

LIIS KASARI

Plant diversity of semi-natural grasslands:
drivers, current status and conservation
challenges



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Plant diversity of semi-natural grasslands:
drivers, current status and conservation
challenges



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

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are denoted in the text by the Roman numerals:

- I Gazol, A., Tamme, R., Takkis, K., **Kasari, L.**, Saar, L., Helm, A. & Pärtel, M. 2012. Landscape- and small-scale determinants of grassland species diversity: direct and indirect influences. *Ecography* 35: 944–951.
- II **Kasari, L.**, Gazol, A., Kalwij, J.M. & Helm, A. 2013. Low shrub cover in alvar grasslands increases small-scale diversity by promoting the occurrence of generalist species. *Tuexenia* 33: 293–308.
- III **Kasari, L.**, Zobel, M., Pärtel, M., Bommarco, R., Bruun, H.H., Gustiņa, L., Heikkinen, R., Honnay, O., Krauss, J., Lindborg, R., Raatikainen, K., Rūsiņa, S. & Helm, A. Plants with good dispersal abilities disappear from European semi-natural grasslands following the payment of extinction debt. *Manuscript*.
- IV **Kasari, L.**, Saar, L., de Bello, F., Takkis, K. & Helm, A. 2016. Hybrid ecosystems can contribute to local biodiversity conservation. *Biodiversity and Conservation* 25: 3023–3041.

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Author's contribution to the publications:

- I participated in data collection and manuscript preparation
- II participated in developing the idea and data collection, had the main responsibility in analysing the data and preparing the manuscript
- III participated in developing the idea, had the main responsibility in analysing the data and preparing the manuscript
- IV participated in developing the idea and data collection, had the main responsibility in analysing the data and preparing the manuscript

1. INTRODUCTION

Semi-natural grasslands are communities of natural biota, which emerged from forest through pastoralism and arable farming approximately 7500–6800 years ago in Europe (Hejcman et al. 2013; Dengler et al. 2014). They harbour a large part of Europe’s biodiversity and hold the world records for small-scale (e.g. 10×10 cm) plant species richness (Quétier et al. 2007; Wilson et al. 2012; Chytrý et al. 2015). There are several types of semi-natural grasslands varying in levels of soil pH and moisture (e.g. dry calcareous grasslands, heaths, coastal meadows, flooded meadows). Most species-rich are dry and semi-dry basiphilous grasslands due to their large species pool (Pärtel 2002; Dengler et al. 2014). In addition to high plant diversity, they are important habitats for a large variety of bird and invertebrate species (Newton 2004; Öckinger & Smith 2006). Semi-natural grasslands offer also multiple ecosystem services (e.g. carbon sequestration, pollination, livestock provision and tourism; Gallai et al. 2009; Hönigová et al. 2012).

Moderate and continuous human influence has played a major role in the development and maintenance of extensive grassland areas in Europe (Poschlod & WallisDeVries 2002; Pärtel et al. 2007; Dengler et al. 2014). Historical continuous management (i.e. grazing or mowing) favoured the connectivity and seed dispersal among grassland patches, resulting in viable species-rich plant communities (Lindborg & Eriksson 2004; Helm et al. 2006). In addition to landscape-scale factors, the diversity of semi-natural grasslands is influenced by local abiotic conditions and biotic interactions. For example, grazing or mowing reduces the light competition between herbaceous species due to biomass removal (Bakker et al. 2006; Jacquemyn et al. 2011), allowing a high number of species to coexist (Pärtel et al. 1999; Dengler et al. 2014). Continuous management is also needed for preventing the encroachment of shrubs as they compete with herbaceous plants for light, nutrients and space (Limb et al. 2010; Miwa & Reuter 2010). At the same time, moderate cover of shrubs can increase species diversity, for instance by offering shade from the sun, or by serving as a grazing refuge (Pihlgren & Lennartsson 2008). For example, in Estonia, low shrub cover of up to 30% is recommended as desirable state for species-rich dry calcareous grassland habitats (Helm 2011), however, its effect on species richness and composition is not yet thoroughly studied. Moreover, shrubs are found to increase the above- and below-ground habitat environmental heterogeneity (Pärtel & Helm 2007). Also, the variability of soil depth can change the temporal availability of soil nutrients and water (Fridley et al. 2011). The influence of environmental heterogeneity on plant diversity is presumed to be positive according to niche theory (Tilman 1982; Clark et al. 1998), however heterogeneity at the plant neighbourhood scale (i.e. centimetres) can have a negative effect on species richness (Pausas & Austin 2001; Tamme et al. 2010; Laanisto et al. 2013). Consequently, landscape- and local-scale factors are often

intertwined, but their direct and indirect influences on local plant species richness have rarely been explored in semi-natural grasslands.

Semi-natural grasslands prevailed in Europe until the end of 19th century (Luoto et al. 2003), but during the last hundred years there has been a drastic reduction in grassland area around 90% and in some regions even more, depending on their land-use history (WallisDeVries et al. 2002; Pärtel et al. 2005; Dengler et al. 2014). Former extensive areas of semi-natural grasslands have been lost due to the cessation of traditional management, conversion to arable fields, afforestation and urbanization (Eriksson et al. 2002; Poschlod & WallisDeVries 2002; Adriaens et al. 2006). In most of Europe only small isolated habitat patches have preserved within a matrix of mainly forest and agricultural land. Remaining fragments are often characterized by poor habitat quality due to the lack of grazing and influx of nutrients from direct fertilization or indirect nutrient deposition through atmosphere and from nearby arable fields (Bobbink et al. 2010). Present-day small and degraded grassland fragments do not support the dispersal between habitat patches and can lead to extinction of the remaining populations without effective restoration and conservation practices (Ovaskainen & Hanski 2002). It has become more evident that restoration and conservation efforts based on ecological theories are needed for successful biodiversity protection (Perring et al. 2015; Török & Helm 2017). Firstly, it is important to know exactly which factors influence the development and maintenance of semi-natural grasslands.

In biodiversity restoration and conservation it is also essential to consider that species extinction might not occur immediately after rapid environmental perturbations due to the slow intrinsic dynamics of populations. This creates an 'extinction debt' in the community, i.e. a number of extant specialist species of the focal habitat are expected to eventually become extinct as the community reaches a new equilibrium after environmental disturbance (Tilman et al. 1994; Kuussaari et al. 2009). Therefore, one has a risk to overestimate the status and conservation value of habitats when disregarding the possible occurrence of extinction debt. Extinction debt has been usually deduced from the relationship between specialist species number and habitat area/connectivity: there is an extinction debt in the community when current species richness of specialists is significantly related to historical but not to current habitat area/connectivity. The extinction debt occurs more probably in landscapes characterised by area loss up to 90% (Cousins 2009). In landscapes where land-use and habitat loss has been more intensive, and extinction debt is probably already paid (i.e. species have gone extinct), significant relationship between current species richness of specialists and current habitat area is expected (Helm et al. 2006; Cousins et al. 2007; Kuussaari et al. 2009). For instance, a study from Estonia, where 30% of the grassland area had remained, estimated that approximately 40% of calcareous grassland specialist species are yet to go extinct due to the onset of habitat loss in the 1930s (Helm et al. 2006). At the same time, Adriaens et al. (2006) could not identify the extinction debt in calcareous grasslands in Belgium, as only 2% of the original habitat area had preserved.

All species are not equally susceptible to land-use changes. Generalist species are expected to be less affected by loss of semi-natural grasslands than species specialised to a particular habitat type (Warren et al. 2001). Susceptibility depends also on species functional traits related to their dispersal, establishment, persistence and reproduction abilities (Aguilar et al. 2006; Walker & Preston 2006; Lindborg 2007; Saar et al. 2012). For example, good dispersal ability can be a disadvantage in highly fragmented landscape, as there is a higher chance to disperse into an unsuitable matrix (Lindborg et al. 2012). Therefore, long life-span and clonal reproduction are considered to be beneficial for long-term persistence (Lindborg et al. 2012; but see Marini et al. 2012). Different susceptibility of species to land-use changes can lead to shifts in community mean trait values. Moreover, land-use changes can alter functional diversity of semi-natural grasslands (i.e. the variability of functional traits in an assemblage of organisms; Suding et al. 2008; Mason & de Bello 2013). Functional diversity has been linked with the maintenance of ecosystem processes and properties (Tilman *et al.* 1997; Girão *et al.* 2007; Gagic et al. 2015). Functional diversity is expected to decline due to a decrease in species richness and habitat filtering in altered landscapes (Sonnier et al. 2014), however, some studies have shown that it can also be delayed in response to rapid habitat loss similarly to taxonomic diversity (Vandewalle et al. 2014). Large-scale comparison of taxonomic diversity and functional characteristics in habitats where extinction debt is either paid or not can reveal valuable information about future changes in community composition and determine which species are most susceptible to land-use change. This in turn helps to make better decisions for habitat restoration and conservation.

Although many species characteristic to European semi-natural grasslands are threatened and declining, there are a number of exotic and invasive species, but also native species from other habitat types, i.e. native 'aliens' (Valéry et al. 2009; Jackson & Sax 2010; Helm et al. 2015) that can benefit from altered conditions. Therefore, total species richness may not change or can even increase despite of the vast habitat loss and degradation, but at the same time, the habitat integrity (i.e. how characteristic is the habitat compared to its historical state prior extensive area and habitat quality loss) and conservation value decrease (Helm et al. 2015). Due to the ongoing degradation of European traditional landscapes, some ecosystems have diverged so much from their original environmental conditions and species composition that they can be considered hybrid (i.e. likely reversible to historical state) or novel (i.e. irreversible to historical state) ecosystems (Hobbs et al. 2014). A thorough evaluation of the level of degradation is needed to understand whether and how to intervene when faced with such highly altered habitats: should one try to restore them, abandon them or value them as they are.

In this thesis I firstly covered the shortcomings in the knowledge of which factors determine the high small-scale plant species richness in semi-natural dry calcareous grasslands. I quantified the direct and indirect influence of historical landscape-scale factors and local environmental conditions on plant species

richness, and the effect of low-cover shrub encroachment (i.e. up to 30%) on specialist and generalist species of dry calcareous grasslands in Estonia (**I, II**). Secondly, I assessed the status of dry to mesic grasslands in central and northern Europe in the light of vast land-use changes during past century (**III, IV**). I detected in which regions the habitat specialists have already gone extinct and where they temporarily persist despite of the unfavourable environmental conditions, creating an extinction debt in the community (**III**). I identified which functional traits and environmental requirements characterise specialist species that are most likely to disappear from European grasslands following the payment of extinction debt. I also found out how the functional diversity of these grasslands responds to habitat loss, and whether the total species richness and composition differs in regions where extinction debt is ‘paid’ or ‘unpaid’ (**III**). In addition, I used a unique dataset compiled in 1920s to compare the historical and current taxonomic and functional diversity in northern Estonian semi-natural dry calcareous grasslands. I also identified which species can survive in these highly altered communities and assessed the habitat integrity of current grassland patches compared to their historical state prior to extensive area and habitat quality loss (**IV**). Finally, based on my study results, I gave implications for habitat restoration and conservation. I provided new perspectives on how to manage habitats (a) where the extinction debt is unpaid, and (b) where extinction debt is already paid and environmental conditions highly altered (**I, II, III, IV**).

The objectives of this doctoral thesis were:

- (1) To determine the drivers of small-scale plant species richness in semi-natural dry calcareous grasslands (**I, II**). More precisely I aimed to clarify:
 - How small-scale species richness in dry calcareous grasslands is related to landscape conditions, and local environmental variables and their heterogeneity (**I**)?
 - How does low shrub cover affect the small-scale specialist and generalist plant species richness in visually well-preserved dry calcareous grassland patches (**II**)?
- (2) To assess the current status of semi-natural dry to mesic grasslands in central and northern Europe (**III, IV**). More precisely I asked:
 - In which dry to mesic grassland systems in central and northern Europe the extinction debt is already paid and where it still exists (**III**)?

- Which functional traits and environmental requirements characterise specialist species that are most likely to disappear from European grasslands following the payment of extinction (**III**)?
 - How functional diversity responds to habitat loss and how taxonomic diversity differs between regions where extinction debt is paid or unpaid (**III**)?
 - How does the taxonomic and functional diversity, and habitat integrity of current highly degraded dry calcareous grassland remnants in northern Estonia differs from their historical status (**IV**)?
 - Which functional traits and environmental requirements characterise species that can survive (‘winners’) in highly altered dry calcareous grassland remnants (**IV**)?
- (3) To give implications for the restoration and conservation of semi-natural dry to mesic grasslands with different level of degradation (**I, II, III, IV**).

2. MATERIALS AND METHODS

2.1. Study sites and data collection

For testing the direct and indirect relationships between environmental variables and small-scale species richness semi-natural dry calcareous grasslands were studied. Thirty-three individual grasslands, representing almost all ungrazed but yet well-preserved habitat patches currently present on the Estonian islands of Saaremaa and Muhu were selected (Fig. 1C, Fig. 2). In Estonia, dry calcareous grasslands, also called alvar grasslands, are located on Ordovician and Silurian limestone bedrock, and characterised by thin soil, low-biomass herbaceous layer, and sparsely distributed *Juniperus communis* shrubs. For describing the small-scale species richness and environmental parameters, a single transect of 0.1×10 m in each grassland was established. Each transect was divided into 100 plots of 10×10 cm (Fig. 2C). In each plot vascular plants, soil pH, soil temperature, soil moisture, soil electrical conductivity, relative light availability and soil depth were recorded. Shrub cover was measured in a 1 m (II) and 2 m (I) buffer zones around each transect. Landscape-scale variables, past human population density and historical habitat availability, were estimated for a 5 km radius around each grassland site (for details see Table 1 in I).

To estimate the current status of semi-natural dry to mesic grassland systems in central and northern Europe, data collected from Belgium, Denmark Jutland and Zealand regions, Estonia, Finland, Germany, Latvia Abava and Zemgale regions, and Swedish mainland and Gotland were used (Fig. 1A). The habitat loss in those regions has been around 90% or more. In total, 493 grassland sites were included from 10 different regions (see Table 1 in III). For each grassland site the habitat area (ha) and total plant species richness were obtained. Species richness was divided into specialist and generalist plant species by local data contributors according to their expert knowledge and locally available information. Detailed information about the studied regions can be found in Table 1 in III.

For comparing the taxonomic and functional diversity as well as habitat integrity in historical and current highly degraded dry calcareous grassland remnants a unique historical dataset collected during 1918–1923 by Estonian botanist Gustav Vilbaste (Vilberg 1927) was used. Historical data were available for eight dry calcareous grassland stands located in northern Estonia (Fig. 1B). The data included maps (scale 1:84 000), descriptions of sampling locations, grassland descriptions and detailed vegetation surveys. The presence/absence data of current plant species from exactly the same locations were gathered during five summers in 2008–2012. For compiling the historical and current species lists the species found from whole habitat area in each site were included. At present these grasslands are highly degraded due to eutrophication, cessation of traditional management and urbanisation, and have lost ~90% of their habitat area.

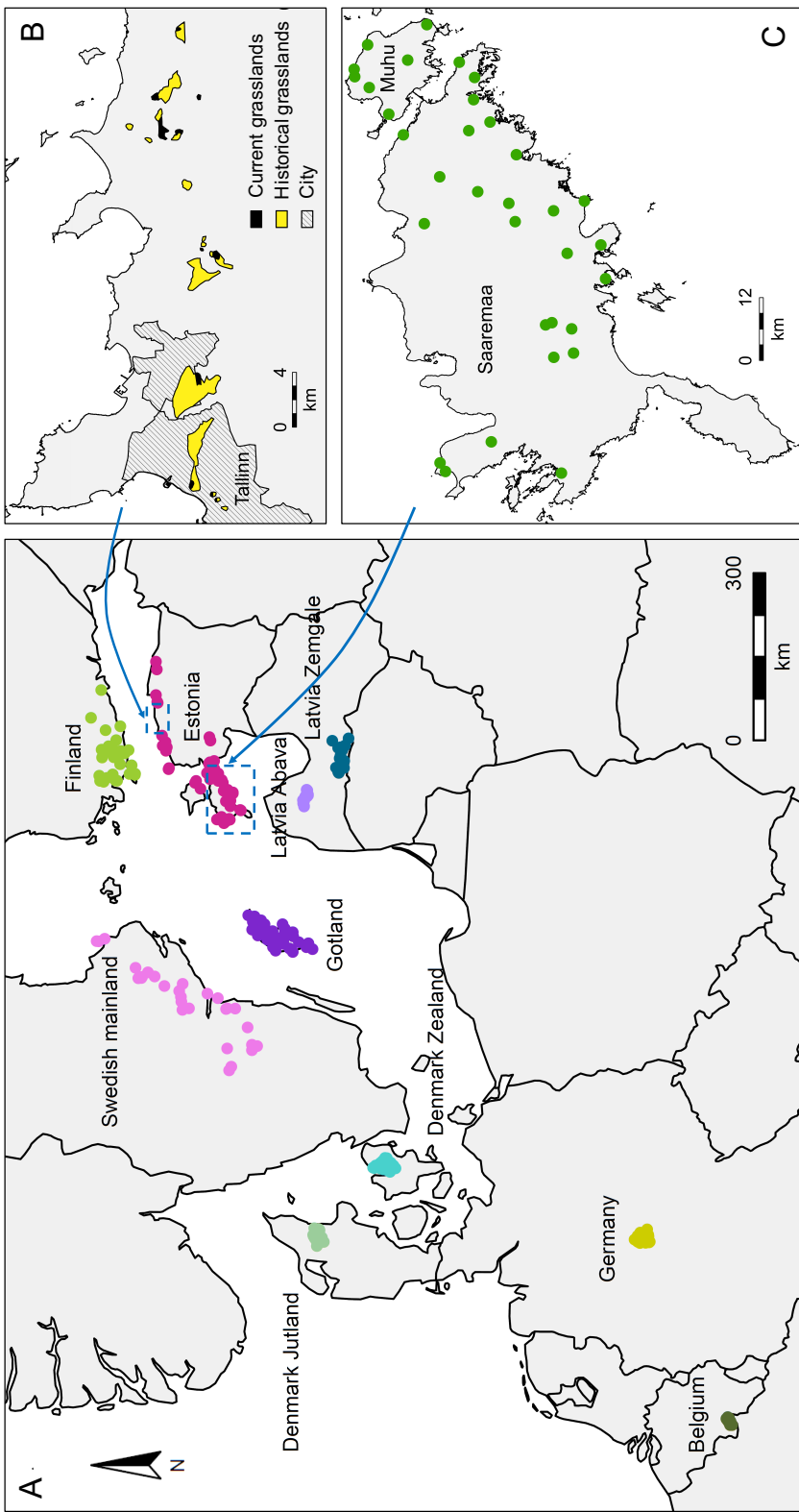


Figure 1. (A) Semi-natural dry to mesic grassland sites in 10 studied regions in central and northern Europe (III). (B) Historical and current distribution of 8 studied dry calcareous grasslands in northern Estonia (IV). (C) Location of the 33 studied dry calcareous grassland patches on the Saaremaa and Muhu islands in Estonia (I, II). Modified from Fig. 1 in III, Fig. 1 in IV and Fig. 3 in II.

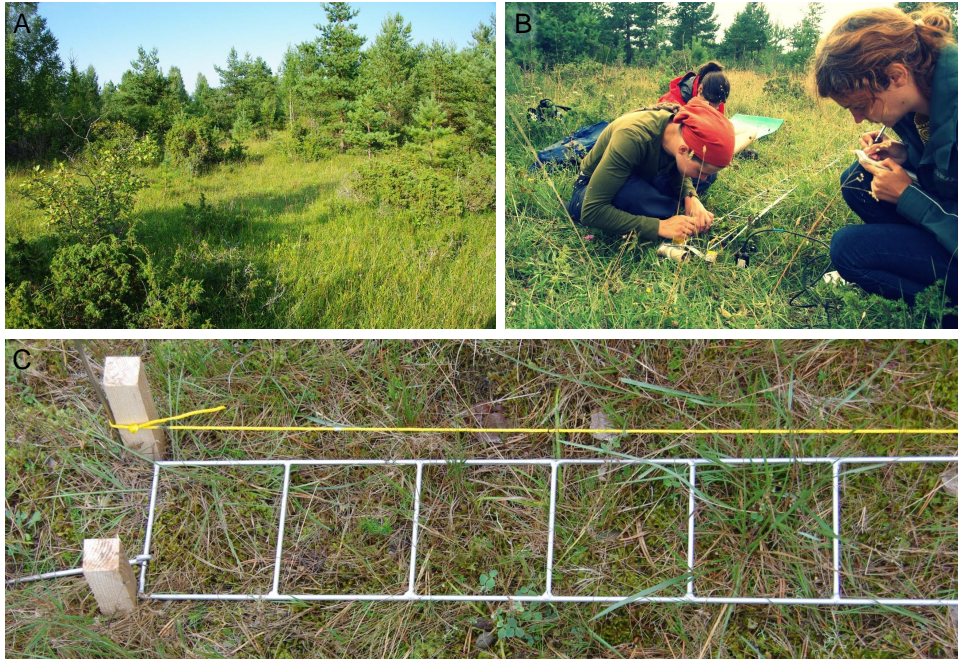


Figure 2. (A) Currently ungrazed but yet well-preserved dry calcareous grassland on Saaremaa island, Estonia. (B) Fieldwork in Võiküla dry calcareous grassland, Muhu island, Estonia for describing the small-scale (10×10 cm) species richness and environmental parameters. (C) Example of a 10×10 cm plot in a transect of 0.1×10 m. (I, II)

2.2. Small-scale species richness and environmental heterogeneity

Small-scale species richness was quantified as the mean total species number of the 10×10 cm plots per transect (I, II). In paper II, the total richness was divided into specialist and generalist species. Specialist species were defined as species that grow preferably on calcareous alvar grasslands and are rarely present in other communities. All other species were designated as generalists.

For studying the effect of local environmental heterogeneity on species richness the coefficient of variation (standard deviation divided by the mean; CV) was calculated, for each measured environmental variable. In paper I, the CV of soil moisture, temperature, electrical conductivity and pH were combined together into one measurement by using a principal component analysis (PCA). The scores of the first axis of the PCA were used as indicators of soil environmental heterogeneity in each site (for details see Table 1 in I). CV of relative light availability was used separately. In paper II, soil moisture, temperature, pH and relative light heterogeneity were used separately. Electrical conductivity data were left out from the analysis as it was strongly correlated with soil moisture.

2.3. Extinction debt and species susceptible to habitat loss

The existence of extinction debt was tested by studying the relationship between current species richness of specialists and current habitat area. The extinction debt likely occurs in regions where habitat specialist species richness is not related to current habitat area, whereas in regions without extinction debt the relationship between the number of specialist species and current habitat area is significant (Cousins et al. 2007; Kuussaari et al. 2009). Only specialist species were used for detecting the extinction debt, as generalists are expected to be less affected by grassland area and quality loss (Warren et al. 2001; Krauss et al. 2010; **III**).

To identify which specialist species are most likely to disappear after the payment of extinction debt the following ten functional traits and species' environmental requirements (hereafter species characteristics) were used, which describe species dispersal, establishment, competitive, persistence and reproduction abilities, and their habitat preferences: (1) maximum potential dispersal distance (m), (2) seed weight (mg), (3) plant height (cm), (4) specific leaf area (SLA; mm²/mg), (5) life span (annual-biennial, perennial), (6) mode of reproduction (vegetative reproduction absent or rare, vegetative reproduction present), (7) flowering duration (months), (8) pollination vector (insect/other), (9) species light requirement (Ellenberg L), and (10) species preference for nutrient conditions (Ellenberg N). Three categorical traits, life span, mode of reproduction and pollination vector, were employed as binary 0/1 variables. Maximum potential dispersal distance (m) values for each species were acquired via predictive modelling using the `dispeRsal` function (Tamme et al. 2014). All other species characteristics were extracted from databases (for detailed information see Material and methods in **III**, **IV**). Species characteristics community mean values (i.e. average trait or environmental requirement value of all species found at one site, not weighted by species abundance as we only had species presence/absence data available; Dias et al. 2013) were compared between grassland systems where extinction debt is paid or unpaid. Community mean values were calculated for each site with the 'FD' package (Laliberté et al. 2014) in R, version 3.1.3 (R Development Core Team 2015; **III**).

2.4. Taxonomic and functional diversity

Species richness, i.e. the total number of vascular plant species from each grassland site was used, to compare taxonomic diversity between regions where extinction debt is paid or unpaid (**III**), and between historical and current highly degraded grassland communities (**IV**). Also log-ratio of generalist to specialist species was used for characterizing the differences in species composition in regions where extinction debt is paid or unpaid (**III**). Grassland specialists were defined as species that are characteristic to studied grassland type and for which the grasslands are main habitat types.

To study how functional diversity is related to habitat area in regions where extinction debt is paid or unpaid the same species characteristics were used as described above. Functional diversity was calculated as a mean pair-wise distance of all possible species pairs (MPD; Pavoine & Bonsall 2011) based on the Gower distance (Gower 1971; modified by Podani 1999). MPD was chosen as it is shown to be intrinsically independent of species richness (e.g. de Bello et al. 2016). Functional diversity values were computed separately within each studied region in central and northern Europe and for each species characteristic individually (III). Same method was used also for comparing the historical and current functional diversity in northern Estonian dry calcareous grasslands (IV). Most of the species characteristics were the same as described above, except dispersal distance and pollination vector. Instead of these two species characteristics dispersal vector (animal/other), seed number per shoot and terminal velocity (m/s^2) were used in paper IV.

2.5. Change in habitat integrity and species that can survive in degraded grassland remnants

To assess the habitat integrity of historical and current highly altered dry calcareous grassland patches in northern Estonia an Index of Favourable Conservation Status (FCS_i) was used, which is a log-ratio of characteristic to derived diversity (Helm et al. 2015). ‘Characteristic diversity’ is defined as the number of species that are typical to a given community and belong to its historically developed habitat-specific species pool. ‘Derived diversity’ consists native and/or non-native species not typical to a given community and whose presence is driven by adverse human impact. Therefore, the more derived and less characteristic is the diversity, the lower is the habitat integrity.

To find out which species can colonise and survive in present-day highly altered grassland patches in northern Estonia historical and current species presence/absence data were compared (IV). Firstly, species were divided into five groups: (1) new species – i.e. species that were not listed in historical dataset in any of the sampled grasslands, (2) increasing species – species whose occurrence increased by at least two sites, (3) stable species – species whose occurrence has remained the same or increased/decreased by one site, (4) decreasing species – species whose occurrence has decreased by at least two sites, and (5) locally extinct species – species that were listed in historical dataset, but are currently absent. For groups 2 and 4, threshold of two sites was selected as species colonization to or extinction from only one site could be random event or a failure to detect species that are actually present. Further, two groups were compiled: ‘winners’, consisting new and increasing species (i.e. species considered to have benefited from recent environmental changes), and ‘losers’, consisting of all decreasing and locally extinct species (see Fig. 3 in IV). After that the species characteristics community mean values of winners and losers described above were compared.

2.6. Statistical analysis

Structural equation modelling (SEM) was used to test the direct and indirect influence of landscape conditions and local environmental factors on total species richness, and low shrub cover on specialist and generalist species. SEM was performed using the IBM SPSS Amos ver. 19 statistical software (Arbuckle 2010; **I**, **II**). Only variables with significant relationships are shown. Overall model fit was assessed using the chi-square statistic (χ^2). A model can be accepted when the P -value associated with a χ^2 is insignificant (Grace 2006).

In order to detect the existence of extinction debt the relationship between the richness of specialist species and current habitat area was analysed with simple regression models. After that linear mixed effect models for regions where extinction debt is paid or unpaid were used to link specialist species richness, and functional diversity to habitat area (**III**). Specifically, a random intercept model was used, where region was included as a random effect. Also, the random intercept and slope model was tested, where both region and habitat area were included as random effects to allow regions to differ in the slopes of their responses and to account for the non-independence of data points that otherwise might pseudoreplicate slope information (Schielzeth & Forstmeier 2009). Models were estimated using the *lme* function in package nlme (Pinheiro et al. 2013) in R (R Development Core Team 2015). Further, the models AIC values were compared with the analysis of variance (*anova*) and only the results of the best models are shown. Random intercept model was chosen when the difference between the two models was insignificant. Random intercept and slope model was chosen when the difference between the two models was significant. Specialist species characteristics community mean values, total species richness and log-ratio of generalist to specialist species between regions where extinction debt is paid or unpaid were also compared with mixed effect model. Region was included as a random effect (**III**).

The total species richness, functional diversity and FCS_i values of current and historical communities were compared with paired t -test. Same method was used to compare the species characteristics community mean values of winners and losers. Analyses were conducted with R, version 3.1.3 (R Development Core Team 2015; **IV**).

Prior to all the analyses species richness, landscape- and local-scale variables, habitat area and functional traits were log transformed, inverted, or square root transformed if deemed necessary to meet the normality criteria. Paired t -tests and linear mixed effect models were considered significant at $P < 0.05$.

3. RESULTS

3.1. Drivers of small-scale species richness

The structural equation model incorporating landscape conditions (past human population density and historical habitat availability) and the local environmental factors explained 49% of the variation in small-scale total species richness (Fig. 3A). Historical landscape habitat availability had a direct positive effect on total species richness. Past human population density had an indirect positive effect on total species richness by increasing historical landscape habitat availability (Fig. 3A; see Table 3 in **I**). At local-scale, light heterogeneity and shrub cover (up to 40%) had a direct positive influence on total species richness, whereas soil environmental heterogeneity decreased species richness. Shrub cover also increased species richness indirectly via its effects on light heterogeneity, and at the same time decreased species richness indirectly by increasing soil environmental heterogeneity. Soil depth heterogeneity had also indirect negative effect on species richness by strongly increasing the soil environmental heterogeneity (Fig. 3A; see Table 3 in **I**).

Low shrub cover (up to 30%) had no effect on the richness of specialist species (Fig. 3B; see Table 1 in **II**). At the same time shrub cover increased generalist species richness both directly and indirectly via light heterogeneity (Fig. 3C; see Table 1 in **II**). Other environmental factors such as soil moisture, pH, and temperature were not significantly related to shrub cover nor generalist richness.

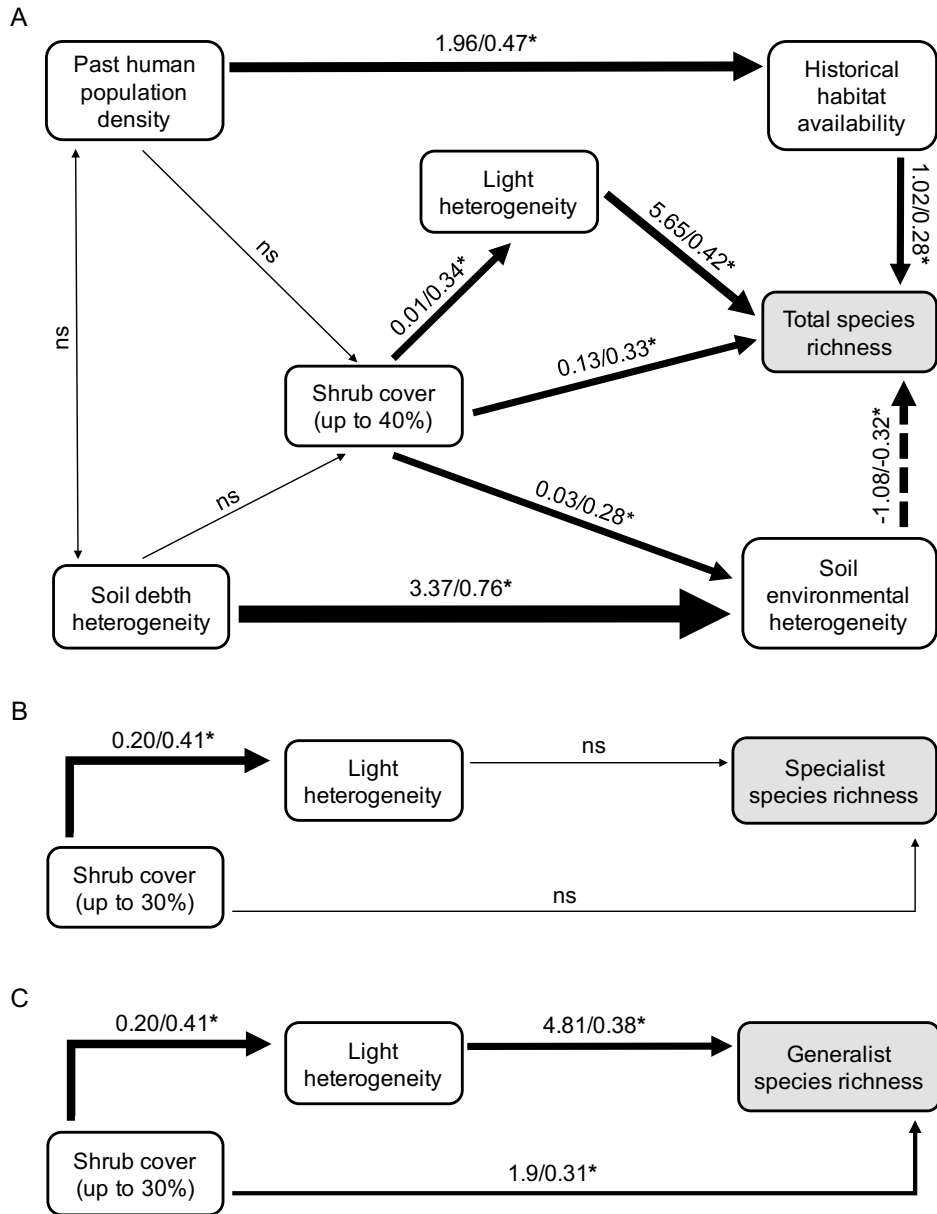


Figure 3. Structural equation models relating landscape conditions and local environmental factors with (A) total species richness, (B) specialist species richness, and (C) generalist species richness (I, II). Single-headed arrows indicate direct causal effects and double-headed arrows indicate partial correlations. The non-standardized and standardized coefficients associated with each path are shown only for the significant relationships; also marked with asterisks (*). The width of the arrow is proportional to the effect of the variable. Solid lines indicate positive, dashed lines negative relationships. The models were statistically significant (A) $\chi^2 = 9.484$, $P = 0.487$, (B) and (C) $\chi^2 = 0.54$, $P = 0.46$. Modified from Fig. 3 in I and Fig. 5 in II.

3.2. Occurrence of extinction debt and species susceptible to habitat loss

The richness of specialist species was significantly related to current grassland area in Belgium, Denmark Jutland and Zealand regions, Finland, Germany and Latvia Zemgale region (Fig. 4A; see Appendix S1 in **III**). In Estonia, Latvia Abava, Swedish mainland and Gotland current habitat area proved to be poor predictor of grassland specialist richness (Fig. 4B; see Appendix S1 in **III**), indicating the existence of extinction debt in those regions. Specialist species appeared to have shorter dispersal distance in the regions where extinction debt is paid (mean 18.33 m) than in regions with extinction debt (mean 29.95 m; $t = -3.33$, $P = 0.009$; see Fig. 3 in **III**). All other community mean values of tested species characteristics showed no differences between regions (Appendix S2 in **III**).

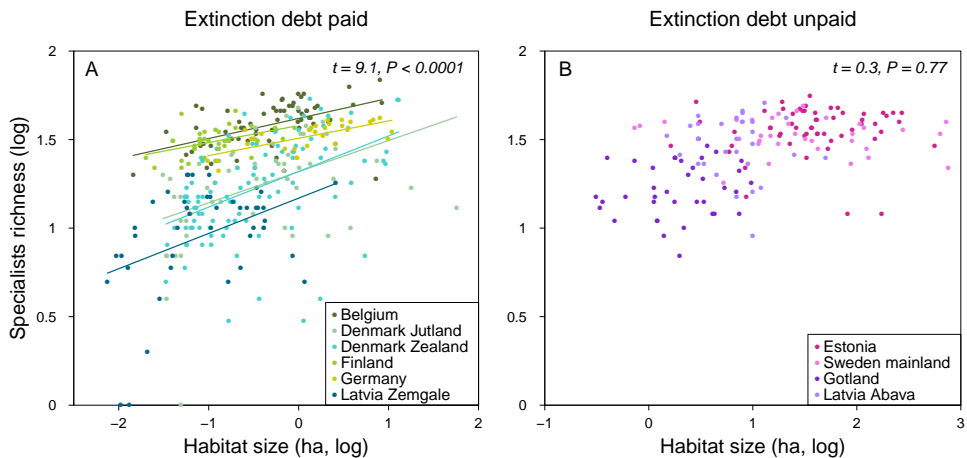


Figure 4. Relationship between habitat area and (A) specialist species richness in European calcareous grasslands where extinction debt is paid, (B) specialist species richness in regions where extinction debt is unpaid (**III**). Tested with linear mixed effect models, where region was included as a random effect. For illustration, regression lines are fitted based on separate linear regressions for each region. Modified from Fig. 2 in **III**.

3.3. Functional and taxonomic diversity in regions where extinction debt is paid or unpaid

The diversity of specialist species specific leaf area, flowering duration and Ellenberg N were positively related to habitat area in regions where extinction debt was paid ($t = 3.22$, $P = 0.001$; $t = 2.30$, $P = 0.02$; $t = 3.93$, $P = 0.0001$ accordingly) and insignificant in regions where extinction debt is unpaid, indicating their possible delayed response to habitat loss. Other functional

diversity values of specialist species were not related to habitat area in any of the regions (see Table 2 in **III**).

Total species richness per site did not differ between regions where the extinction debt is paid or unpaid ($t = -0.54$, $P = 0.60$). There were on average 55 species in regions where the debt is already paid and 47 species in regions where extinction debt still exists. However, the ratio of generalists to specialists was higher in regions where extinction debt is paid, indicating that there are relatively more generalist species and less specialists in those regions, compared to grasslands where extinction debt is unpaid ($t = 2.35$, $P = 0.04$; **III**).

3.4. Comparison of historical and current highly degraded grasslands in northern Estonia

Species richness per site in northern Estonian dry calcareous grasslands was significantly greater in current than in historical records ($t = 3.99$, $df = 7$, $P = 0.005$; Fig. 5). Four traits (seed weight, dispersal type, SLA, terminal velocity) showed increased functional diversity in current communities, whereas functional diversity of plant height had decreased (Table 1). There was no change in the functional diversity of other studied species characteristics. Compared to the losers, winners had a shorter life span, longer flowering duration, heavier seeds, more seeds per shoot, higher terminal velocity, taller height, lower light requirement and higher soil fertility requirement (Table 1). There were 66 increasing and 104 new species among winners. All new colonisers were native to Estonian flora (**IV**).

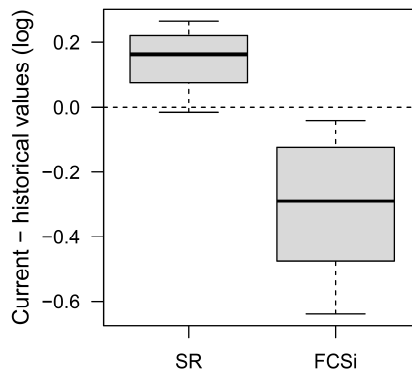


Figure 5. Differences between current and historical plant communities SR – species richness and FCS_i – index of Favourable Conservation Status at the study sites (**IV**). The dotted line indicates no difference, results > 0 indicate current higher values and < 0 current lower values. SR was higher in current grasslands ($P = 0.005$) and FCS_i was lower in current grasslands ($P = 0.004$). Modified from Fig. 4 in **IV**.

Index of Favourable Conservation Status (FCSi; i.e. log-ratio of characteristic to derived diversity) is today significantly smaller than 90 years ago ($t = -4.098$, $df = 7$, $P = 0.004$; Fig. 5), indicating a considerable decline in habitat integrity and conservation value despite the increase in total number of species. Historically there were on average 35 derived species per site, whereas in current communities the average number of derived diversity is 75. The mean number of characteristic species had not changed significantly in time; both historical and current communities contain about 60 characteristic species per site (IV).

Table 1. Results of paired t -tests comparing current and historical functional diversity (calculated as mean pairwise distance), and winners and losers' community mean trait values (IV). Statistically significant tests ($P < 0.05$) are marked in bold. Three categorical traits were coded 0/1 for binary representation. Modified from Table 1 in IV.

Species characteristics	Current vs. historical functional diversity			Winners vs. losers community mean values		
	t	df	P	t	df	P
Dispersal vector (animal/other)	3.10	7	0.01	1.52	7	0.17
Seed number per shoot (log)	1.84	7	0.10	15.14	7	<0.0001
Terminal velocity (log) (m/s ²)	3.25	7	0.01	6.59	7	0.0003
Seed weight (log) (mg)	2.48	7	0.04	7.19	7	0.0001
Flowering duration (months)	1.76	7	0.12	4.34	7	0.003
Mode of reproduction (vegetative reproduction absent or rare/vegetative reproduction present)	0.09	7	0.92	-1.57	7	0.15
Life span (annual-biennial/perennial)	1.98	7	0.08	-3.02	7	0.01
Plant height (log) (cm)	-3.05	7	0.01	12.35	7	<0.0001
Specific leaf area (log) (mm ² /mg)	3.09	7	0.01	0.21	7	0.83
Ellenberg L	2.19	7	0.06	-5.96	7	0.0005
Ellenberg N	1.50	7	0.17	9.85	7	<0.0001

4. DISCUSSION

4.1. Drivers of semi-natural dry calcareous grasslands diversity

The high small-scale plant diversity of semi-natural dry calcareous grasslands is driven by a combination of landscape- and local-scale factors. Structural equation modelling revealed their direct and indirect effects on species richness and confirmed that the effect of regional and local factors is complementary rather than mutually exclusive (I). Also, low shrub cover (up to 30%) was already found to increase the number of generalist species, but it did not yet hinder the richness of habitat specialist species (II).

At the landscape scale, current species richness was significantly related to historical habitat availability, which in turn was highly dependent on past human population density (I). Previous studies have also shown that patterns of land-use intensity from the Iron Age (1200 BC–1 BC) and onwards have contributed significantly to the diversity of local species pools, and thereby to the species richness of grassland communities (Bruun et al. 2001; Pärtel et al. 2007). Therefore, the long-lasting sustainable management and extensive grassland areas are essential for the development and maintenance of species-rich grassland communities.

At the local scale, the shrub cover (up to 40%) had a direct positive effect on total plant diversity, supporting the previous findings that moderate shrub cover can promote plant species coexistence at small spatial scales (Pykälä et al. 2005; Pihlgren & Lennartsson 2008; I). Shrubs can have facilitative abilities, especially in habitats with harsh environmental conditions, by creating suitable microhabitats for germination; by changing nutrient quantity, availability, and variability; by transforming soil chemical composition, offering wind shelter, protecting from herbivores, or changing the composition of soil microorganisms (Callaway 2007; Franco & Nobel 1989). Shrubs also influenced species richness indirectly by increasing light variability and soil environmental heterogeneity, although the latter was mostly determined by the soil depth variability.

Light heterogeneity in turn had a significant positive influence on species richness (I), probably because it allows the coexistence of light- and shade-demanding species (Valladares 2003; Rūsiņa et al. 2013). At the same time belowground small-scale environmental heterogeneity lowered species richness (I). Novel explanations such as microfragmentation theory, have been proposed to explain the counterintuitive negative diversity-heterogeneity relationship (Tamme et al. 2010). Microfragmentation is a community influencing process of changing habitat into a more heterogeneous environment that can have negative effects on the diversity through habitat loss and subsequent isolation, occurring at the plant neighbourhood scale (Tamme et al. 2010; Laanisto et al. 2013). Soil heterogeneity can also alter competitive hierarchies among co-existing species since plants with large root systems can forage among soil

patches, increasing resource competition and lowering species richness (heterogeneity as a separate niche axis, *sensu* Tamme et al. 2010).

Generalist species richness was influenced by shrub cover (up to 30%) similar to total species number – directly and indirectly by increasing light heterogeneity. Species richness of grassland specialists, however, showed no direct or indirect relationship with shrub cover (**II**). Many species, characteristic to dry calcareous grasslands originate from steppe and tundra regions, and are adapted to open habitats with good light availability and stressful conditions (Laasimer 1965), hence do not benefit from the occurrence of shrubs. Previously, Rejmánek & Rosén (1992) have found that a juniper cover exceeding 10% already decreased the number of habitat-characteristic species in Swedish alvar grasslands. However, my results indicate that a shrub cover of 30% can be considered suitable for the coexistence of habitat specialist and generalist species.

4.2. Current status of semi-natural dry to mesic grasslands in Europe

In most of Europe, there are only small and isolated semi-natural grassland fragments left due to considerable land-use changes during the last hundred years. We found that in several of the studied regions in central and northern Europe, species susceptible to grassland area and quality loss have already gone extinct, but in some regions species still persist temporally despite of the unfavourable habitat conditions, creating an extinction debt in the community. Although many species are threatened, the total species richness did not change after the payment of extinction debt and in northern Estonian highly degraded grasslands, the diversity had even increased after 90 years. At the same time, integrity of current communities had considerably declined due to the relative decrease in the number of habitat characteristic species.

The extinction debt occurred in four out of ten regions in central and northern Europe. In regions where extinction debt is already paid specialist species had considerably lower dispersal ability (**III**). It shows that the hindered movement between habitat patches due to unsuitable matrix area and lack of dispersal vectors (i.e. domestic and wild animals) in the landscape have led to the disappearance of good dispersers (Ozinga et al. 2009; Öckinger et al. 2012). Better dispersers may disappear also because of the trade-off between dispersal and competitive ability as in current small and low-quality grassland patches competitive ability is more advantageous (Westoby et al. 1996; Saar et al. 2012).

Similar to species richness, the diversity of specialist species' specific leaf area, flowering duration and Ellenberg N showed possible delayed response to habitat loss in central and northern European grasslands, being positively related to habitat area in regions where extinction debt is paid and having no relationship in regions with a debt (**III**). Comparison of historical and current highly degraded dry calcareous grasslands in northern Estonia also revealed

probable delayed response of functional traits related to species establishment and competitive abilities (IV). Current diversity of seed weight and SLA were higher compared to the historical values, although they are expected to decrease after the abandonment of grazing management (de Bello et al. 2006; Vandewalle et al. 2014). Previously, Vandewalle et al. (2014) also found that current functional diversity of dry calcareous grasslands in Öland, Sweden is partly a legacy from past habitat conditions. At the same time, higher diversity of dispersal type may indicate that species with certain dispersal type were historically favoured, but this limitation has disappeared by now, allowing species with differing dispersal type to co-exist. Presumably, dispersal ability does not determine species survival in the current highly degraded environment. Only the functional diversity of plant height had already decreased in response to ceased grazing (IV).

Despite the loss of habitat area and quality, the total species richness did not decrease after the payment of extinction debt in central and northern Europe (III), indicating that although some species disappear, others can find a suitable habitat in altered communities. In northern Estonian highly degraded grasslands the total richness per site had even increased after 90 years as they still contain a number of specialists, but also due to the colonization of 104 new species (IV). Similar trends have been found in other studies, mostly influenced by the invasion of exotic species exceeding the loss of native species during the observed time period (Abbott et al. 2000; Stohlgren et al. 2008; Ellis et al. 2012). However, northern Estonian degraded grasslands were not colonized by exotic invaders but by native species from other open habitat types in the surroundings, such as road verges, nutrient-rich cultural grasslands and fallows. Species that benefitted from current conditions (i.e. 'winners') were characterized by better establishment and competitive abilities, such as heavier seeds, more seeds per shoot, higher terminal velocity, longer flowering duration, taller height, shorter life-span, higher soil nitrogen preference and lower light requirement, which is in accordance with previous findings (e.g. Lindborg et al. 2012; Saar et al. 2012; Timmermann et al. 2015).

Functional traits of winners refer to a change towards less disturbed and more fertile habitat conditions during 90 years, which are likely the reasons of current higher biodiversity (IV). Historically, the grasslands were relatively intensively grazed, limiting community composition to a specific set of species i.e. those with high tolerance to continuous high disturbance (Vilberg 1927; Petit & Elbersen 2006). This effect is especially pronounced in low productivity ecosystems, such as dry calcareous grasslands, where harsh conditions (e.g. thin soil and related summer droughts and spring floods) additionally limit the number of species able to inhabit these communities (Proulx & Mazumder 1998; Schultz et al. 2011). Cessation of grazing and influx of nutrients from nearby arable fields, through atmospheric nitrogen deposition and/or possible direct addition of fertilizers during the agricultural intensification in the 1950s has led to increased soil fertility, higher grass layer and litter accumulation, which in turn helps to retain soil moisture during summer droughts. This is one

of the possible explanations why the species richness, which is mostly found to decrease in response to nitrogen deposition (Payne et al. 2013), has increased in studied grassland patches. The absence of a negative effect of increasing productivity may be also related to the fact that in calcareous grasslands the soil phosphorous is more limiting factors for plant growth than nitrogen availability (Carrol et al. 2003; Diekmann et al. 2014). Consequently, more productive, less stressful (i.e. with more optimal moisture conditions) and less disturbed conditions may be conducive to more species in the region, resulting in a shift towards more mesotrophic grassland communities (Newton et al. 2012).

At the same time habitat integrity (i.e. how characteristic is the habitat compared to its historical state prior extensive area and/or habitat quality loss) of northern Estonian grasslands had decreased considerably. Current communities contained relatively more species that have not been historically characteristic to a given habitat than historical communities (IV). This thorough change in species composition, coupled with the change in environmental conditions, has led to the development of hybrid communities' *sensu* Hobbs et al. (2014). Also in central and northern European grasslands the relative amount of generalist species increased after the payment of extinction debt (III). Therefore, simply the total number of species would lead us to erroneous conclusions concerning habitat quality (Pärtel 2014; Helm et al. 2015).

4.3. Implications for conservation

Based on the results of my thesis, I provide new implications for restoration and conservation of semi-natural dry to mesic grasslands. I found that species richness is dependent on historical habitat area and connectivity as well as suitable local environmental conditions, indicating the importance of considering both landscape- and local-scale factors in habitat restoration and conservation (I). Results about the effect of low shrub cover on specialist and generalist species confirmed that previously recommended 30% shrub cover can be considered suitable for the maintenance of specialist species richness and high plant diversity in semi-natural dry calcareous grasslands (II). The findings of this thesis also showed that habitat specialists and generalists or characteristic and derived diversity need to be separated while studying species response to land-use changes in order not to overestimate the habitat quality and conservation value (II, III, IV). In addition, I stress the need to consider that habitat loss and degradation might not lead immediately to observable changes in biodiversity or community composition due to the extinction debt (III). In regions where species predicted to eventually become extinct still persist in the habitat patch and its vicinity and there have not been alterations in ecosystem functions yet, habitat restoration is urgently needed to prevent the loss of susceptible species, infiltration of generalist species and change in functional diversity. First, it is important to increase habitat quality by resuming the appropriate management regime, which reduces the impact of the loss of past grassland area and inhibits

the payment of an extinction debt by providing suitable microhabitats and eliminating the competition from generalist species (Hylander & Ehrlén 2013; Otsu et al. 2017). Second, the study results showed that good dispersers are especially susceptible in declining and degrading grasslands, therefore it is essential to increase habitat quantity and restore functional connectivity between habitat patches (Lindborg & Eriksson 2004; Auffret et al. 2017; Török & Helm 2017). The distance to possible seed sources should not be more than 1 km as it is highly unlikely that migration or gene flow will occur over larger distances (Aavik et al. 2013; Prach et al. 2015). Traditional shepherding and landscape-scale grazing networks could help to disperse the seeds over longer distances, even in greatly fragmented landscape, but is currently uneconomical and therefore mostly replaced by stationary paddocks (Fischer et al. 1996; Poschod & WallisDeVries 2002). Finally, increasing the quality of surrounding anthropogenic matrices is found to have a significant effect on the recovery of viable species populations (Aguilar et al. 2006; Donald & Evan 2006; Öckinger et al. 2012).

Habitat restoration requires comprehensive approach in grassland systems where the extinction debt is already paid, the community includes a considerable amount of species that do not belong to their historical habitat specific species pool and there have been changes in ecosystem functions. For instance, in northern Estonian highly degraded dry calcareous grasslands the current biotic and abiotic conditions are potentially reversible to their historical state via restoration, but as the remnant small grassland patches have become isolated from other grasslands in Estonia by more than 100 km, restoration without introduction of propagules of specialist species and without re-creating large landscape-scale functional connectivity of habitat patches might fail to create conditions necessary for long-term persistence of dry calcareous grassland biota (Helm et al. 2006; Auffret et al. 2017; **IV**). Hence, it would be perhaps worthwhile to consider the alternative of managing and maintaining such habitats as hybrid or novel ecosystems given that their remaining species richness contributes to the conservation of local biodiversity. The aim would be to avoid further habitat loss and extinction of the remaining specialist species by resuming the appropriate management regime, improve functional connectivity between habitat patches and if possible then reintroduce the propagules of locally missing specialist species rather than attempting complete restoration to historical state or continuing their abandonment.

Current landscapes often consist of an increasing number of hybrid and novel communities in varying states of degradation (Hobbs et al. 2014). Therefore, nature conservation and restoration practices should be broadened and transcend traditional approaches, by considering also the role of hybrid and novel ecosystems in biodiversity protection. However, the priority must be set to restoration and preservation of historically developed habitat patches.

5. CONCLUSIONS

The high diversity of semi-natural grasslands has developed during hundreds of years in a combination of landscape-scale historical factors and local environmental conditions. During the past century, ~90% of the grassland area has been lost due to the intensive management practices, rendering many species vulnerable to local extinctions. Effective habitat restoration and conservation, based on the knowledge from theoretical ecology, is extremely important for preserving the remaining biodiversity. My thesis helps to understand the mechanisms involved in the maintenance of plant species diversity in semi-natural dry calcareous grasslands. I also assessed the status of semi-natural dry to mesic grasslands in central and northern Europe after vast land-use changes during the past century. Finally, I provided new implications for biodiversity restoration and conservation of communities where the extinction debt is unpaid or already paid and environmental conditions highly altered.

The results of my thesis showed that different environmental factors can have both positive and negative influence on the small-scale species richness of dry calcareous grasslands. At the landscape-scale, historical habitat availability had a direct and past human population density indirect (via its positive influence on historical habitat availability) positive effect on species richness. At the local-scale, light heterogeneity and shrub cover had a positive direct influence on the species richness (I). My results confirmed that a shrub cover of 30% can be considered suitable for the coexistence of habitat specialist and generalist species (II). In contrast to the positive heterogeneity–diversity relationship we found that small-scale soil environmental heterogeneity decreased species richness (I). These findings indicate that the development and maintenance of species-rich grassland communities in Europe depends on the continuous moderate habitat management, availability of extensive grassland areas in the surrounding and suitable local environmental conditions, which should be taken into account in the habitat restoration and conservation.

I detected that in four out of ten European semi-natural dry to mesic grassland regions the species predicted to eventually become extinct still persist in the grassland patch and its vicinity, despite of the current unfavourable environmental conditions. In six regions, where the extinction debt could not be detected, specialist species appeared to have considerably lower dispersal ability. This suggests that species with better dispersal ability are more prone to disappear from European semi-natural grasslands following the payment of extinction debt. Therefore, in regions where extinction debt is still unpaid, restoration of extensive habitat area and functional connectivity is urgently needed to prevent the loss of susceptible species (III).

In the grassland system, where the extinction debt is already paid and there has been a considerable decline in habitat integrity, complete restoration to historical state prior extensive area and habitat quality loss might fail. Hence, instead of abandoning them, it would be worthwhile to consider managing and

maintaining (e.g. avoiding further habitat area and quality loss, improving functional connectivity) such habitats as hybrid or novel ecosystems (i.e. habitats out of their historical range) as they are often still species-rich and can contribute to the local biodiversity protection. In the studied European grassland regions the total species richness did not change after the payment of extinction debt due to the infiltration of generalist species. In northern Estonian highly degraded grasslands the species richness had even increased after 90 years as they still contain a number of specialist species, but also due to the colonization by more competitive and nutrient-demanding native species (**III, IV**).

The priority in biodiversity conservation is to restore and preserve the historical communities as much as possible. However, current landscapes contain an increasing number of hybrid and novel communities, more so in light of ongoing land-use and climate change, and not all of them can be restored. In this thesis I recommend to consider also the role of highly altered ecosystems (i.e. hybrid and novel ecosystems) in biodiversity conservation. I suggest to carefully determine the status of the habitat, and to decide whether it is possible and reasonable to restore the historical community or manage it as a hybrid/novel ecosystem.

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SUMMARY IN ESTONIAN

Pool-looduslike niidukoosluste taimede mitmekesisus: kõrge liigirikkuse taganud tegurid, praegune seisund ja looduskaitsetised väljakutsed

Pool-looduslikeks kooslusteks ehk pärandkooslusteks loetakse loodusliku elustikuga kooslusi, mis on kujunenud kestva niitmise või karjatamise tulemusel ning mida pole mõjutatud kündmise, heinaseemne külvamise ega väetamisega. Suur osa Euroopa soontaimede liigirikkusest on seotud just pool-looduslike maastikega ning väikesel skaalal on nad erakordselt liigirikkad ka kogu maailma mastaabis. Näiteks Eestist, Laelatu puisniidult on 10×10 cm ruudult leitud 25 liiki soontaimi, mis on selles skaalas maailmarekord. Pool-looduslike kooslusi on mitut erinevat tüüpi (nt. loo-, ranna-, luha-, nõmme- ja puisniidud), neist liigirikkaimad on lubjarikkad niidud, kuna suur osa pool-looduslike koosluste liike on pärit Lõuna-Euroopa ja Kaukaasia jääaja refuugiumitest, kus on valdavad olnud kõrge lubjasisaldusega aluselised mullad. Lisaks kõrgele taimede liigirikkusele on pool-looduslikud niidukooslused elupaigaks ka paljudele linnu ja selgrootute liikidele ning pakuvad mitmeid inimkonna heaolu toetavaid looduse hüvesid (nt. tolmeldamise hüve, looduslik kahjuritõrje ja kultuurilised hüved).

Pool-looduslike koosluste ja nende kõrge liigirikkuse kujunemisel ja säilimisel on olulist rolli mänginud mõõdukas inimõju niitmise ja karjatamise näol. Traditsiooniline majandamine tagas elujõuliste taimepopulatsioonide püsimeks vajaliku suurte ja omavahel seotud elupaigalaikude süsteemi (nn. metapopulatsioonide võrgustiku), kus taimeseemnete peamiseks levitajateks olid kariloomad. Lisaks maastikuskaalal toimuvatele protsessidele mõjutavad pool-looduslike niidukoosluste väikeseskaalalist liigirikkust kohalikud keskkonnatingimused, näiteks mulla niiskus, põõsaste katvus ning nende ruumiline varieeruvus. Ei ole aga täpselt teada, milline on erinevate keskkonnategurite otsene ja kaudne mõju pool-looduslike koosluste väikeseskaalalisele taimede mitmekesisusele.

Pool-looduslike niidukoosluste leviku kõrgaeg Euroopas jääb 19. sajandi lõppu. Alates 20. sajandi algusest on kogu Euroopas inimasustuse tihenemise, põllumajanduse intensiivistumise ning traditsiooniliste majandamisviiside lakkamise tõttu nende elupaikade pindala ja kvaliteet drastiliselt vähenenud. Järele on enamasti jäänud vaid väikesed, isoleeritud ja kehva kvaliteediga elupaigalaigud, mis ei toeta elujõuliste populatsioonide säilimist. Ilma efektiivse elupaikade taastamise ja kaitseta on tulevikus oodata mitmete pool-looduslikele niitudele iseloomulike liikide väljasuremist. Tänapäevaks on selge, et elurikkuse säilitamiseks on vaja ökoloogilistel teooriatel põhinevat looduskaitset. Selleks on vaja täpselt teada, millised ja kuidas erinevad keskkonnategurid mõjutavad kooslusele iseloomulike soontaimede mitmekesisust.

Lisaks on looduskaitstes on oluline arvesse võtta liikide aeglast reageerimist keskkonnatingimuste ja maastikustruktuuri muutustele. Paljude taimeliikide populatsioonid suudavad veel lühemat või pikemat aega koosluses püsida, isegi kui keskkonnatingimused on muutunud neile sobimatuks. Nende tegelik väljasuremine on aga vaid aja küsimus. Seda nähtust nimetatakse „väljasuremisvõlaks“. Väljasuremisvõla olemasolule viitab väikeste ja isoleeritud pärandkoosluste laikude endiselt kõrge liigirikkus ning seotus pigem ajaloolise kui tänase maastikustruktuuriga. Jättes võla olemasolu tuvastamata on oht koosluse seisundit ülehinnata. Näiteks on leitud, et Eesti läänesaarte igalt loopealse laigult võib tulevikus kaduda kuni 40% ehk ligikaudu 20 iseloomulikku soon-taimeliiki. Tähtis on ka arvestada, et erinevate tunnustega liigid reageerivad elupaiga muutustele erinevalt. Näiteks pikema levimiskaugusega liigid võivad olla ohustatumad, kuna neil on tänases tugevalt killustunud maastikus suurem tõenäosus sattuda ebasobivasse keskkonda. Võrreldes kooslusi kus väljasuremisvõlg on veel olemas või juba makstud (s.t. liigid kadunud) võib anda olulist informatsiooni selle kohta, millised liigid on kõige tundlikumad ning kuidas võib koosluse elurikkus tulevikus muutuda. See omakorda võimaldab teha õigemaid otsuseid koosluste ning nende mitmekesisuse taastamiseks ja säilitamiseks.

Muutused koosluse keskkonnatingimustes ning liigirikkuses ja koosseisus toovad kaasa muutusi ökosüsteemide funktsioonides. Seega on elupaiga seisundi ja looduskaitse väärtuse hindamiseks oluline uurida ka funktsionaalset mitmekesisust. Funktsionaalne mitmekesisus on bioloogilise mitmekesisuse mõõde, mis näitab kooslustes esinevate organismide funktsionaalsete tunnuste erinevuste hulka. Sarnaselt liigirikkusele võib ka funktsionaalne mitmekesisus elupaigakaole hilinemisega reageerida.

Looduses ei ole aga tühja kohta ning kui ühed liigid kaovad, võivad teised liigid leida muutunud keskkonnatingimustes enda jaoks uue elupaiga. Degradunud kooslusesse võivad siseneda nii invasiivsed tulnukliigid kui ka kohalikud, teistest kooslusetüüpidest pärit liigid. Seega kogu liigirikkus ei pruugigi alati väheneda ning võib teinekord isegi tõusta, kuid samal ajal elupaiga rikkmatus ehk liigilise koosseisu sarnasus algele kooslusele väheneb. Sageli on tulemuseks hübriidsed või täiesti uudsed kooslused, mida ajalooliselt pole esinenud. Hübriidseid kooslusi on võimalik veel algsel kujul taastada, kuid uudsed kooslused on juba pöördumatult ajaloolisest seisundist teisenenud. Praeguse ni ei ole veel jõutud ühisele arvamusele kas ja kuidas oleks mõistlik selliseid tugevalt degradeerunud, kuid liigirikkaid kooslusi majandada.

Minu doktoritöö eesmärgiks oli esiteks kindlaks määrata, millised tegurid on taganud pool-looduslike kuivade lubjarikaste niidukoosluste kõrge soontaimede liigirikkuse (**I**, **II**). Täpsemalt selgitasin välja (a) kuidas erinevad keskkonnategurid mõjutavad otseselt ja kaudselt lubjarikaste niitude väikeseskaalalist (10×10 cm) liigirikkust (**I**) ning (b) milline mõju on põõsaste madalal katvusel (<30%) lubjarikaste niitude spetsialistide ja generalistide liigirikkusele (**II**). Teiseks hindasin Kesk- ja Põhja-Euroopa pool-looduslike kuivade kuni parasniiskete niidukoosluste praegust seisundit jätkuvate maakasutuse muutuste

valguses, kokku kümnes regioonis (III, IV). Täpsemalt tuvastasin (a) milliste regioonide niitudel esineb väljasuremisvõlg ja millistel on võlg juba makstud, (b) milliste funktsionaalsete tunnustega niiduliigid kaovad kooslusest pärast väljasuremisvõla maksmist, (c) kuidas funktsionaalne mitmekesisus on elupaiga pindala vähenemisest mõjutatud ning (d) kas kogu liigirikkus ja liigiline koosseis erinevad regioonides kus väljasuremisvõlg maksmata või makstud (III). Lisaks oli mul võimalus hinnata muutusi tänaseks tugevalt degradeerunud Põhja-Eesti kuivade lubjarikaste niidulaikude taksonoomilises ja funktsionaalses mitmekesisuses ning nende elupaiga rikkumatuses, võrreldes ajaloolise seisundiga. Selgitasin välja ka, millised funktsionaalsed tunnused iseloomustavad liike, mis suudavad tugevalt degradeerunud koosluses püsima jääda (IV). Viimaseks eesmärgiks oli, uurimustulemustele toetudes, välja pakkuda uusi soovitusi koosluste taastamiseks ja nende elurikkuse säilitamiseks, olukorras mil väljasuremisvõlg maksmata või võlg juba makstud ja kooslus tugevalt degradeerunud (I, II, III, IV).

Struktuurse võrrandi mudeli tulemused näitasid, et erinevatel keskkonnafaktoritel on nii positiivseid kui ka negatiivseid mõjusid lubjarikaste niitude väikeseskaalalisele rohttaimede kogu liigirikkusele. Ajaloolisel elupaiga suurusel ja elupaikade omavahelisel sidususel oli otsene positiivne mõju liigirikkusele ning ajaloolisel inimasustuse tihedusel kaudne positiivne mõju liigirikkusele. Kogu liigirikkust suurendasid otseselt ka väikeseskaalaline valguse heterogeensus ja mõõdukas põõsaste katvus. Samas väikeseskaalaline mulla heterogeensus mõjutab liigirikkust negatiivselt. Antud tulemused näitavad, et liigirikaste niidukoosluste teke ja püsimine sõltub nii suurekaalalistest teguritest nagu pidev mõõdukas majandamine, piisava hulga niidulaikude olemasolu ja sidusus maastikus kui ka kohalikest keskkonnatingimustest, mida tuleb arvesse võtta elupaikade taastamisel ja säilitamisel. Elupaiga spetsialiste ja generaliste eraldi analüüsid, selgus, et madalal, kuni 30%, põõsaste katvusel ei ole spetsialistide liigirikkusega veel mingit seost. Samas, generalistide arvule oli põõsaste katvusel positiivne mõju nii otseselt kui ka kaudselt läbi valguse heterogeensus suurendamise. Seega, minu töö tulemused kinnitavad, et pool-looduslikel lubjarikastel niitudel on sobivaks puittaimede katvuseks ligikaudu 30%, mis lubab kooseksisteerida nii elupaiga spetsialistidel kui ka generalistidel.

Väljasuremisvõlg esines neljas uuritud Euroopa piirkonnas – Eestis, Läti Abava regioonis, Rootsi maismaa kooslustes ja Gotlandil. Neis neljas piirkonnas oli spetsialistide liigirikkuse ja elupaiga pindala omavaheline seos ebaoluline, mis viitabki väljasuremisvõla olemasolule. Ka funktsionaalne mitmekesisus näitas neis piirkondades viibega reageerimist. Belgias, Taani Jutlandi ja Zealandi regioonides, Soomes, Saksamaal ja Läti Zengale regioonis oli liigirikkuse ja pindala vahel positiivne seos, mis näitab, et nendel niitudel on võlg juba makstud. Piirkondades, kus võlg juba tasutud, oli elupaiga spetsialistidel oluliselt lühem levimiskaugus. See näitab, et head levijad on pindalakaole kõige tundlikumad. Seega, regioonides, kus väljasuremisvõlg on veel maksmata tuleks võimalikult kiiresti alustada elupaiga taastamisega, et takistada hea levimisvõimega elupaiga spetsialistide kadumist. Kuna liigid on veel koosluselaigus ja

selle lähiümbruses alles, siis elujõuliste populatsioonide taastumise tõenäosus on väga kõrge. Esmalt tuleks tõsta alles oleva elupaiga kvaliteeti alustades taas karjatamise/niitmise ja vajadusel vähendada põõsaste katvust ~30 protsendini. Seejärel tuleks suurendada elupaiga pindala ja sidusust teiste maastikus paiknevate niidulaikudega. Varasemad uurimused on näidanud, et vahemaa elupaigalaikude vahel ei tohiks olla rohkem kui 1 km, kuna ka kõige paremad levijad ei suuda enamasti pikemaid vahemaid läbida. Võla tasumist ennetaks ka ümbritseva maastiku muutmine liikidele läbitavamaks, näiteks kasutades ökoloogilisemaid põllumajandusvõtteid.

Niidulaikudes, kus võlg juba makstud ja elupaiga rikkumatus oluliselt vähenenud, on täielik koosluse taastamine keerulisem ja ajaloolise seisundi saavutamiseks vähem tõenäoline. Samas on sellised degradeerunud ja algsest kooslusest oluliselt teisenenud elupaigalaigud tihtipeale siiski väga liigirikkad. Uuritud Euroopa regioonides, kus võlg makstud, ei olnud kogu liigirikkus generalistide saabumise tõttu kahanenud. Põhja-Eesti lämmastiku saaste ning karjatamise lakkamise tõttu degradeerunud niitudel oli kogu liigirikkus isegi oluliselt kõrgem kui 90 aastat tagasi, ka mõnede funktsionaalsete tunnuste mitmekesisus oli tõusnud. Samal ajal oli elupaiga rikkumatus ehk liigilise koosseisu sarnasus ajaloolisele kooslusele oluliselt vähenenud. Osad ajalooliselt esinenud niiduliigid on tänaseks juba piirkonnast kadunud ja mõningad kadumas ning kooslusesse on sisenenud hulgaliselt uusi teistest elupaigatüüpidest pärit kohalikke liike (kokku 104). Samas on need niidud endiselt elupaigaks ka üsna suurele hulga lubjarikastele rohumaadele iseloomulikele liikidele. Seega tuleks võimalikult kaaluda selliste liigirikaste, samas tugevalt degradeerunud koosluste majandamist ja säilitamist hübriidsete või uudsete kooslustena. Tuleks taas alustada karjatamise/niitmise ja parandada elupaigalaikude funktsionaalset sidusust, mis hoiaks ära nende edasise degradeerumise ja järelejäänud ajaloolisele kooslusele iseloomulike liikide kadumise ning annaks panuse piirkonna elurikkuse säilimisele.

Arvestades hübriidsete ja uudsete ökosüsteemide üha kasvavat hulka jätkuvate maakasutuse ja kliima muutuse valguses, tuleks neile tähelepanu pöörata ka bioloogilise mitmekesisuse kaitses. Selle asemel, et neid ignoreerida ja tähtsusetuks pidada, peaksime leidma võimalusi ja perspektiive nende kasutamisel elurikkuse ja ökosüsteemide funktsioonide ning teenuste säilitamiseks regioonides. Seda muidugi olukorras, mil algne kooslus on tugevalt või lausa pöördumatult muutunud. Prioriteediks peab alati siiski seadma looduslike ja poollooduslike koosluste taastamise ja säilitamise.

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PUBLICATIONS

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2009–2011 University of Tartu, MSc in biology
2006–2009 University of Tartu, BSc in biology
1998–2006 Rapla Vesiroosi Gymnasium
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Language skills:

Estonian (mother tongue)
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Russian (basic)

Institution and position held:

2015–present University of Tartu, specialist
2012–2016 Estonian University of Life Sciences, field work assistant
2013 Nordic Botanical, field work assistant
2011 University of Tartu and Estonian Physical Society, UT Science
Camp, assistant of biology workshop
2011 Tartu Environmental Education Centre Foundation, referee of
biodiversity competitive match
2009–2011 Science Centre AHHA Foundation, assistant of biology work-
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Research interests:

Drivers of high small-scale plant species richness, taxonomic and functional diversity in degraded landscapes, biodiversity and conservation value of hybrid and novel ecosystems, conservation and restoration of semi-natural grasslands.

Publications:

Kasari, L., Zobel, M., Pärtel, M., Bommarco, R., Bruun, H.H., Gustiņa, L., Heikkinen, R., Honnay, O., Krauss, J., Lindborg, R., Raatikainen, K., Rūsiņa, S. & Helm, A. Plants with good dispersal abilities disappear from European semi-natural grasslands following the payment of extinction debt. *Manuscript*.

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Conference presentations:

- Kasari, L.**, Zobel, M., Pärtel, M., Bommarco, R., Bruun, H.H., Gustiņa, L., Heikkinen, R., Honnay, O., Krauss, J., Lindborg, R., Raatikainen, K., Rūsiņa, S. & Helm, A. Plants with good dispersal abilities disappear from European semi-natural grasslands following the payment of extinction debt. 60th Symposium of the International Association for Vegetation Science (IAVS), 20–24 June 2017, Palermo, Italy. *Poster presentation*.
- Kasari, L.**, et al. & Helm, A. Does habitat size influences the functional diversity similarly to species richness? 58th Symposium of the International Association for Vegetation Science (IAVS), 19–24 July 2015, Brno, Czech Republic. *Oral presentation*.
- Kasari, L.**, Takkis, K., Saar, L. & Helm, A. Increase in species richness and functional diversity after habitat degradation and fragmentation. 57th Symposium of the International Association for Vegetation Science (IAVS), 1–5 September 2014, Perth, Australia. *Oral presentation*.
- Kasari, L.**, Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? 56th Symposium of the International

Association for Vegetation Science (IAVS), 26–30 June 2013, Tartu, Estonia. *Poster presentation.*

Kasari, L., Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? 2nd International Conference of Doctoral School of Earth Sciences and Ecology, 16–17 May 2013, Tallinn, Estonia. *Oral presentation.*

Kasari, L., Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? 26th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 9–11 May 2013, Tartu, Estonia. *Poster presentation.*

Awards and scholarships:

- 2017 Honourable mention for an outstanding poster presentation in the 60th International Association for Vegetation Science (IAVS) symposium, 19–24 June, Palermo, Italy
- 2017 International Association for Vegetation Science (IAVS), partial travel grant
- 2014, 2015 Doctoral School of Earth Sciences and Ecology, travel grants
- 2013 Archimedes foundation, part-time studies scholarship

Courses attended:

- 2017 International Association for Vegetation Science (IAVS) symposium workshop for young scientists: “How to write a successful grant application20 ,” June, Palermo, Italy.
- 2013–2014 Quantitative Ecology Module for Master and PhD students, 30 September – 31 January, University of South Bohemia, České Budějovice, Czech Republic.
- 2013 International Association for Vegetation Science (IAVS) post-symposium course in R for community assembly analyses, 1–2 July, Tartu, Estonia.
- 2012 Graduate course ‘Issues in Diversity’ by Prof. Susan Harrison, 3–7 September, University of Oulu, Finland.

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Väikeseskaalalist taimede liigirikkust mõjutavad tegurid, degradeerunud maastike taksonoomiline ja funktsionaalne mitmekesisus, hübriidsete ja uudsete ökosüsteemide bioloogiline mitmekesisus ja looduskaitse väärtus, pool-looduslike koosluste kaitse ja taastamine.

Publikatsioonid:

Kasari, L., Zobel, M., Pärtel, M., Bommarco, R., Bruun, H.H., Gustiņa, L., Heikkinen, R., Honnay, O., Krauss, J., Lindborg, R., Raatikainen, K., Rūsiņa, S. & Helm, A. Good dispersers disappear from European semi-natural grasslands following the payment of extinction debt. *Käsi*.

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Konverentsiettekanded:

- Kasari, L.**, Zobel, M., Pärtel, M., Bommarco, R., Bruun, H.H., Gustiņa, L., Heikkinen, R., Honnay, O., Krauss, J., Lindborg, R., Raatikainen, K., Rūsiņa, S. & Helm, A. Good dispersers disappear from European semi-natural grasslands following the payment of extinction debt. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 60. sümpoosion, 20.–24. juuni 2017, Palermo, Itaalia. *Posterettekanne*.
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- Kasari, L.**, Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 56. sümpoosion, 26.–30. juuni 2013, Tartu, Eesti. *Posterettekanne*.

Kasari, L., Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? Maateaduste ja ökoloogia doktorikooli 2. rahvusvaheline konverents, 16.–17. mai 2013, Tallinn, Eesti. *Suuline ettekanne*.

Kasari, L., Takkis, K., Saar, L. & Helm, A. Which plant species are ‘winners’ in degraded grassland habitats? Saksamaa, Austria ja Šveitsi Ökoloogiaühingu (GfÖ) Taimede populatsioonibioloogia sektsiooni 26. konverents, 9.–11. mai 2013, Tartu, Eesti. *Posterettekanne*.

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- 2017 Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) osaline välissõidutoetus
- 2014, 2015 Maateaduste ja ökoloogia doktorikooli välissõidutoetused
- 2013 SA Archimedese Kristijan Jaagu osalise õppe stipendium

Erialane enesetäiendus:

- 2017 Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) sümpoosioni raames toimunud noorteadlastele suunatud kursus „Kuidas kirjutada edukat granditaotlust“, 20. juuni, Palermo, Itaalia.
- 2013–2014 Rahvusvaheline kvantitatiivse ökoloogia moodul, 30. september – 31. jaanuar, Lõuna-Cechy Ülikool, České Budějovice, Tšehhi.
- 2013 Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) sümpoosionijärgne kursus taimekoosluste kokkupaneku analüüsimiseks statistika programmiga R, 1.–2. juuni, Tartu, Eesti.
- 2012 Prof. Susan Harrisoni poolt läbi viidud kursus ‘Issues in Diversity’, 3.–7. september, Oulu Ülikool, Soome.

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- 2007–... Tartu Üliõpilaste Looduskaitseringi liige

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