study system takes place very rapidly, making it possible for even the species with moderate water dispersal ability to disperse relatively far from their origin in the upstream part of the river. In our system, the river has a very low descent (3.6 cm/km; Järvekülg 2001) and the relatively slow movement of water even during the peak spring floods could hamper the dispersal of propagules with shorter floating times.

4.5. Changes in functional diversity and plant community assembly during early succession

Boedeltje et al. (2003) found that buoyancy, number of seeds produced per plant and abundance of species in the established riparian vegetation explained 50% of the variation in the number of diaspores carried in a river flow. Our analysis also showed that seed buoyancy is an important aspect of dispersal in a flooded meadows system. The community-weighted mean proportion of good water dispersers increased in early successional stages after the disturbance.

The dispersal-related functional diversity in large scale showed significant convergence during early stages (Figure 5 in IV), suggesting that dispersal filters might shape the initial plant community structure. This is in line with the results of Fraaije et al. (2015) who found that patterns of initial seed arrival were more significant in shaping the developing plant community than environmental filtering. Also, Purschke et al. (2013) found that deterministic processes generate biodiversity during post-disturbance ecosystem development and that the relative importance of assembly processes changes over time. Trait-mediated abiotic filtering appears to play an important role in community assembly during the early and early-mid stages of arable-to-grassland succession, whereas the relative importance of competitive exclusion appears to have increased towards the later successional stages.

We did register a decrease in community-weighted mean plant height in early stages compared to later stages, which is indicative of competition gaining more importance throughout succession. This is supported also by several other studies (e. g Prach et al. 1997; Loranger et al. 2016). Contrary to our expectations, on the local scale, we did not detect either functional convergence (indicative of niche differentiation, or competitive exclusion of similar plants) or divergence (indicative of weaker competitor exclusion). One possible reason why the local-scale assembly patterns were random rather than indicative of

competition could be that the studied period (3 years for eight sites, 4 years for two sites) is still too short to reflect the outcome of competition-related processes. Also, when looking at the species richness, we did not detect a considerable decrease even after three or four years – the proportion of tall growing species did increase, but the small growing species were still present in the vegetation. On the other hand, the presence of a random, rather than a convergent pattern (which could be expected in such a productive environment; Mayfield and Levine 2010) is in part probably due to the annual management, since mowing is shown to remove disproportionately more tall plants, thus reducing the asymmetry in competition for light (Grime et al. 1987; Lepš 1999).

5. CONCLUSIONS

Floodplain meadows are plant species rich complex ecosystems that host both terrestrial and fresh-water species, and provide people with different ecosystem services (e. g flood mitigation, water purification, animal fodder). These semi-natural plant communities require moderate human intervention in the form of mowing to prevent overgrowth by shrubs and trees.

The restoration management that started in Alam-Pedja NR in 2000 had a significant effect on the vegetation diversity of the floodplain meadows. The removal of shrubs resulted in re-creation of open landscapes, and consecutive mowing increased the floristic diversity of the meadows. The number of plant species increased during the ten years of management (I–III), and, by the end of the studies, the managed and unmanaged plots also exhibited different plant community compositions (I–II). The observed changes both in the community composition and in diversity were the most pronounced on the relatively drier meadow types (I–III). In the wettest communities, the tall sedge meadows, the species compositions of mown and unmown plots did not differ. A possible explanation is a relatively slower species turnover rate in wetter communities with a high standing crop in comparison to drier communities. The different response to management in the species diversity can on the one hand be attributed to a relatively larger species pool in the drier communities (notably mesic meadows). On the other hand, when comparing the tall forb meadow to the sedge meadow, the relatively more improved light conditions may play a crucial role for the regeneration and survival success for smaller plant species, hence promoting an increase in species richness. The relatively rich – both in absolute number of species and in the proportion of typical floodplain meadow species – soil seed bank of the sedge meadows (III) could provide a useful source of propagules in restoration, if measures suitable to activating the soil seed bank in large scales are used.

In study I we proposed a number of easily identifiable management indicator species that could prove useful in practical decision making and assessment of the management quality. In addition to certain species serving as indicators of mowing or abandonment, the plant functional groups responded differently to mowing (I, II). In general, mowing favoured sedges and, in the tall forb meadow, also small herbs (II). The latter showed a rather fine-tuned response that could help to identify suitable and unsuitable ways of management: in one case the cover of small herbs responded negatively to management. The specific management type used was mulching, by which the biomass was not removed from the meadow but stayed in the ecosystem in the form of litter, causing several negative effects on the meadow. The positive effect of litter removal on species richness was significantly larger than that of either aboveground living biomass or the nutrient concentrations in the living plant tissues (II). Thus, a proper management for floodplain meadows must include biomass removal to promote floristic diversity.

Several studies of floodplain meadows in more fragmented landscapes and in river systems with less natural hydrology have reported both lack of diaspores and a negligible effect of river water as a dispersal vector for floodplain meadow species. In our study (IV) we found that rivers with natural spring floods can act as an effective vector of plant species dispersal, favouring especially the species with seeds that float for longer periods. The initial dispersal-related effects on plant community assembly seemed to outweigh those related to competition.

The results and conclusions presented in this thesis:

- 1) provide management indicator species for some floodplain plant communities;
- 2) underline the importance of encompassing several plant communities in the evaluation of management efficiency of floodplain meadows, as a response to management can vary substantially between communities;
- 3) encourage nature managers to use the soil seed bank as a source for propagules in floodplain meadow restoration;
- 4) demonstrate the importance of running river water as a vector for seed dispersal in hydrologically well preserved floodplain systems;
- 5) show that proper management by removal of hay and of litter is essential in targeting floodplain grasslands diversity.

These findings are applicable not only to Estonian Northern Boreal alluvial meadows, but also to similar floodplain ecosystems elsewhere in the world, given similarly preserved hydrology and landscapes that have escaped intensive agriculture. From a more local perspective, the results can provide detailed insights to nature managers and decision makers in Estonia, where the area of managed flooded meadows is expected to increase considerably in the coming years.

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SUMMARY IN ESTONIAN

Taimkattemuutused luhtadel: niitmise ja jõesetete ladestamise mõju

Lamminiidud ehk luhad on mitmekesised elupaigakompleksid, mida saab käsitleda nii rohumaade kui märgaladena. Ajalooliselt on inimesed neid alasid kasutanud eelkõige loomasööda varumiseks. Heinamaadena olid luhad hinnatud eelkõige tänu lopsakale taimkattele, mida looduslikult väetab kevadeti suurveega luhale kantav jõesete. Just see toitaineterikas lammimuld on ka üheks põhjuseks, miks alates 20. sajandi keskpaigast rajati mitmel pool (eriti Kesk-Euroopas) luhtade asemele kultuurrohumaad või põllud. Põllumajandusega kaasnes tihti luha-alade kraavitamine, jõgede õgvendamine ja kallastele tammide rajamine. Niimoodi muutus järsult luhtade loomulik veerežiim ning kuivendatud alad ei pakkunud enam ökoloogiliselt sobivaid tingimusi luhtadele iseloomulikele taimedele ja muule elustikule. Lisaks luhataimedele vajavad “viiendat aasta-aega” ehk kevadist üleujutust ka luhtadele kudema tulevad kalad ja üleujutuse taandumise järel luha pehmes mullas toitu otsivad kurvitsalised, nt rohunepp. Lisaks elustiku säilitamisele pakuvad luhad väga mitmesuguseid ökosüsteemiteenuseid: vee puhastamine (toitainete settimine luhale vähendab nende hulka jõeveses ja niimoodi vähendab otseselt veekogude eutrofeerumist), üleujutuste leevendamine, turismiks sobivad maastikud jne.

Paljud Eesti lamminiidud on Kesk-Euroopa luhtadega võrreldes suhteliselt heas seisus: jõgede veerežiim on valdavalt rikkumata ja jõed looklevad oma looduslikus sängis. Raske ligipääsetavuse ja tehnikaga majandamiseks liialt pehmete muldade tõttu pole luhtadele rajatud ka kultuurrohumaad või põlde ja seega on luhale iseloomulik taimestik säilinud. Küll aga ähvardab Eesti luhtasid inimtegevuse lakkamisele järgnev kinnikasvamine. Eelkõige võsastumise tõttu on luhtade pindala 20. sajandi algusega võrreldes vähenenud ligi kümme korda, ulatudes täna umbes 16 000 hektarini.

Luhtade kui kogu Euroopas ohustatud elupaikade seisundi parandamiseks on asutud nende ökoloogilisele taastamisele. Kesk-Euroopas tähendab see hüdroloogilise režiimi ennistamist, liigsete toitainete (eriti lämmastiku) eemaldamist (nt pealmise mullakihi koorimisega) ja taimelveste kohaletoomist luhale, kuna looduslik taimestik on hävinud. Eestis on sageli võimalik piirduda põõsaste eemaldamise ja varasema majandamise (niitmise või karjatamise) taasalustamisega. Taastamisele peab kindlasti järgnema pidev niitmine või karjatamine, mis eemaldab suhteliselt enam kõrgekasvulisi taimi ja loob seega soodsamaid tingimusi madalakasvulistele.

Koos taimedega eemaldavad nii niitmine (koos heina või silo koristamisega) kui karjatamine ökosüsteemist toitaineid, mis omakorda võivad suurendada liigirikkkust. Toitainete eemaldamine pärsib taimede kasvu, vähendades seega ka valguskonkurentsi. Valguskonkurentsi mõju taimedele on tugevam ja ebasümmeetrilisem kui juurkonkurentsi oma ning just valgustingimuste parandamine võimaldab väikesekasvulistel nõrgemal konkurentsivõimega taimeliikidel rohu-

maakooslustes ellu jääda. Lisaks toitainete vähendamisele eemaldatakse koos heinasaagi koristamisega kooslusest ka surnud taimne mass ehk kulu. Kulu on rohumaadel väga oluline tegur. Vähene kulu võib lokaalse mikrokliima muuta mõnedele liikidele soodsamaks, liigne aga hoopis takistab taimede idanemist, nii seeläbi, et taimede seemned lihtsalt ei jõua mullani kui ka varjates idanemiseks ja kasvamiseks vajalikku valgust.

Tihti pärsib ökoloogilise taastamise edukust kooslusele iseloomulike liikide puudumine nii kohalikus taimkattes kui ümberkaudsetel aladel, mistõttu kasutatakse erinevaid meetodeid sihtliikide kohaletoomiseks (külvamine, istutamine, sihtliikide seemneid sisaldava heina laotamine alale). Lisaks doonorladelt kohale toodud levistele on uuritud ka mulla seemnepanga võimalikku rolli taimekoosluste taastamisel. On leitud, et rohumaaliikide seemnepank on vähepüsiv ja eriti põlluna kasutatud alade mullas taastamiseks sobilikke seemneid ei leidu. Teisalt on näidatud, et märgadel rohumaadel võiks seemnepank olla suhteliselt tihe ($nt > 800\,000$ seemet m^{-2}) ja liigirohke. Lisaks on leitud, et taastamiseks sobiv seemnepank võib esineda ka kuivadel rohumaadel (nt Eesti loopealsed) ja seda isegi pikka aega hüljatud aladel.

Taimede levikut käsitlevates töödes on uuritud ka jõe (eriti üleujutuseaegset) võimalikku rolli taimeleviste transportijana ehk levikuvektorina. Paraku aga – vähemalt rikutud veerežiimiga jõgede puhul – on see mõju osutunud väikeseks, kuigi potentsiaalselt võib vooluvesi seemneid kanda ka sadade kilomeetrite kaugusele.

Eesti aladele jääb ligi 50% põhjamaiste lamminiitide (Natura 2000 elupaigatüüp 6450) kogupindalast Euroopas ning siinsed niidud on unikaalsed tänu hästi säilinud hüdrooloogilisele režiimile ja põllumajandusest mõjutamata taimestikule. Pindalaliselt pole Eesti lamminiidud meie pärandkoosluste seas kõige ohustatumad, aga siiski on leitud, et just luhtade hooldamise kvaliteet on sageli madal. Madala hoolduskvaliteedi põhjustele on kindlasti võimalik vastata põhjalikult kavandatud teadusuuringutega. Paljud uuringud vaatlevad rohumaade taastamist suhteliselt lühikese aja jooksul (vähem kui kümme aastat), väga harva pööratakse tähelepanu mulla seemnepangale või uuritakse täpsemaid mehhanisme, mille kaudu rohumaade majandamine taimkatet muudab. Käesolev uurimus sai luhtade ökoloogilise taastamise mõju uurida suhteliselt pika aja (kümme aastat) jooksul, vaatlesime komplekselt nii taimkatet kui mulla seemnepanka ning selgitasime konkreetseid mehhanisme ja protsesse, mille kaudu majandamine luhataimestiku mitmekesisusele mõjub.

Käesoleva doktoritöö eesmärkideks on:

- 1) hinnata majandamise (taastamise ja hooldamise) mõju luhtade taimekoosluse mitmekesisusele (**I, II, III**);
- 2) selgitada, kas majandamise mõju on kasvuvormiti (**II**) erinev ja kas mõned liigid võiksid olla majandamisrežiimi indikaatoriteks (**I**);
- 3) leida, kas majandamise positiivset mõju liigirikkusele vahendab toitainete eemaldamine (**III**) või sobivate elupaigalaikude loomine kulu (**II**) või tiheda taimkatte eemaldamisel (**II, IV**);

- 4) uurida, kas taastamise edukust pärsib maapealsete (IV) või mullas paiknevate (III) leviste puudumine;
- 5) kirjeldada protsesse (levimine, liikidevaheline valguskonkurents), mis mõjutavad taimekoosluse häiringujärgset kujunemist (IV).

Leidsime, et majandamine suurendas luhtade taimekoosluste liigirikkust, kusjuures enam suurenes liigirikkus suhteliselt kuivematel aladel. Üks võimalik selgitus, miks liigirikkus suurenes enim kõige kuivematel, aruniidu-laadsetel aladel, on nende koosluste suhteliselt suurem liigifond. Angervaksa domineerimisega alade suhteliselt tugevam positiivne reaktsioon niitmisele võib olla seotud sellega, et võrreldes tarnastikega on angervaksaga kooslustes valgustingimused madalakasvulistele taimedele eriti halvad. Kuigi niitmine eemaldas biomassi tarnastikest ja angervaksastikest sarnastes kogustes, paranesid valgustingimused ja vähenes konkurents viimastes enam. Tarnastike nõrk reaktsioon majandamisele võib olla seotud ka sellega, et tänu oma väga väikesele suhtelisele kõrgusele jõepinnast jäid nad uurimisperioodil u. ühel või kahel aastal viiest niitmata. Lisaks on teadustöodes leitud, et püsivamalt liigniisked tarnastikud reageerivad väga aeglaselt ka hooldamise lakkamisele; seega võib oletada, et paarikümne aasta pikkune hooldusvaba periood ei olnud tarnastikes palju muutusi esile kutsunud ning seetõttu pole ka hoolduse taasalustamisel (kiired) muutused märgatavad.

Lamminiitude mulla seemnepanga kogu liigirikkus moodustas u. 70% maapealse taimkatte liigirikkusest. Siinkohal on huvitav märkida, et väikeses skaalas (1 m²) oli liigirikkus seemnepangas kaks kuni viis korda kõrgem kui taimkattes; see võib olla seotud seemnepanga ruumiliselt heterogeense jaotusega mullas. Kuni 25 aastat hüljatud alade seemnepank sisaldas üle 60% luhtadele tüüpiliste liikide seemneid, olles seega luhtade ökoloogilisel taastamisel arvestatava tähtsusega levisereservuaar.

Majandamine tõstis taimkattes tarnade ja angervaksastikes ka väiksekasvulisteh rohundite osakaalu. Ootamatult ühel alal niitmise mõjul aga väikeste rohundite osakaal hoopis langes. Kuna seda ala oli uurimisperioodi jooksul majandatud ainult hekseldamise teel (purustatud hein jäeti luhale), võib see olla üheks tõestuseks asjaolule, et liigirikkuse tõusu on võimalik tagada vaid kohase hooldamisega. Hekseldamisega luhale jääv kulu takistab liikide idanemist. Leidsime ka, et kulul oli liigirikkuse selgitamisel suurem osatähtsus kui toitainetel (mille kontsentratsiooni mõõtsime taimede maapealsetes kudedes). Teatud piirväärtuseni (u. 300 g/m²) oli kulul liigirikkusele positiivne mõju, sellest suurematel väärtustel liigirikkus langes. Tarnastikes jäi kulu osakaal ka majandamata aladel allapoole nimetatud piirväärtust, mis omakorda seletab, miks tarnastikes majandamise mõju vähemärgatav oli. Majandatud luhtade indikaatorliikidena tuvastasime nt kuldtulika (*Ranunculus auricomus*) ja värvmadara (*Galium boreale*); mõlemat on majandatud ja kõrge väärtusega poollooduslike rohumaadega seostatud ka teiste autorite uuringutes. Majandamata alade indikaatoriteks olid mätaastarn (*Carex cespitosa*) ja sookastik (*Calamagrostis canescens*).

Taastamiseks sobivaid taimede leviseid leidis ohtralt mulla seemnepangas (vt eespool), samuti osutus loodusliku üleujutusrežiimiga jõgi oluliseks levikuvektoriks paljudele liikidele. Meie uuritud vanajõesuudmetest eemaldatud setete ladestusalad sisaldasid enne häiringut (sette ladestamist) kokku 35 erinevat soontaimeliiki, esimesel aastal peale häiringut lisandus aladele 85 liiki. Algselt suur ruderaalide summaarne katvus (u. 40%) taandus teiseks aastaks peale sette ladestamist algsele tasemele (< 1%). Häiritud aladele saabus esimese kolme aasta jooksul palju veega levimisele kohastunud liike. Nende aastate jooksul oli uuritud kooslustes kauaujuvate seemnetega liikide osakaal oluliselt suurem kui see on keskmiselt kogu luhale omases liigifondis. Erinevalt varasematest uuringutest ei tuvastanud me, et edasises suktsessioonis mõjutaks liikidevaheline valguskonkurents taimekoosluse kujunemist. Üheks põhjuseks võib olla uurimisperioodi liiga lühike kestus (neli aastat), teiseks aga luhtade niitmine, mis, nagu eelnevastki selgus, vähendab liikidevahelise konkurentsi mõju.

Kokkuvõtvalt võib öelda, et käesolev töö:

- 1) esitab mõningate luhakoosluste jaoks hooldamise indikaator-taimeliigid;
- 2) rõhutab, et luhtade majandamise tulemuslikkust uurides tuleb kaasata erinevaid taimekooslusi, kuna reaktsioon majandamisele võib tihti olla koosluse-spetsiifiline;
- 3) julgustab luhtade hooldajaid taimekoosluste taastamisel pöörama tähelepanu ka mullas sisalduvale seemnepangale;
- 4) näitab, et rikkumata hüdroloogilise režiimiga jõgede puhul on vooluvesi oluliseks taimede levikuvektoriks;
- 5) kinnitab, et luhtade taimekoosluste mitmekesisuse taastamisel on väga olulised õiged hooldusvõtted, millega eemaldatakse kooslusest nii hein kui ka kulu.

Töö tulemusi saab kasutada mitte ainult Eesti põhjamaiste lamminiitide, vaid ka muude analoogsete ökosüsteemide puhul kogu maailmas, kus jõgede hüdroloogiline režiim on rikkumata ning pole esinenud intensiivset põllumajandust. Uurimuste tulemused on heaks ülevaateks luhaniitide taimekattes toimuvatest muutustest, millele saavad toetuda Eesti luhaniitide hooldajad ja looduskaitseliste otsuste tegijad, arvestades, et luhaniite peaks lähiajal ootama oluline hooldatava pindala tõus.

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APPENDIX

Vascular plant species registered in the studies

Table 1. List of vascular plant species registered in the studies. Taxa identified to a genus level only are omitted. Roman numerals refer to studies in the publication list. In study **III**, data for vegetation and soil seed bank are listed separately. In study **IV**, data for the ten sediment deposit sites and the habitat type species pool are listed separately. In parentheses, the total number of species per study is given as well as grand total over all studies. Nomenclature: Kukk T. 1999. *Eesti taimestik*, Tallinn: Teaduste Akadeemia kirjastus.

Species	Study					
	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
(281)	(117)	(60)	(87)	(55)	(157)	(186)
<i>Achillea millefolium</i>	+	+	+	+		+
<i>Achillea ptarmica</i>						+
<i>Achillea salicifolia</i>					+	+
<i>Acorus calamus</i>			+			
<i>Aegopodium podagraria</i>	+				+	
<i>Agrostis canina</i>						+
<i>Agrostis capillaris</i>	+			+		+
<i>Agrostis gigantea</i>	+				+	+
<i>Agrostis stolonifera</i> subsp. <i>stolonifera</i>	+				+	+
<i>Alchemilla vulgaris</i> auct.	+		+	+	+	
<i>Alisma plantago-aquatica</i>	+				+	+
<i>Alnus glutinosa</i>					+	+
<i>Alnus incana</i>			+		+	+
<i>Alopecurus aequalis</i>					+	
<i>Alopecurus geniculatus</i>						+
<i>Alopecurus pratensis</i>	+	+	+			+
<i>Angelica sylvestris</i>	+		+		+	+
<i>Anthoxanthum odoratum</i>	+	+	+			+
<i>Anthriscus sylvestris</i>	+	+	+	+	+	+
<i>Arrhenaterum elatius</i>		+	+			
<i>Artemisia campestris</i>				+		
<i>Artemisia vulgaris</i>					+	+
<i>Atriplex patula</i>					+	
<i>Barbarea stricta</i>	+				+	
<i>Betula humilis</i>						+
<i>Betula nana</i>						+

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Betula pendula</i>					+	+
<i>Betula pubescens</i>					+	+
<i>Bidens cernua</i>						+
<i>Bidens tripartita</i>					+	
<i>Briza media</i>	+		+			
<i>Bromus inermis</i>				+		
<i>Butomus umbellatus</i>					+	+
<i>Calamagrostis canescens</i>	+	+	+		+	+
<i>Calamagrostis epigeios</i> subsp. <i>epigeios</i>					+	+
<i>Calamagrostis neglecta</i> subsp. <i>stricta</i>						+
<i>Calamagrostis purpurea</i> subsp. <i>purpurea</i>	+					
<i>Caltha palustris</i>	+	+	+	+	+	+
<i>Calystegia sepium</i>	+		+		+	+
<i>Campanula glomerata</i>	+	+				+
<i>Campanula patula</i>					+	+
<i>Campanula persicifolia</i>					+	
<i>Cardamine pratensis</i> s.l.		+	+		+	+
<i>Carduus crispus</i>	+				+	
<i>Carex acuta</i>	+	+	+	+	+	+
<i>Carex acutiformis</i>	+				+	+
<i>Carex cespitosa</i>	+	+	+	+		+
<i>Carex disticha</i>	+	+	+	+	+	+
<i>Carex elata</i>	+	+	+			+
<i>Carex flava</i>						+
<i>Carex hartmanii</i>						+
<i>Carex hirta</i>	+				+	+
<i>Carex lasiocarpa</i>						+
<i>Carex leporina</i>						+
<i>Carex nigra</i>						+
<i>Carex pallescens</i>	+					+
<i>Carex panicea</i>	+	+	+		+	+
<i>Carex riparia</i>					+	+
<i>Carex rostrata</i>						+
<i>Carex vaginata</i>					+	+
<i>Carex vesicaria</i>	+	+	+		+	+
<i>Carex viridula</i>					+	

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Carex vulpina</i>	+	+	+			
<i>Carum carvi</i>	+					
<i>Centaurea jacea</i>	+	+	+			+
<i>Cerastium fontanum</i>				+	+	
<i>Chenopodium album</i>					+	
<i>Chenopodium polyspermum</i>				+		
<i>Chenopodium rubrum</i>					+	
<i>Chrysosplenium alternifolium</i>			+			
<i>Cirsium arvense</i>	+			+	+	+
<i>Cirsium oleraceum</i>	+	+	+		+	+
<i>Cirsium palustre</i>						+
<i>Cirsium vulgare</i>					+	
<i>Cnidium dubium</i>						+
<i>Convallaria majalis</i>						+
<i>Conyza canadensis</i>				+		
<i>Corylus avellana</i>						+
<i>Crepis paludosa</i>					+	
<i>Cuscuta europea</i>	+					
<i>Dactylis glomerata</i>	+	+	+	+		+
<i>Dactylorhiza incarnata</i>						+
<i>Deschampsia cespitosa</i>	+		+	+	+	+
<i>Dianthus arenarius</i> s.l.						+
<i>Eleocharis acicularis</i>					+	
<i>Eleocharis palustris</i> subsp. <i>palustris</i>					+	+
<i>Elymus repens</i> subsp. <i>repens</i>	+		+	+	+	+
<i>Epilobium adenocaulon</i>						+
<i>Epilobium ciliatum</i>					+	
<i>Epilobium hirsutum</i>	+			+	+	
<i>Epilobium montanum</i>	+					
<i>Epilobium palustre</i>					+	+
<i>Epilobium parviflorum</i>					+	
<i>Equisetum arvense</i>	+				+	+
<i>Equisetum fluviatile</i>	+	+	+		+	+
<i>Equisetum hyemale</i>						+
<i>Equisetum palustre</i>						+
<i>Equisetum pratense</i>	+			+		+
<i>Eriophorum angustifolium</i>						+

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Erysimum cheiranthoides</i> subsp. <i>cheiranthoides</i>	+					
<i>Eupatorium cannabinum</i>						+
<i>Fallopia convolvulus</i>					+	
<i>Festuca pratensis</i>	+	+	+			
<i>Festuca rubra</i> subsp. <i>rubra</i>	+		+		+	+
<i>Filipendula ulmaria</i> s.l.	+	+	+	+	+	+
<i>Frangula alnus</i>					+	+
<i>Fraxinus excelsior</i>			+			+
<i>Galeopsis bifida</i>	+					
<i>Galium album</i>	+	+	+			+
<i>Galium aparine</i>					+	
<i>Galium boreale</i>	+	+	+			+
<i>Galium mollugo</i>	+					
<i>Galium odoratum</i>	+					
<i>Galium palustre</i> subsp. <i>palustre</i>	+	+	+	+	+	+
<i>Galium spurium</i>					+	
<i>Galium verum</i> subsp. <i>verum</i>	+					
<i>Galium uliginosum</i>		+	+		+	+
<i>Geranium palustre</i>	+	+	+			+
<i>Geranium pratense</i>	+	+	+			+
<i>Geum rivale</i>	+	+	+	+	+	+
<i>Glechoma hederacea</i>	+	+	+	+	+	+
<i>Glyceria fluitans</i>					+	+
<i>Glyceria maxima</i>	+	+	+		+	+
<i>Gnaphalium uliginosum</i>				+	+	
<i>Helictotrichon pubescens</i>	+	+	+			
<i>Heracleum sibiricum</i>	+	+	+			
<i>Hieracium umbellatum</i>						+
<i>Hierochloa odorata</i>						+
<i>Humulus lupulus</i>	+				+	+
<i>Hydrocharis morsus-ranae</i>					+	
<i>Hypericum maculatum</i>	+				+	+
<i>Impatiens noli-tangere</i>		+	+			
<i>Impatiens parviflora</i>					+	
<i>Inula salicina</i>		+	+			
<i>Iris pseudacorus</i>	+	+	+		+	+
<i>Iris sibirica</i>					+	

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Juncus alpinoarticulatus</i> subsp. <i>nodulosus</i>						+
<i>Juncus articulatus</i>					+	+
<i>Juncus bufonius</i>				+	+	
<i>Juncus compressus</i>					+	
<i>Juncus conglomeratus</i>						+
<i>Juncus effusus</i>					+	+
<i>Juncus filiformis</i>						+
<i>Lathyrus palustris</i>	+		+		+	+
<i>Lathyrus pratensis</i>	+	+	+	+	+	+
<i>Lemna minor</i>	+				+	+
<i>Lemna trisulca</i>						+
<i>Leucanthemum vulgare</i>				+	+	
<i>Luzula campestris</i>						+
<i>Luzula multiflora</i>	+				+	+
<i>Luzula pilosa</i>				+		
<i>Lychnis flos-cuculi</i>	+			+	+	+
<i>Lycopus europaeus</i>			+	+	+	+
<i>Lysimachia nummularia</i>	+		+	+	+	+
<i>Lysimachia thyrsoflora</i>			+			
<i>Lysimachia vulgaris</i>	+	+	+		+	+
<i>Lythrum salicaria</i>	+	+		+	+	+
<i>Malus domestica</i>						+
<i>Melampyrum nemorosum</i>	+					+
<i>Mentha aquatica</i>						+
<i>Mentha arvensis</i>					+	+
<i>Mentha x verticillata</i>					+	+
<i>Menyanthes trifoliata</i>						+
<i>Moehringia trinervia</i>				+	+	
<i>Molinia caerulea</i>						+
<i>Myosotis scorpioides</i>	+		+	+	+	+
<i>Myosoton aquaticum</i>					+	
<i>Oenanthe aquatica</i>					+	+
<i>Padus avium</i>			+			+
<i>Paris quadrifolia</i>			+			
<i>Peucedanum palustre</i>	+				+	+
<i>Phalaris arundinacea</i>	+	+	+	+	+	+
<i>Phleum pratense</i> subsp. <i>pratense</i>	+	+	+			+

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Phragmites australis</i>			+		+	+
<i>Picea abies</i>					+	
<i>Plantago lanceolata</i>	+					
<i>Plantago major</i>				+	+	+
<i>Plantago media</i>						+
<i>Platanthera bifolia</i>						+
<i>Poa angustifolia</i>	+	+	+		+	
<i>Poa compressa</i> subsp. <i>compressa</i>					+	
<i>Poa palustris</i>	+	+	+		+	+
<i>Poa pratensis</i>	+	+		+		
<i>Polygala amarella</i>						+
<i>Polygonum amphibium</i>	+	+	+		+	+
<i>Polygonum lapathifolium</i> subsp. <i>lapathifolium</i>					+	
<i>Polygonum viviparum</i>						+
<i>Populus tremula</i>					+	+
<i>Potentilla anserina</i>					+	+
<i>Potentilla erecta</i> s.l.	+	+	+		+	+
<i>Potentilla norvegica</i>					+	
<i>Potentilla palustris</i>				+		+
<i>Prunella vulgaris</i>	+				+	+
<i>Pyrola rotundifolia</i>						+
<i>Quercus robur</i>						+
<i>Ranunculus acris</i>	+	+	+		+	+
<i>Ranunculus auricomus</i> s.l.	+	+	+			+
<i>Ranunculus cassubicus</i> s.l.	+	+	+			
<i>Ranunculus ficaria</i> subsp. <i>bulbilifer</i>		+	+	+	+	
<i>Ranunculus flammula</i>				+	+	
<i>Ranunculus lingua</i>					+	+
<i>Ranunculus repens</i>	+		+	+	+	+
<i>Ranunculus reptans</i>						+
<i>Ranunculus sceleratus</i>					+	
<i>Ranunculus trichophyllus</i> s.l.					+	
<i>Rhamnus catharticus</i>	+		+			+
<i>Ribes nigrum</i>					+	+
<i>Ribes rubrum</i>					+	
<i>Rorippa amphibia</i>	+					+
<i>Rorippa palustris</i>				+	+	+

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Rubus caesius</i>	+				+	+
<i>Rubus idaeus</i>	+		+			
<i>Rubus saxatilis</i>			+		+	
<i>Rumex acetosa</i>	+	+	+			+
<i>Rumex aquaticus</i>	+		+	+		+
<i>Rumex hydrolapathum</i>					+	
<i>Rumex longifolius</i>	+					
<i>Rumex maritimus</i>					+	+
<i>Sagina nodosa</i>				+		
<i>Sagittaria sagittifolia</i>					+	
<i>Salix alba</i>					+	+
<i>Salix aurita</i>	+					
<i>Salix cinerea</i>					+	+
<i>Salix x dasyclados</i>					+	
<i>Salix myrsinifolia</i>						+
<i>Salix pentandra</i>						+
<i>Salix phylicifolia</i>			+			+
<i>Salix rosmarinifolia</i>	+					+
<i>Salix triandra</i>					+	+
<i>Schoenoplectus lacustris</i>					+	+
<i>Scirpus sylvaticus</i>					+	
<i>Scolochloa festucacea</i>						+
<i>Scorzonera humilis</i>	+	+	+			
<i>Scrophularia nodosa</i>	+			+	+	+
<i>Scutellaria galericulata</i>			+		+	+
<i>Senecio paludosus</i>	+				+	+
<i>Sesleria caerulea</i>	+					
<i>Sium latifolium</i>					+	+
<i>Solanum dulcamara</i>					+	+
<i>Sonchus arvensis</i> s.l.				+	+	
<i>Sonchus asper</i>						+
<i>Sorbus aucuparia</i>						+
<i>Sparganium emersum</i>					+	
<i>Sparganium erectum</i> s.l.					+	
<i>Sparganium erectum</i> subsp. <i>microcarpum</i>						+
<i>Stachys officinalis</i>						+
<i>Stachys palustris</i>	+		+		+	+

Table 1. Continued

	I	II	III Vegetation	III Seed bank	IV Ten sites	IV Species pool
<i>Stachys sylvatica</i>						+
<i>Stellaria graminea</i>	+				+	+
<i>Stellaria holostea</i>			+			
<i>Stellaria media</i>					+	
<i>Stellaria palustris</i>	+			+	+	+
<i>Succisa pratensis</i>	+			+		+
<i>Symphytum officinale</i>	+				+	+
<i>Taraxacum officinale</i> s.l.		+	+	+	+	+
<i>Thalictrum aquilegiifolium</i>	+		+			
<i>Thalictrum flavum</i>	+	+			+	+
<i>Thalictrum lucidum</i>						+
<i>Thelypteris palustris</i>						+
<i>Thlaspi arvense</i>				+		
<i>Trifolium medium</i>	+				+	
<i>Trifolium pratense</i> subsp. <i>pratense</i>	+					+
<i>Trifolium repens</i>	+			+	+	+
<i>Trollius europaeus</i>	+	+	+			
<i>Tussilago farfara</i>					+	+
<i>Typha angustifolia</i>					+	
<i>Typha latifolia</i>					+	+
<i>Ulmus laevis</i>		+	+			
<i>Urtica dioica</i> subsp. <i>dioica</i>	+	+	+	+	+	+
<i>Valeriana officinalis</i> subsp. <i>officinalis</i>	+		+		+	+
<i>Veronica anagallis-aquatica</i>					+	
<i>Veronica beccabunga</i>					+	
<i>Veronica chamaedrys</i> s.l.	+	+	+	+	+	+
<i>Veronica longifolia</i>	+	+	+	+	+	+
<i>Veronica scutellata</i>				+	+	
<i>Viburnum opulus</i>			+			+
<i>Vicia cracca</i>	+	+	+		+	+
<i>Vicia sepium</i> subsp. <i>sepium</i>	+					+
<i>Viola canina</i> subsp. <i>canina</i>					+	+
<i>Viola riviniana</i>					+	
<i>Viola uliginosa</i>						+

PUBLICATIONS

CURRICULUM VITAE

Name: Jaak-Albert Metsoja
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Education:

2010–... University of Tartu, PhD studies in botany and ecology
2007–2010 University of Tartu, MSc (plant and fungal sciences)
2003–2007 University of Tartu, BSc (biology)
1997–2002 University of Tartu, bachelor's studies in semiotics and culture studies
1994–1997 Tallinn School No. 21
1986–1994 Sõle Gymnasium

Institution and position:

2016–2016 University of Tartu, Institute of Ecology and Earth Sciences, Department of Botany, Specialist
2011–2012 University of Tartu, Institute of Ecology and Earth Sciences, Department of Botany, Specialist, 0.1 p.
2006–... Association for Nature Conservation “Kotkas” (Eagle), member of board
2006–... Estonian Seminatural Community Conservation Association, member of board

Research interests:

Plant ecology, vegetation diversity and dynamics in seminatural grassland communities

Publications:

Metsoja, J.-A., Neuenkamp, L., Zobel, M. 2013. Seed bank and its restoration potential in Estonian flooded meadows. *Applied Vegetation Science*. doi: 10.1111/avsc.12057
Neuenkamp, L., **Metsoja, J.-A.**, Zobel, M., Hölzel, N. 2013. Impact of management on biodiversity-biomass relations in Estonian flooded meadows. *Plant Ecology*, 214: 845–856. doi: 10.1007/s11258-013-0213-y
Metsoja, J.-A., Neuenkamp, L., Pihu, S., Vellak, K., Kalwij, J. M., Zobel, M. 2012. Restoration of flooded meadows in Estonia – vegetation changes and management indicators. *Applied Vegetation Science*, 15: 231–244. doi: 10.1111/j.1654-109X.2011.01171.x

Conference presentations:

- Püssa, K., Kalamees, R., **Metsoja, J.-A.**, Neuenkamp, L. & Zobel, M. The importance of the unseen – can soil seed bank contribute to grassland restoration? Two Estonian examples – alvars and flooded meadows (oral presentation). SER Europe Conference 2016 – Best Practice in Restoration. 22.–26.08. Freising, Germany.
- Metsoja, J.-A.**, Luuk, O. & Zobel, M. Drivers of plant community assembly on sediment deposition sites at River Emajõgi floodplain, Estonia (oral presentation). 57th Annual Symposium of the International Association for Vegetation Science “Biodiversity & Vegetation: Pattern, Processes, Conservation”. 5.–7.09.2014. Perth, Australia.
- Metsoja, J.-A.**, Luuk, O. & Zobel, M. Restoring a flooded meadow in Central Estonia. Can we aim at benefits for fish and plant communities in parallel? (oral presentation). 9th European Conference on Ecological Restoration “Restoration, Ecosystem Services and Land Use Policy” 03.–08.08.2014, Oulu, Finland.
- Metsoja, J.-A.**, Luuk, O. & Zobel, M. Protecting flooded meadows in Estonia – examples from Alam-Pedja Nature Reserve (oral presentation). Conference: “Floodplain Meadows and Society – A Two-Way Relationship!”, 14–15.05.2014, South Cerney, Gloucestershire, Great Britain.
- Metsoja, J.-A.**, Luuk, O., Vellak, K. & Zobel, M. Vegetation recovery on sediment deposition sites on the River Emajõgi floodplain, Alam-Pedja NR, Estonia (poster presentation). 26th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ) (PopBio 2013), 9–11.05.2013, Tartu, Estonia.
- Metsoja, J.-A.**, Luuk, O., Vellak, K. & Zobel, M. Vegetation recovery on sediment deposition sites on the River Emajõgi floodplain, Alam-Pedja NR, Estonia (workshops and poster presentation). Seminar „AWARE: Approaches in Wetland Restoration“ 21.–25.04.2013, Warsaw, Poland.
- Metsoja, J.-A.**, Neuenkamp, L., Zobel, M. Persistent soil seed bank in successional floodplain meadows in Estonia – potential for grassland restoration (oral presentation). 8th European Conference on Ecological Restoration, 09.–14.09.2012, České Budějovice, Czech Republic.
- Metsoja, J.-A.**, Neuenkamp, L., Pihu, S., Vellak, K., Kalwij, J. M., Zobel, M. Vegetation changes and management indicators in restored flooded meadows of Alam-Pedja Nature Reserve, Estonia (oral presentation). 54th Symposium of the International Association for Vegetation Science 20.–24.06.2011, Lyon, France.
- Metsoja, J.-A.**, Neuenkamp, L., Pihu, S., Vellak, K., Kalwij, J. M., Zobel, M. Vegetation changes and management indicators in restored flooded meadows of Alam-Pedja Nature Reserve, Estonia (oral presentation). Conference: “Next generation insights into geosciences and ecology” 12.–13.05.2011, Tartu, Estonia.
- Metsoja, J.-A.** & Kuresoo, A. Experience in restoration and management of the floodplain meadows with focus on threatened breeding bird species in Alam-

Pedja Nature Reserve (Estonia) (oral presentation). Conference: “Conservation of the Great Snipe (*Gallinago media*) breeding population: status, trends, habitat selection and management”. 6.–7.12.2010, Vilnius, Lithuania.
Vellak, K., **Metsoja, J.-A.** & Pihu, S. Vegetation recovery on floodplain meadows of Estonia (poster presentation). 7th SER European Conference on Ecological Restoration. 23.–27.08.2010, Avignon, France.

Additional studies:

Learning and Teaching in Higher Education. 28.01–06.05.2016. University of Tartu, Tartu, Estonia.
Interactive teaching methods. 16.–17.01.2014. University of Tartu, Tartu, Estonia.
Course “Designing and conducting ethnobiological research”. 29.06–05.07.2014, Estonian University of Life Sciences, Tartu, Estonia.
IAVS 2013 “R course on community assembly”. 1.–2.07. Tartu, Estonia.
Intensive course for master’s programme: “Graduate course “Issues in Diversity””. 02.–08.09.2012. Oulu, Finland.
BOVA course “Energy Crops and biogas Production”, 3.–7.03.2008. Estonian University of Life Sciences, Tartu, Estonia.

Other scientific activities:

Refereed papers for: Agriculture, Ecosystems and Environment; Ecological Engineering; Journal of Ecology; PLoS ONE.

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Publikatsioonid:

Metsoja, J.-A., Neuenkamp, L., Zobel, M. 2013. Seed bank and its restoration potential in Estonian flooded meadows. *Applied Vegetation Science*. doi: 10.1111/avsc.12057

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Konverentsiettekanded:

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- Metsoja, J.-A.**, Luuk, O. & Zobel, M. Drivers of plant community assembly on sediment deposition sites at River Emajõgi floodplain, Estonia. Suuline ettekanne konverentsil „57th Annual Symposium of the International Association for Vegetation Science “Biodiversity & Vegetation: Pattern, Processes, Conservation”. 5.–7.09.2014. Perth, Australia.
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- Metsoja, J.-A.**, Luuk, O., Vellak, K. & Zobel, M. Vegetation recovery on sediment deposition sites on the River Emajõgi floodplain, Alam-Pedja NR, Estonia. Õpitoad ja posterettekanne tööseminaril „AWARE: Approaches in Wetland Restoration“ 21.–25.04.2013, Warsaw, Poola.
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- Vellak, K., **Metsoja, J.-A.** & Pihu, S. Vegetation recovery on floodplain meadows of Estonia. Posterettekanne konverentsil 7th SER European Conference on Ecological Restoration. 23.–27.08.2010, Avignon, Prantsusmaa.

Täiendkoolitused:

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Interaktiivsed õppemeetodid. 16.–17.01.2014. Tartu Ülikool, Tartu, Eesti.

Kursus “Designing and conducting ethnobiological research”. 29.06–5.07.2014, Eesti Maaülikool, Tartu, Eesti.

IAVS 2013 kursus “R course on community assembly”. 1.–2.07. Tartu, Eesti.

Magistriastme intensiivkursus “Graduate course “Issues in Diversity””. 02.–08.09.2012. Oulu, Soome.

BOVA kursus “Energy Crops and biogas Production”, 3.–7.03.2008. Eesti Maaülikool, Tartu, Eesti.

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Retsenseerinud artikleid ajakirjades Agriculture, Ecosystems and Environment; Ecological Engineering; Journal of Ecology; PLoS ONE.

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