

KERSTI RIIBAK

Importance of dispersal limitation
in determining dark diversity
of plants across spatial scales



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Dissertation was accepted for the commencement of the degree of *Doctor Philosophiae* in botany and mycology at the University of Tartu on April 9, 2018 by the Scientific Council of the Institute of Ecology and Earth Sciences University of Tartu.

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Commencement: Room 218, 40 Lai Street, Tartu, on May 28, 2018 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479

ISBN 978-9949-77-718-1 (print)

ISBN 978-9949-77-719-8 (pdf)

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University of Tartu Press

www.tyk.ee

CONTENTS

LIST OF ORIGINAL PUBLICATIONS	6
1. INTRODUCTION.....	7
1.1. The objectives of the thesis.....	9
2. MATERIALS AND METHODS	11
2.1. Study area and vegetation data	11
2.2. Estimating dark diversity and community completeness.....	13
2.3. Invasion success and biotic effects on invasion.....	14
2.4. Seed production and dispersal distances.....	14
2.5. Environmental factors.....	15
2.6. Statistical analyses	16
3. RESULTS	18
3.1. Dispersal limitation determines dark diversity in Central and Northern Europe.....	18
3.2. Dispersal limitation decreases with environmental stress and human activities	18
3.3. Species with good dispersal abilities disappear in fragmented grasslands	20
3.4. Dispersal limitation decreases at smaller spatial scales	21
3.5. Relationship between environment, diversity and invasion success..	24
4. DISCUSSION	26
5. CONCLUSIONS.....	31
6. REFERENCES.....	32
7. SUMMARY IN ESTONIAN	38
ACKNOWLEDGEMENTS	41
PUBLICATIONS	43
CURRICULUM VITAE	113
ELULOOKIRJELDUS.....	115

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers denoted in the text by Roman numerals:

- I. **Riibak, K.**, Ronk, A., Kattge, J. & Pärtel, M. (2017) Dispersal limitation determines large-scale dark diversity in Central and Northern Europe. *Journal of Biogeography*, 44, 1770–1780.
- II. **Riibak, K.**, Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Znamenskiy, S., Bengtsson, K., Rosén, E., Prentice, H.C. & Pärtel, M. (2015) Dark diversity in dry calcareous grasslands is determined by dispersal ability and stress-tolerance. *Ecography*, 38, 713–721.
- III. **Riibak, K.**, Bennett, J.A., Kook, E., Reier, Ü., Tamme, R., Bueno C.G. & Pärtel, M. Plant dispersal limitation influencing observed and dark diversity in agricultural landscapes is stronger at larger spatial scales. *Submitted manuscript*.
- IV. Bennett, J.A., **Riibak, K.**, Kook, E., Reier, Ü., Tamme, R., Bueno, G.C. & Pärtel, M. (2016) Species pools, community completeness and invasion: disentangling diversity effects on the establishment of native and alien species. *Ecology Letters*, 19, 1496–1505.

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Author's contribution to the publications:

- I. participated in developing the idea and assembled the dispersal data, had the main responsibility in data analysis as well as in manuscript writing
- II. participated in developing the idea and compiled the dispersal data, had the main responsibility in data analysis as well as manuscript preparation
- III. participated in field works and data collection, had the main responsibility to develop the idea, data analysis as well as manuscript writing
- IV. participated in the field works, data collection and manuscript preparation

1. INTRODUCTION

Dispersal is among the most important ecological processes influencing plant community assembly, colonization of new habitats, maintenance of biodiversity, and biological invasions (Wang & Smith 2002; Chase 2003; Levine & Murrell 2003). Restricted seed dispersal could be one of the main reasons why many species are absent from potentially suitable sites (i.e. these sites are dispersal limited). Yet linking seed dispersal to observed diversity patterns has been challenging, because tracking seeds from parent plants to their deposition is difficult (Wang & Smith 2002). The extent to which dispersal limitation determines plant species occurrences within their distribution ranges is still poorly quantified at the macroecological scale. Knowing what the role of dispersal limitation is in shaping local plant assemblages and how it depends on natural and anthropogenic factors is essential for biodiversity conservation (Lewis et al. 2017).

The most common way to detect dispersal limitation in local communities is by using seed addition experiments (Zobel et al. 2000; Clark et al. 2007; Myers & Harms 2009). These studies have found that biodiversity typically increases after propagule addition, indicating that communities are not saturated, i.e. they are not complete. Alternatively, to better understand which ecological processes (dispersal limitation, competition, stochastic events) restrict local biodiversity, we could compare functional traits of observed species to dark diversity – the species that are currently absent from sites although present in the surrounding region and adapted to the prevailing environmental conditions (Pärtel et al. 2011; de Bello et al. 2012; Pärtel 2014). For instance, if species in dark diversity are typically characterized by lower dispersal abilities than observed species, it indicates that the poor dispersal ability of species likely restricts local biodiversity.

Dark diversity represents the absent part of the habitat- or site-specific species pool and is expected to vary between different sites (Huston 1999; Pärtel et al. 2000). Dark diversity can be estimated, in addition to seed additions experiments, on the basis of expert knowledge, by considering suitable species for specific habitats (Sádlo et al. 2007; Zobel et al. 2011). Another method, more suitable for large-scale studies, involves the use of eco-informatics to define species pools, such as using habitat suitability models with GIS (Guisan & Rahbek 2011) or analyzing species co-occurrence patterns (Ewald 2002; Münzbergová & Herben 2004; Lewis et al. 2016). By using the species co-occurrence approach, a species is considered to be a part of dark diversity if it is absent from a site characterized by a set of species it is typically found to co-occur with. By calculating the log-ratio of observed diversity to dark diversity [$\ln(\text{observed diversity}/\text{dark diversity})$], we can estimate how much of the site-specific species pool is represented in local communities – the community completeness (Pärtel et al. 2013). The estimate of completeness differs from the raw values of species richness or other biodiversity metrics, because it allows comparison of different

sites, habitats and regions at a relative scale, taking into account the natural variation of their species pool sizes (Pärtel et al. 2013; Ronk et al. 2015).

Species dispersal ability depends on the number of seeds produced (seed abundance) and the dispersal distance of seeds (Muller-Landau et al. 2002). Direct measures of seed abundance and dispersal distances are difficult to collect for vast range of species in field conditions, yet plant trait databases, such as LEDA (Kleyer et al. 2008), provide some data on seed abundance and other dispersal traits for macroecological studies. Seed abundance can also be estimated indirectly via seed mass, because seed mass and abundance are inversely related (Turnbull et al. 1999; Jakobsson & Eriksson 2000; Henery & Westoby 2001). Additionally, potential dispersal distance of seeds can be estimated with the help of statistical tools using a combination of specific plant traits, such as dispersal syndrome, growth form, selected seed characteristics, and information on species phylogeny (Tamme et al. 2014).

The inability to disperse to potentially suitable sites after the Last Glacial Maximum restricts plant diversity within Europe (Svenning & Skov 2007; Normand et al. 2011). However, the extent to which both dispersal limitation mechanisms, species' seed production ability and potential seed dispersal distance, determine plant species absences within their occurrence range and how it depends on climatic and anthropogenic factors has remained largely unexplored at biogeographical scales. Dispersal limitation might be less important in very stressful environments where diversity is restricted more by establishment than by dispersal (Foster et al. 2004; Stein et al. 2008). In dry or cold conditions, abiotic stress likely limits establishment of less adapted species, whereas in warm and wet regions, competitive resident vegetation might exert strong resistance against dispersed seeds (Rejmánek et al. 2005). Additionally, dispersal limitation might be lower in human-disturbed (or naturally) open landscapes where seeds get trapped within vegetation less often than in closed canopy forests (Chambers & MacMahon 1994; Nathan et al. 2008). Agricultural activities, such as livestock grazing or usage of agricultural machinery, may also enhance dispersal of some plant taxa (Strykstra et al. 1996; Poschlod et al. 2005). Knowing which sites are most limited by dispersal and how it relates to local climatic and anthropogenic factors allows also prediction of how future global change (e.g. warmer conditions and increasing human activities) will influence the extent of dispersal limitation in particular regions.

The relative importance of dispersal limitation in determining community completeness could also depend on the studied spatial scale and on habitat availability in the surrounding landscape. The extent of dispersal limitation might be greater at larger (regional) scales whereas at smaller scales, local environmental conditions and biotic interactions, such as competition, mostly determine species assemblages (Weiher & Keddy 1995; Münzbergová 2004). Additionally, dispersal limitation is likely less detected in fragmented landscapes. High-dispersal ability is thought to increase species' ability to respond to disturbance (Tscharrntke et al. 2005). Yet in areas that have suffered from significant habitat loss, persistence might be more beneficial than dispersal, because

seeds may often reach unsuitable sites (Fahrig 2001; Tremlová & Münzbergová 2007; Saar et al. 2012). Therefore, if only a few fragments of suitable habitats are embedded in the landscape, the species with good dispersal abilities might more often belong to dark diversity, while clonal species belong to observed diversity.

Seed dispersal is successful when seeds are able to establish in newly colonized habitats (Wang & Smith 2002). Which sites are better to invade, and more specifically, what the relationship is between local diversity and invasion success is still poorly understood (Levine et al. 2004; Fridley et al. 2007). The species pool and dark diversity concepts may help to better understand the diversity-invasion relationship than species richness as the first two metrics allow to separate environmental and biotic effects. Large species pools result from benign and heterogeneous environmental conditions, as there are fewer abiotic limitations on establishment and more niches. Those conditions are also suitable for a greater number of invaders (Richardson et al. 2012). Comparing sites with different species pool sizes can thus result in positive richness-invasion relationships irrespective of biotic resistance (Levine 2000; Fridley et al. 2007). As species richness and invasion success both increase with species pool size, it is important to estimate richness relative to the species pool size (Shea & Chesson 2002; Perelman et al. 2007). Community completeness represents the effects of local biotic interactions on the species pool. Consequently, we propose that biotic resistance to seeds is greater (i.e. dispersal limitation is weaker) in more complete communities, whereas seed establishment success increases with species pool size since larger pools reflect more broadly favorable environmental conditions and reduce abiotic limitation of seed establishment.

1.1. The objectives of the thesis

The purpose of the thesis was to estimate the extent to which low seed production and short dispersal distances may cause the absence of vascular plant species from suitable sites at the biogeographical scale in Central and Northern Europe and within two different grassland ecosystems in the Baltic Sea Region. At the European scale, we explore how the levels of dispersal limitation (inferred as trait differences between observed and dark diversity) depend on the natural and anthropogenic factors (e.g. climate, landscape heterogeneity, human population size, agricultural intensity). Further, within grassland ecosystems we study how dispersal limitation depends on habitat availability in the landscape, and explore the effect of dispersal limitation, habitat availability and local environmental conditions on community completeness at different spatial scales. Lastly, we also explore which grassland sites are better to invade and if species pool and dark diversity as biodiversity metrics can better explain plant invasions than species richness.

Our main hypothesis are as follows:

- 1) Dispersal limitation is one of the main reasons why species belong to dark diversity at both biogeographical and regional scales (i.e. species in dark diversity likely produce fewer seeds and disperse shorter distances than observed species).
- 2) The relative importance of dispersal limitation reduces under severe abiotic and biotic stress. In cold and dry areas, abiotic limitation restricts biodiversity more than dispersal. In productive warm and moist conditions, biotic resistance limits biodiversity more than dispersal.
- 3) Anthropogenic activities generally facilitate seed dispersal; therefore, dispersal limitation decreases in highly human populated areas with intensive agriculture.
- 4) Species in dark diversity have better dispersal abilities than observed species in regions containing only fragments of suitable habitats (because species with good dispersal abilities disperse to unsuitable sites).
- 5) The importance of dispersal limitation decreases at smaller spatial scales, where local environmental conditions and biotic interactions, such as competition, determine species occurrence more than dispersal.
- 6) The dark diversity and species pool concepts help to predict better species invasion success and the relationship between diversity and invasion, because these metrics allow separation of environmental and biotic effects. Seeds establish better in sites with large species pools, whereas biotic resistance to seeds is greater in more complete sites (i.e. dispersal limitation is less important).

2. MATERIALS AND METHODS

2.1. Study area and vegetation data

To study observed and dark diversity at the European and regional scales, we used three different vascular species datasets. In paper **I** we analysed available species distribution data from seven areas in Northern and Central Europe: Iceland (www.floraislands.is/blom.html), Finland (www.luomus.fi/kasviatlas; Lampinen & Lahti 2013), Estonia (<http://efloora.ut.ee/Eesti/index.html>), the British Isles (www.brc.ac.uk/plantatlas/), the Netherlands (<http://soortenbank.nl/>), Germany (www.floraweb.de), and Switzerland (<http://www.infoflora.ch/de/flora/art-abfragen.html>) (Fig. 1A). Climatic conditions vary greatly between the study areas. Annual mean temperature is much lower in Iceland and Finland than in the other study areas (1.5 °C and 7.3 °C respectively). Switzerland, Iceland, the British Isles, and the Netherlands receive annually more precipitation than the rest (on average 87.8 and 53.8 cm respectively) (Hijmans et al. 2005). The spatial resolution of datasets was typically 10 × 10 km. However, the grid cell size for the Netherlands and Switzerland were 5 × 5 km, so we merged the grid cells into groups of four (10 × 10 km). The German dataset had a spatial resolution of roughly 12 × 11 km.

In paper **II** we analyzed the species dataset covering the entire distributional area of dry calcareous grasslands in the Baltic Sea region of northern Europe that can be divided into nine, distinct subregions in Sweden (Västergötland, Öland, Gotland), Estonia (Saaremaa, Hiiumaa, western Estonia, northern Estonia), and western Russia (Izborsk, Izhora) (Fig. 1A). The presence of herbaceous species was recorded in 1223 1 × 1 m vegetation plots. The total area of dry calcareous grasslands on the large Swedish islands and in Estonia is much higher than on the Swedish mainland (Västergötland) (Ekstam & Forshed 2002) and in western Russia (Znamenskiy et al. 2006). There were 3–36 study sites per subregion and 3–15 plots per site. The vegetation data were assembled from previous studies by Reitalu et al. (2014).

In papers **III** and **IV** we collected small- and landscape-scale vegetation data from 31 grassland sites scattered within an agricultural area in South-East Estonia (Fig. 1B). These sites were mostly comprised of perennial species, typical for grasslands in the region. All grassland sites were situated on dry to mesic soils, and none of them were recently disturbed. In May 2014 we established fifteen 0.5 × 0.5 m plots, arranged in a grid of three rows and five columns comprising a 1.5 × 2.5 m area, and also two smaller adjacent seed plots (0.2 × 0.8 m) in each site. As in the paper **IV**, we were interested in isolating the biotic effects of the plant community on plant invasion, we removed all vegetation from one seed plot per site by applying herbicide. We then added 100 seeds of 15 herbaceous species to the small plots. The majority of the added species were typical grassland species in Estonia. After two growing seasons, we counted all individuals belonging to the 15 focal species (recruits) in seed

plots, excluding large established plants. In each grassland area, we recorded all vascular plant species within the 1.5×2.5 m area and compiled a landscape-scale plant species list for a 10 ha circular area around each site, irrespective of habitat type. The 10 ha circular area was searched systematically by two experienced botanists for three to four hours with the help of GPS tracking, private gardens and the interior of agricultural fields were excluded from the survey.

In each paper we standardized species nomenclature according to The Plant List (2010, 2013). This resulted in a total of 5088 vascular species in paper **I** and 291 species in paper **II**. A total of 154 species were observed on 1.5×2.5 m plots across the grassland sites in papers **III** and **IV**.

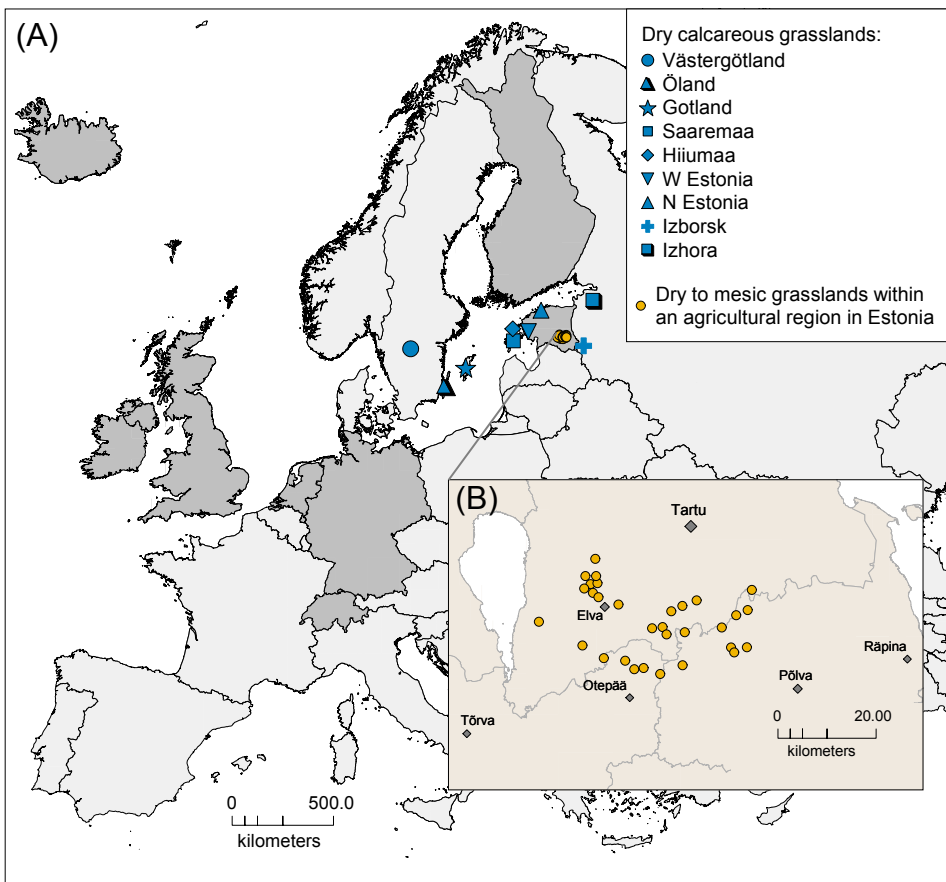


Figure 1. (A) Study areas in Central and Northern Europe (indicated by *dark grey* colours) and dry calcareous grasslands in the Baltic Sea region divided into nine subregions (analyzed in papers I and II, respectively). (B) Dry to mesic grassland sites within an agricultural area in South-East Estonia (analyzed in papers III and IV).

2.2. Estimating dark diversity and community completeness

To estimate dark diversity for each grid cell in paper **I**, we applied geographical, biogeographical, and environmental filters. First, we determined the geographical species pool for each 9834 grid cell in our dataset by including all species found within a 300-km radius. This left out the species with little possibility of dispersing to that particular grid cell from dark diversity. Within the geographical species pool, we determined the biogeographical species pool by using dispersion fields (Borregaard & Rahbek 2010; Carstensen et al. 2013) to identify other grid cells with similar conditions. Specifically, we selected only grid cells within the 300-km radius with at least a 50% species overlap with the grid cell for which we were estimating dark diversity. From within the biogeographical species pool, we obtained a site-specific species pool by selecting only absent species with a high probability of co-occurrence with those species present within the grid cell, thereby selecting only species with similar environmental tolerances. For that, we estimated the probability of co-occurrence with other species using the Beals index (Beals 1984; Ewald 2002), implemented in the *beals* function in the R package ‘vegan’ (Oksanen et al. 2012). The Beals index is defined as

$$p_{ij} = \frac{1}{S_i} \sum_k \frac{N_{jk} I_{ik}}{N_k}$$

where p_{ij} is probability that species j occurs at site (grid cell) i , S_i is number of species at site i (minus 1 if species j is present), N_{jk} is the number of joint occurrences of species j and k ($j \neq k$), N_k is the number of occurrences of species k , and I_{ik} is the incidence (0 or 1) of species k in the study plot i .

We calculated the species co-occurrence probability for each species in each grid cell, including both presences and absences. Each species was assigned a species-specific threshold value for inclusion in dark diversity. This threshold was derived from the estimated probabilities of occurrence in which the species was present and was set at the 5% quantile of those probabilities. This method accounts for variation in species frequency, but excludes possible bias due to outliers, which are common in co-occurrence probability distributions (Botta-Dukát 2012). In other words, a species was included in dark diversity when it was absent from a grid cell and its occurrence probability was greater than 5% of the values in grid cells where the species was found.

Since in papers **II–IV** vegetation data were collected within a single biogeographic region, we applied only environmental filtering by analyzing species co-occurrences using Beals index. In paper **II** we analyzed species co-occurrences obtained from all 1223 1×1 m plots, in papers **III** and **IV** we analyzed species data collected from fifteen 0.5×0.5 m plots across all 31 sites (465 plots in total). Yet in paper **IV**, we had to omit two grasslands sites from the analyses

because seed plots got heavily damaged by wild boar activities, not allowing estimation of biotic effects on plant invasion. Although dark diversity was found for every 0.5×0.5 m plot within a 1.5×2.5 m site in papers **III** and **IV**, we estimated the site-level observed and dark diversity cumulatively for the 1.5×2.5 m area. We subsequently divided dark diversity between the landscape scale and regional dark diversity, depending on if the species was present within the 10 ha circular area around the site, or was present only in some other visited grassland sites within the study region, respectively. Site completeness was calculated for the regional and landscape scale as the ratio of site-level observed species richness to respective dark diversity, $\ln(\text{observed diversity} / \text{dark diversity})$ (sensu Pärtel et al. 2013). To minimize the effect of dispersal limitation in our species pool estimates in paper **IV**, community completeness was calculated only at the landscape scale.

2.3. Invasion success and biotic effects on invasion

In paper **IV**, we calculated two site-level metrics on plant invasion: invasion (or establishment) success and biotic effects on seeds (i.e. biotic resistance/acceptance). Invasion success was calculated as the number of recruits summed across all 15 species, only the data from intact vegetation were used. Biotic effects were calculated as the log-ratio of summed recruits in intact vegetation to cleared vegetation [$\ln(\text{intact/cleared})$]. In this study, biotic effects represent the effects of the intact plant community on invasion, but ignore the effects of herbivores and pathogens.

2.4. Seed production and dispersal distances

We estimated species seed production using direct measures (average number of seeds per ramet/tussock or individual) from the LEDA traitbase (Kleyer et al. 2008) (in papers **I** and **III**), or via seed mass (**II**), as seed mass is inversely related to seed abundance (Jakobsson & Eriksson 2000; Henery & Westoby 2001).

To estimate potential dispersal distance of species in papers **I–III**, we used simple plant traits and the *dispeRsal* function in R (Tamme et al. 2014). This function incorporates traits, such as dispersal syndrome, growth form and seed characteristics (terminal velocity, seed-release height and seed mass), in different combinations to estimate the maximum potential dispersal distance for each species. For these analyses, trait values were obtained from the LEDA traitbase (Kleyer et al. 2008), the BiolFlor database (Klotz et al. 2002), the Kew Gardens Seed Information Database (SID, Royal Botanic Gardens Kew 2012), the Ecological Database of the British Isles (Fitter & Peat 1994), the Dispersal and Diaspore Database (Hintze et al. 2013), the PLANTS database (USDA, NRCS 2015), and the TRY database (Kattge et al. 2011). If the species had

several dispersal syndromes, we calculated the geometric mean of all its potential dispersal distances. In paper **III**, species clonal ability was estimated using the Clonal Index of a species from the CLO-PLA3 database (Klimešová et al. 2017).

2.5. Environmental factors

To test the effect of natural and anthropogenic factors on dispersal limitation in Central and Northern Europe (**I**), we obtained data on the climatic and land use patterns for each 10×10 km grid cell. Average temperature and precipitation values were obtained from WorldClim database (Hijmans et al. 2005). Information on human population density was obtained from the HYDE 3.1 database (Goldewijk et al. 2010). The agricultural land use index was calculated as $\log[\text{Agricultural areas}/(\text{Forest and semi-natural areas} + \text{Wetland areas})]$ based on Corine level 1 land use types (Bossard et al. 2000). The landscape heterogeneity index was estimated as the Shannon index on Corine level 2 land use types.

To estimate how the differences in dispersal traits between observed and dark diversity and site completeness depend on the current and historical size of grasslands in the surrounding landscape in paper **III**, we used GIS data. We estimated the percentage of current grasslands within a 500 m radius around the sites. Both current orthophotos and topographic maps were used to distinguish dry to mesic grasslands from other areas, typically not suitable for dry to mesic grassland species. The percentage of historical grassland area was estimated similarly as the current grassland area but using a topographic map from the 1940s. To estimate how completeness depends on disturbance history of grasslands, we estimated the age of grassland sites using available orthophotos from 1990s and early 2000s. Sites were classified as “younger grasslands” if the sites were disturbed (e.g. ploughed) on any of these orthophotos. Twelve sites were classified as “younger grasslands”; the rest, 19 sites, as “older grasslands”.

To estimate how community completeness and plant invasion success depend on the local environmental conditions in papers **III** and **IV**, we measured various soil characteristics, light availability and plant productivity at each site. Small-scale environmental heterogeneity was estimated as the average of the coefficients of variation for soil depth and moisture, and light availability across the 15 plots in each site. In paper **III**, the measured environmental variables were used in principal components analysis to extract three axes representing the local soil conditions and site productivity. These three axes represented 1) soil texture (clay and silt), pH, soil phosphorus (P), and total plant biomass; 2) soil nitrogen (N) and potassium (K); 3) soil carbon (C). These axes explained 75.3% of the measured environmental variation (41.8%, 18.1%, and 15.4% respectively).

2.6. Statistical analyses

Comparing dispersal traits of observed and dark

We calculated the geometric mean of each dispersal trait (seed production, potential dispersal distance, seed mass or clonal index) across species in observed and dark diversity for each grid cell, plot, or site (in papers **I**, **II**, and **III**, respectively). In papers **I** and **III** we subsequently calculated the log-ratio of the mean trait values between observed and dark diversity. Positive log-ratios indicated that species in observed diversity produce more seeds and have longer potential dispersal distance than the species in dark diversity (indicating potential dispersal limitation). Positive log-ratio of clonal index showed that observed species are more clonal than dark diversity species.

To test whether the log-ratios of dispersal traits were overall significantly different from zero (i.e. if sites are dispersal limited) across the study areas in Central and Northern Europe (**I**), we used linear mixed effects models (*lme* function) with study area as a random factor in the ‘nlme’ R package (Pinheiro et al. 2013). To analyze study areas individually, we used generalized least squares fitted linear models using the *gls* function. To test if log-ratios of dispersal traits differ significantly from zero in paper **III**, we used two simple linear regression models separately for the regional and landscape scale. To test if dispersal limitation (expressed as log-ratios of dispersal traits) differed significantly between the study areas in Northern and Central Europe (**I**) we applied Tukeys HSD test using *glht* function in the ‘multcomp’ R package (Hothorn et al. 2008). To detect if there was difference in the levels of dispersal limitation between two study scales in South-East Estonia we tested the effect of scale on the log-ratios using the analyses of variance (**III**).

To compare dispersal traits of observed and dark diversity across all subregions in the dry calcareous grasslands area in the Baltic Sea region (**II**), we used linear mixed effects models with “subregion”, “study site”, and “vegetation plot” as random factors. Plots were nested within sites and sites within subregions. To analyze if observed and dark diversity species traits differ significantly within the subregions, the “subregion” was set as an explanatory variable.

The effect of environmental variables on dispersal limitation and completeness

To analyze the effects of natural and anthropogenic factors on dispersal limitation across the study areas in Central and Northern Europe (**I**), we regressed log-ratios of dispersal traits against temperature, precipitation, landscape heterogeneity index, human population density, and agricultural land use index in the linear mixed effects models using *lme* function. We checked for the presence of spatial autocorrelation by calculating the Moran’s I value of model residuals using the ‘spdep’ (Bivand et al. 2013) and ‘ncf’ (Bjornstad 2013) R packages. If a significant autocorrelation was detected, we included an exponential spatial

correlation structure in the model. To analyse whether the difference in dispersal traits between observed and dark diversity depends on the habitat availability in the surrounding landscape (III), we regressed log-ratios of dispersal traits against current and historical habitat area.

To test the importance of different environmental variables on the community completeness within an agricultural area in South-East Estonia (III), we regressed completeness against current and historical grassland area, grassland age, small-scale heterogeneity, local soil conditions and site productivity in two separate linear models for the regional and landscape scale. In both models, we ran all possible subsets of the predictor variables using the *dredge* function in the 'MuMIn' R package (Bartoñ 2017). We selected the best model(s) based on the AIC_c values. If multiple models were weighted similarly on the basis of the $\Delta AIC_c = < 2$ criteria, we averaged those models using the *model.avg* function in the 'MuMIn' package. To quantify the relative importance of different predictors of community completeness, we summed the Akaike weights for each explanatory variable over the models with $\Delta AIC_c = < 2$ in which the variable occurred. The greater the sum, the more important the variable is compared to the other explanatory variables.

Relationship between diversity, environment, and invasion

To test the relationships between each aspect of diversity (richness, completeness, species pool) and invasion (IV), we developed two sets of structural equation models (SEM). One focused on species richness and the other on species pool size and community completeness. For each model we first modelled the relationship among the abiotic environment, productivity and diversity. Then using those models we constructed two SEM using richness and two using completeness and species pools. These SEM models tested which of the factors within the previous models determined invasion (establishment) success and biotic effects on seeds. For all SEM, we initially assumed that each abiotic, productivity and diversity variable could directly influence invasion outcomes. From these models, we repeated the backward removal of terms based on AIC. For the final models we assessed model fit using multiple indices and bootstrapped estimates of parameter significance. These analyses were conducted using SPSS with AMOS (IBM SPSS, Chicago, Illinois, USA).

3. RESULTS

3.1. Dispersal limitation determines dark diversity in Central and Northern Europe

Depending on the study area, the average number of vascular plant species observed in the 10×10 km grid cells ranged between 125 and 1014, while on average 61–489 species were estimated to belong to dark diversity. Across all study areas in Central and Northern Europe, we found that log-ratios of seed production and dispersal distance were significantly higher than zero ($t = 2.0$, $DF = 9825$, $P = 0.046$; $t = 6.0$, $DF = 9826$, $P < 0.001$, respectively), indicating that species in dark diversity produced generally fewer seeds and dispersed shorter distances than observed species (i.e. potential dispersal limitation was detected) (Fig. 2). However, seed production did not differ between observed and dark diversity in Estonia. In Iceland, the species in dark diversity produced more seeds than observed species (Fig. 2A), accompanied by the lowest difference in dispersal distances between observed and dark diversity relative to other regions (Fig. 2B).

3.2. Dispersal limitation decreases with environmental stress and human activities

Across all study areas in Central and Northern Europe, the difference in dispersal traits between observed and dark diversity decreased with drier conditions (Table 1). Additionally, in most areas (Estonia, the British Isles, Switzerland, and Germany), dispersal limitation decreased significantly with warm temperatures ($P < 0.05$). Inversely, in areas characterized by high rainfall (the British Isles, the Netherlands, and Switzerland) or cold climate (Finland), dispersal limitation decreased with precipitation and lower temperatures ($P < 0.05$), respectively. These results indicate that dispersal limitation decreases under stressful abiotic conditions (in dry and cold areas) or under potential biotic resistance (in warm and wet areas).

Both the log-ratios of seed production and potential dispersal distance decreased with increasing agricultural land use index (Table 1). In addition, the log-ratio of potential dispersal distance decreased in regions with higher human population density. These results indicate that besides environmental stress, human activities have helped to reduce the importance of dispersal limitation.

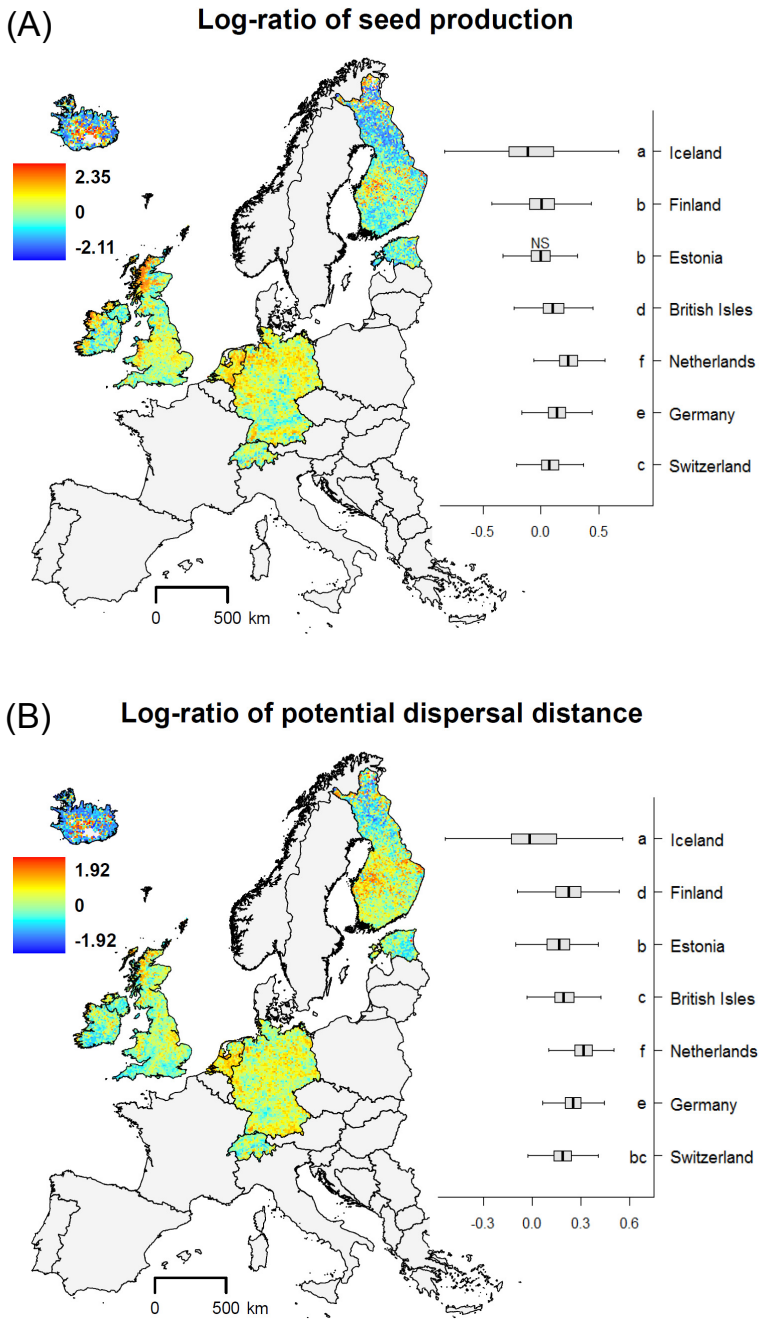


Figure 2. The log-ratio of seed production (A) and potential dispersal distance (B) between observed and dark diversity across seven study areas in Europe (calculated for each ca. 10×10 km grid cell). Positive values indicate dispersal limited sites (in which absent vascular plant species produced fewer seeds and dispersed shorter distances than observed species), whereas negative values indicate the opposite. The log-ratio of seed production was greater than zero in most study areas ($P < 0.001$), although the opposite pattern was found in Iceland, and no pattern was found in Estonia (NS). The log-ratio of potential dispersal distance was greater than zero in each study area ($P < 0.001$). Different lower case letters indicate significant differences between study areas (Tukey test, $P < 0.05$). Figures are from Riibak et al. (2017).

Table 1. Effects of natural and anthropogenic factors on the log-ratio of seed production, potential dispersal distance in vascular plant observed and dark diversity in Central and Northern Europe (bold values indicate significant relationship). Study area was used as a random factor in the linear mixed effect models (DF = 8198). Table from Riibak et al. (2017).

Effect	Log-ratio of seed production				Log-ratio of dispersal distance			
	Estimate	SE	<i>t</i> -value	<i>P</i> -value	Estimate	SE	<i>t</i> -value	<i>P</i> -value
<i>Intercept</i>	-0.344	0.135	-2.5	0.011	0.110	0.095	1.1	0.251
Temperature	0.003	0.003	0.9	0.377	0.000	0.002	0.2	0.823
Precipitation	0.092	0.027	3.4	0.001	0.022	0.018	1.2	0.222
Landscape heterogeneity	-0.005	0.006	-0.8	0.416	-0.001	0.004	-0.3	0.790
Human population	0.000	0.002	0.0	0.999	-0.004	0.001	-3.9	< 0.001
Agricultural land use	-0.006	0.001	-4.7	< 0.001	-0.002	0.001	-2.0	0.043

3.3. Species with good dispersal abilities disappear in fragmented grasslands

In dry calcareous grasslands across the Baltic Sea Region (Fig. 1A), the average number of plant species present in a 1×1 m plot was 21.1, whereas on average 36.8 species belonged to dark diversity. Dispersal limitation was detected also in this study, as dark diversity species had overall shorter potential dispersal distances and heavier seeds (i.e. species likely produced fewer seeds) than observed species ($t = -20.0$, $P < 0.001$; $t = 14.0$, $P < 0.001$; DF = 1222, respectively) (Fig. 3).

However, potential dispersal distance values did not differ between observed and dark diversity in the subregions characterized by small fragments of dry grasslands – in Västergötland on the Swedish mainland ($t = -1.8$, $P = 0.075$, N = 13) and in the two Russian grassland regions, Izborsk and Izhora ($t = -1.6$, $P = 0.121$, N = 79; $t = 1.4$, $P = 0.173$, N = 75; respectively). Additionally, in dry to mesic grasslands within an agricultural region in South-East Estonia (Fig. 1B), we found that the species dispersing potentially long distances were more often present in 1.5×2.5 m grassland sites that had larger areas of historical grasslands nearby ($z = 3.0$, $P = 0.003$) (Fig. 4A). Furthermore, although clonal species belonged more likely to observed diversity than to dark ($t = 9.2$, $P < 0.001$), they were less often present in sites having historically large areas of grasslands in the surrounding landscape ($z = 2.8$, $P = 0.005$) (Fig. 4B). Neither log-ratio of dispersal distance or clonal index was related to the current habitat size ($P > 0.05$).

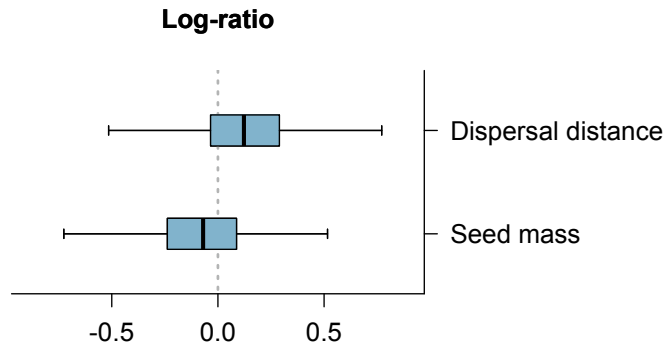


Figure 3. Log-ratio of potential dispersal distance and seed mass of observed and dark diversity in dry calcareous grasslands in the Baltic Sea Region. Species in dark diversity had significantly shorter dispersal distance and heavier seeds than observed species, indicated by the positive and negative log-ratios on the graph, respectively. The figure is based on data used in Riibak et al. (2015).

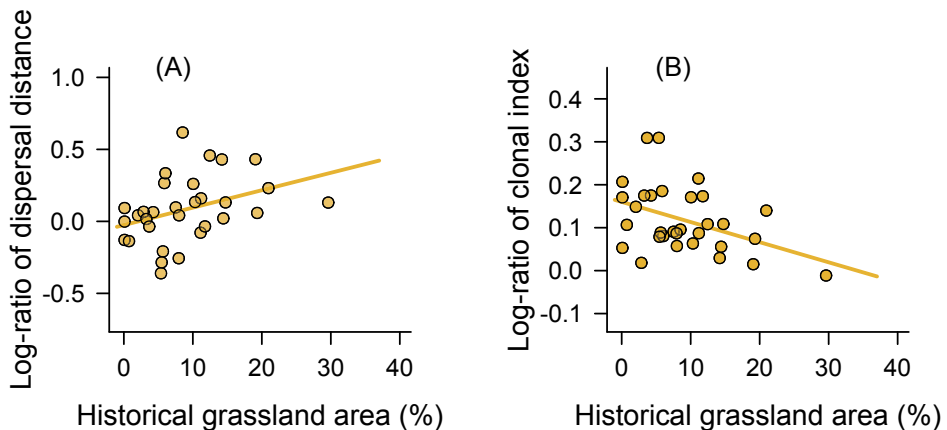


Figure 4. Relationship between log-ratio of dispersal distance (A) and clonal index (B) of observed and dark diversity, and percentage of historical grasslands in the surrounding landscape in grassland sites in South-East of Estonia. Dark diversity species were all present in close vicinity to a site, within the 10 ha area. Figures are from paper III.

3.4. Dispersal limitation decreases at smaller spatial scales

We observed on average 30.8 herbaceous species on 1.5×2.5 m sites across all visited grasslands within an agricultural region in South-East Estonia (Fig. 1B). On average 38.2 species were estimated to dark diversity at the landscape scale (i.e. those suitable species were absent from the sites, but present within the 10 ha landscape around the site). At the regional scale, we estimated on average 39.8 species to dark diversity (i.e. those suitable species were absent from the

1.5 × 2.5 m sites and the 10 ha landscape around the site, but present in other visited grassland sites in the region).

Dispersal limitation restricted local biodiversity also in these grasslands. More specifically, if we compared the dispersal traits of species we observed on 1.5 × 2.5 m sites to the regional scale dark diversity, both log-ratio of seed production and maximum potential dispersal distance were significantly greater than zero ($t = 2.5$, $P = 0.016$; $t = 7.1$, $P < 0.001$, respectively; $DF = 60$) (Fig. 5AB). By comparing dispersal traits of observed and dark diversity at the landscape scale, log-ratio of seed production was significantly lower than zero, but the log-ratio of maximum potential dispersal distance was greater than zero ($t = -3.8$, $P < 0.001$; $t = 2.2$, $P = 0.030$; respectively, $DF = 60$) (Fig. 5AB). Study scale had significant effect on both log-ratio of seed production and dispersal distance models ($F_{1,60} = 19.6$, $P < 0.001$; $F_{1,60} = 11.9$, $P = 0.001$, respectively) (Fig. 5AB), indicating that the importance of dispersal limitation decreased at smaller spatial scales.

(A) Log-ratio of seed production (B) Log-ratio of dispersal distance

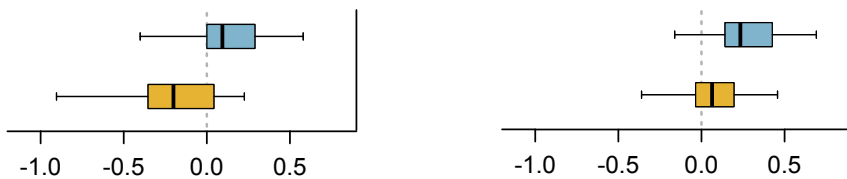


Figure 5. Log-ratio of seed production (A) and potential dispersal distance (B) of observed and dark diversity calculated using plant data from dry to mesic grasslands within agricultural region in South-East of Estonia. Log-ratios were calculated at two different spatial scales, by comparing observed diversity of 1.5 × 2.5 m grassland sites between the dark diversity species that were absent from sites but present at some other visited grassland plots in the region (i.e. regional scale, indicated by *blue* colours), and between the dark diversity species that were present in the close vicinity, within a 10 ha circular area around the site (i.e. landscape scale, indicated by *yellow* colours). Positive log-ratios indicate that species in dark diversity produce fewer seeds and have shorter potential dispersal distance than species in dark diversity (i.e. dispersal limitation). All log-ratios differed significantly from zero ($P < 0.05$) and between the study scales ($P \leq 0.001$). Figure from paper **III**.

Furthermore, among the analysed landscape and local scale factors, such as current and historical grassland area, grassland age, small-scale soil and light heterogeneity, local soil conditions and productivity, we found that the current grassland area mostly determined the extent to which species from other visited grassland sites in the region had reached to potentially suitable sites (i.e. completeness at the regional scale), whereas local environmental conditions, such as soil P and texture, pH, and plant total biomass (representing the first

PCA axis) determined how well species in close vicinity to sites (10 ha area) had reached the sites (i.e. completeness at the landscape scale) (Fig. 6A). More specifically, at the regional scale we found a positive relationship between completeness and current grassland area ($z = 2.0$, $P = 0.046$, Fig. 6B), whereas no relationship was found between completeness and other analysed variables. Conversely, at the landscape scale, we only found a significant negative relationship between completeness and PCA1, where greater values indicated more productive site conditions ($z = 2.299$, $P = 0.022$; Fig. 6C).

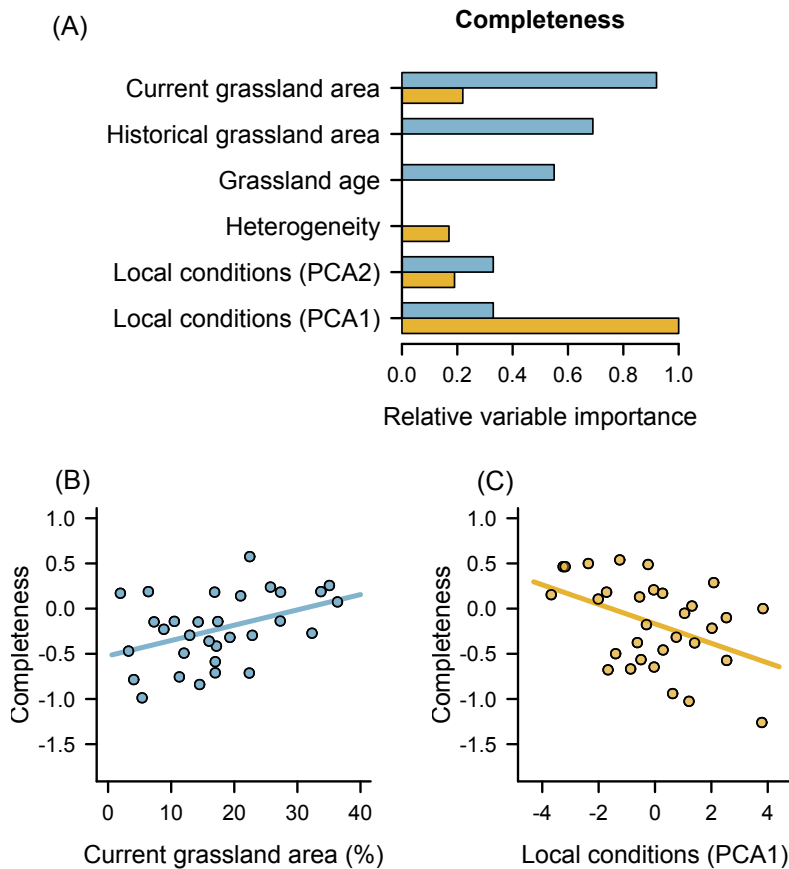


Figure 6. Relative importance of current and historical grassland area, grassland age (older/younger), small-scale soil and light heterogeneity, and local soil conditions and productivity (characterized by two PCA axes) in determining completeness of 1.5×2.5 m grassland sites in South-East Estonia (A); and the relationships between completeness, current grassland area, and local soil conditions and productivity (PCA1) at the regional scale (*blue* colours) (B) and landscape scale (*yellow* colours) (C). Soil N and K associated mostly to PCA2, whereas soil P, texture, pH, and plant biomass to PCA1. Greater PCA1 values indicated sites characterized by acidic deep soils with high soil P and low clay content, and with high biomass production. Results of model averaging of the best fitted ($\Delta AICc = <2$) linear models. Only significant relationships are presented on scatterplots. Figures are from paper III.

3.5. Relationship between environment, diversity and invasion success

We found that species pools and completeness explained invasion success better in dry to mesic grasslands in South-East Estonia than species richness as species richness explained overall less variation (i.e. had lower R^2 values) in the structural equation model (SEM) (Table 2). This result suggests that partitioning richness into species pool size and completeness enhances our understanding of the relationship between diversity and invasion.

Table 2. Model fit for structural equation models and the variation explained (R^2) in two aspects of invasion of 15 species. Degrees of freedom from the Chi-squared tests are shown as subscripts. Model fit is considered adequate if $P > 0.05$. Based on the results from Bennett et al. (2016).

Invasion model	Richness		Species pool/ completeness		Difference in R^2
	Model fit	R^2	Model fit	R^2	
Invasion success	$X_{20}^2 = 6.37$ P = 0.998	0.69	$X_{25}^2 = 8.70$ P = 0.999	0.80	0.10
Biotic effects	$X_{23}^2 = 8.50$ P = 0.997	0.27	$X_{24}^2 = 8.17$ P = 0.999	0.33	0.06

Furthermore, although many environmental factors influenced invasion, including environmental paths in our models did not diminish the importance of species pools and completeness (Fig. 7). We found that seed establishment increased (Fig. 7A) and biotic effects became less negative (i.e. resistance reduced) with species pool size (Fig. 7B). Additionally, seeds established better in more complete sites (Fig. 7A), but biotic resistance on seeds increased with completeness (Fig. 7B). These results support our initial hypothesis that seed establishment success is positively related to species pool size and more complete communities pose stronger biotic resistance against invaders. Productive environments (high litter and shoot biomass) generally inhibited seed establishment (Fig 7A) and had negative biotic effects on invasion (i.e. dispersal limitation was less important) (Fig. 7B).

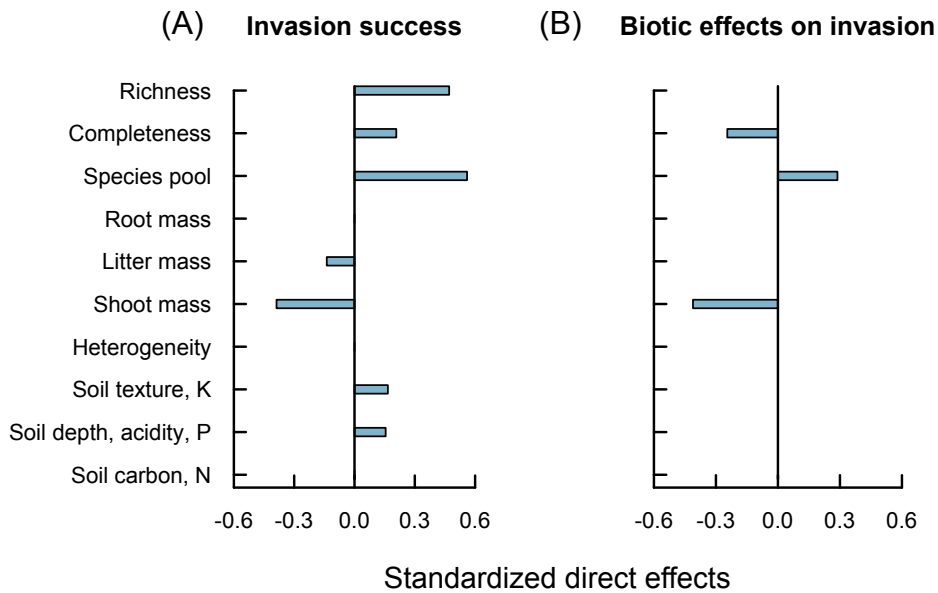


Figure 7. Standardized direct effects of diversity (richness, completeness and species pool size), productivity and the environment on invasions of 15 plant species across the 29 sites taken from structural equation models (SEMs). Bars represent the standardized parameter estimate of the relationship between that variable and invasion. Only variables retained after SEM simplification are shown. Invasion was measured as establishment in intact vegetation of sown seed (A), and as the biotic effect on establishment [$\ln(\text{intact}/\text{disturbed})$] (B); negative values denote increasing resistance for seed. Separate SEMs were used to generate the results for species richness and for community completeness/species pool effects, with effects for productivity and environmental variables taken from the latter. Modified figure from Bennett et al. (2016).

4. DISCUSSION

The overall aim of this thesis was to estimate the extent to which poor dispersal abilities of plant species may cause absences from suitable sites at the biogeographical scales in Central and Northern Europe and within two different grassland ecosystems in the Baltic Sea Region. Additionally, we explored how the importance of dispersal limitation relates to local natural and anthropogenic factors. Our results showed that only a fraction of the habitat-specific species pool had reached suitable sites from the surrounding region, indicating that plant assemblages are generally not saturated with suitable species (I–IV). Comparison of functional traits between observed and dark diversity enabled us to understand which ecological mechanisms cause species absences. We found that both mechanisms of dispersal limitation, low seed production and the inability to disperse long distances assigned many species to dark diversity in Central and Northern Europe (I), and also within two different grassland ecosystems in the Baltic Sea Region (II, III). The importance of both dispersal limitation mechanisms was previously largely unexplored at the macro-ecological scale. The extent of dispersal limitation depended on various natural and anthropogenic factors. Dispersal limitation decreased with higher levels of abiotic stress, biotic resistance, and human activities (I), and at smaller spatial scales (III). Species with good dispersal abilities often belonged to dark diversity in landscapes characterized by small areas of suitable habitats (II, III).

Seed dispersal can be successful only if seeds are able to establish in newly colonized habitats (Wang & Smith 2002). Which sites are better to invade, and more specifically, how invasion success depends on local diversity is still poorly understood in ecology. Our experimental seed addition study showed that species pool and completeness predicted species invasion success in grasslands better than species richness, as these biodiversity metrics allowed separation of environmental and biotic effects (IV). Establishment success of seeds was greater in sites with larger species pools most likely because such sites contain more favorable environmental conditions and more niches. Biotic resistance to seeds was greater in more complete communities (i.e. the extent of dispersal limitation was lower in such sites) (IV).

The level of dispersal limitation decreases under severe abiotic and biotic stress

The ability of species to disperse over long distances and to produce a sufficient number of seeds influenced species range filling in Central and Northern Europe (I). However, the level of dispersal limitation was less important in more stressful environments. More specifically, the extent of dispersal limitation decreased in warm and dry conditions, except in areas with cold climate (Finland) or high overall rainfall (the British Isles, Netherlands, and Switzerland) (I). In cold or relatively dry areas, abiotic environmental stress likely limits the establishment

of plants more than dispersal (Foster et al. 2004). The low levels of dispersal limitation found in Iceland (**I**) can also be explained by severe abiotic stress. Iceland has suffered from ecosystem degeneration since human settlement (Arnalds 2006). Infertile soils cover large parts of Iceland and strong winds in these relatively cold, open, and sparsely vegetated habitats have likely helped to disperse many plant species, thereby reducing dispersal limitation (Chambers & MacMahon 1994; Arnalds 2006). It is also possible that Darwin's wind hypothesis applies to Iceland: species with poor dispersal abilities are evolutionary more successful on islands as relatively fewer seeds deposit into the ocean (see also Cody & Overton 1996). In relatively productive warm and wet areas (the British Isles, the Netherlands, and Switzerland), strong biotic resistance by resident vegetation has likely inhibited the establishment of some species. We tested the latter assertion in paper **III** and found that establishment success of experimentally added grassland seeds was indeed the lowest, and biotic resistance to seeds the strongest in productive environments, as characterized by high shoot and litter biomass. The shifting limitation hypothesis along productivity gradients, often found in grassland ecosystems, states that the importance of dispersal limitation is highest at intermediate productivity levels (Foster et al. 2004; Stein et al. 2008). We can conclude from our results that this hypothesis does not operate only in grassland ecosystems, but also at broad, biogeographical scales.

Anthropogenic activities facilitate seed dispersal

We predicted that besides environmental stress, human activities help to reduce the extent of dispersal limitation. Consistent with this hypothesis, our results showed that both potential dispersal distances and seed production were less important in determining species' occurrences when human activity was greater (**I**). Previous studies have shown that habitat loss and fragmentation in urbanized and agricultural landscapes restrict seed dispersal between habitat patches (McEuen & Curran 2004). Yet European plant species have a long evolutionary history of growing in human-dominated environments (Balmford 1996), and at larger scales biodiversity and human population size are frequently positively correlated (Araújo 2003). Human activities have likely facilitated the dispersal of many vascular plants across Europe, thereby decreasing dispersal limitation. Our findings also coincide with the review by Nathan et al. (2008), summarizing that dispersal is facilitated in open, human-disturbed landscapes. Yet Ronk et al. (2017) showed that even while large-scale site completeness in Europe is positively related to land use heterogeneity and human population density in Europe, it is negatively related to agricultural land use. Consequently, although moderate agricultural activities may help to promote seed dispersal and plant biodiversity, too intensive agricultural practices in modern landscapes likely result in biodiversity loss in local plant assemblages.

Loss of species with good dispersal abilities in fragmented landscapes

Although high-dispersal ability is thought to increase species' ability to respond to disturbance (Tschardt et al. 2005), the ability to disperse long distances across landscapes may not always represent an advantageous strategy (Fahrig 2001). Within dry calcareous grassland area in the Baltic Sea region, we found that species' dispersal distances did not differ between observed and dark diversity in areas characterized only by small fragments of dry calcareous grasslands: in Västergötland on the Swedish mainland and in the Russian sites (II). Additionally, in isolated grassland patches in South-East Estonia, the species belonging to dark diversity (although present in the surrounding landscape) produced more seeds than observed species (III). In fragmented landscapes, species with good dispersal abilities are probably less frequently present in suitable sites because their seeds often disperse into unsuitable parts of the habitat matrix (see also Purschke et al. 2012; Saar et al. 2012). In paper III, we found a clear link between the dispersal ability of species and habitat size; species with longer potential dispersal distances were relatively more frequent and clonal species were less frequent in sites surrounded by large areas of historical grasslands. No relationship was found with the current habitat area (III). These results support the assertion that species investing in dispersal are just a legacy of historical landscapes and can be extirpated from the region in the future (Kasari 2017). Consequently, our results imply that it is essential to increase the area of grassland habitats in fragmented agricultural landscapes to avoid the loss of functional and taxonomic diversity in local communities.

Dispersal limitation decreases at smaller spatial scales

According to our estimations, on average 70 percent of the site-specific species pool was absent from grassland sites within the agricultural region in South-East Estonia, and half of them were also absent in the surrounding 10 ha landscape (III). Such low completeness may not provide ecosystem functioning and services (e.g. natural pest control and pollination of surrounding crop fields) (Tschardt et al. 2005; Hautier et al. 2018). We found that dispersal limitation was one of the main reasons why suitable species present in the region had not reached local sites (III). Yet dispersal limitation was less evident at the smaller, landscape scale, where competitive interactions can be more important. These findings are in accordance with some previous seed addition experiments, showing that dispersal limitation is less prevailing at smaller spatial scales (Münzbergová 2004; Pinto & MacDougall 2010; Germain et al. 2017). For example, Germain et al. (2017) found that species richness in Californian serpentine meadows increased significantly after receiving seeds collected from 100 m and greater distance, whereas no increase was found when seeds collected from ≤ 5 m were added.

Additionally, our results showed that the grassland species present within the agricultural region were more likely to reach suitable sites if larger areas of grassland habitats were available in the landscape. Higher grassland connectivity enhances dispersal of seeds into unoccupied sites after agricultural disturbances or other stochastic events (Fischer & Lindenmayer 2007). Moreover, well-functioning seed exchange between grassland patches helps to avoid negative inbreeding effects in local populations (Aavik & Helm 2017). At the landscape scale, community completeness was determined by local environmental conditions, with more productive sites being less complete, consistent with our hypothesis. In fertile grassland soils, more competitive species typically start to dominate, which leads to exclusion of weaker competitors and decreased biodiversity despite ongoing dispersal (Kull & Zobel 1991; Janssens et al. 1998; Liira et al. 2012; Bennett et al. 2016).

We conclude that the effect of ecological mechanisms shaping local biodiversity clearly varies across spatial scales. Dispersal limitation and habitat availability determine community completeness at larger scales, whereas local environmental conditions and site productivity shape biodiversity at smaller scales. Consequently, both landscape scale and local environmental factors should be taken into account in nature conservation planning (Aavik & Helm 2017).

Disentangling the effects of environment and diversity on invasion success

We predicted that the unclear relationship between species richness and invasion success (Fridley et al. 2007) occurs because richness is a product of both the species pool and local processes. Our results showed that species pool and completeness predicted species invasions better than species richness (**IV**), supporting the assertion that environmental and biotic processes have distinct effects on invasion (Shea & Chesson 2002; Fridley et al. 2007). Therefore, not considering species pools and completeness may limit our understanding of the processes driving invasion.

Furthermore, we found support for the hypothesis that invasion rates will be higher in sites with large species pools as they represent environments where the conditions are favorable for a greater number of species (Shea & Chesson 2002; Fukami 2004). Yet even if initial establishment success is higher in sites with larger species pools, such sites have also higher probability to contain strongly competitive species (Herben 2005). Therefore, at later life stages, these same habitats may become more competitive and pose strong biotic resistance against recruits.

We also predicted that more complete communities hold greater biotic resistance to recruits as they are more saturated and therefore exploit more resources (Moore et al. 2001; Shea & Chesson 2002; Fukami 2004). Across the fifteen sown species, establishment success increased with completeness, yet biotic resistance on seeds also increased with completeness, supporting our initial

hypothesis. Taking account both environmental and diversity effects on plant invasion, we can conclude from our results that the sites with large species pools promote seed establishment, whereas more productive and complete communities are more difficult to invade (i.e. dispersal limitation is less important in such sites). Consequently, any disturbances reducing completeness of sites can also enhance invasions of unwanted species (e.g. alien plants).

5. CONCLUSIONS

We conclude that (1) the ability of species to produce sufficient numbers of seeds and disperse over long distances influences both large-scale species distribution range filling in Central and Northern Europe and small-scale species assemblage patterns in temperate grasslands in the Baltic Sea Region. (2) Abiotic stress and biotic resistance decrease the relative importance of dispersal limitation. (3) Human activities have generally helped to promote dispersal of various seeds at large scales in Europe. (4) In fragmented landscapes, the species with good dispersal abilities often belong to dark diversity because their seeds deposit into unsuitable parts of the habitat matrix. (5) We also found that dispersal limitation is less important at smaller spatial scales where local environmental conditions and competitive interactions largely determine species assemblages. (6) Lastly, community completeness and the species pool as biodiversity metrics indeed have more power to predict species invasions than species richness.

We can infer from our results that if global change is accompanied by warmer and moister conditions at high latitudes (Jacob et al. 2014), dispersal limitation may become more prevalent in the sparsely human-inhabited regions of Northern Europe (**I**). Additionally, our results from grassland ecosystems show that the remnant patches of historical grasslands and ex-arable fields have a potential to be plant diversity “hotspots” in agricultural landscapes, yet this diversity is only partially realized in local communities (**II**, **III**). Sites with low completeness are more susceptible to species invasions, which can also promote the spread of alien plants (**IV**). Because community completeness is largely dependent on dispersal-based processes (**II**, **III**), it is particularly important to increase the area of species rich habitats in agricultural landscapes to avoid the loss of species with good dispersal abilities, and to promote successful seed dispersal of native species between different grassland patches, for instance, with the help of grazing animals (Poschlod et al. 1998; Couvreur et al. 2004).

Overall, our studies show that the dark diversity concept and the comparison of functional traits between observed and dark diversity can be applied to study the ecological mechanisms driving diversity patterns in different ecosystems and at different spatial scales. Knowing which sites are less diverse relative to their potential species pool and which ecological mechanisms restrict local diversity at different scales has great value in nature conservation planning as only diverse communities can provide sufficiently ecosystem functions and services (Tschamntke et al. 2005; Hautier et al. 2018).

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7. SUMMARY IN ESTONIAN

Levimispiirangu osatähtsus taimede tumeda elurikkuse kujunemisel

Elurikkuse hoidmine on looduskaitse ülim eesmärk, ent sageli on elurikkus võimalikust liikide hulgast palju väiksem. Kuna vaid elurikkad kooslused suudavad inimkonnale pakkuda erinevaid looduse hüvesid nagu mullateke, (kultuur)-taimede tolmeldamine ja looduslik kahjuritõrje, on äärmiselt oluline teada, miks osad liigid on sobivatest elupaikadest puudu ja moodustavad *tumeda elurikkuse*. Takistatud seemnelevi (ehk levimispiirang) võib olla üks peamisi põhjuseid, miks osad taimeliigid on puudu neile sobivatelt aladelt. Makroökoloogilisel skaalal on seda senini vähe hinnatud. Looduskaitsete tegevuste planeerimiseks on aga oluline teada, mil määral võib taimede piiratud levimisvõime (vähene seemnetoodang ja levimiskaugus) põhjustada koosluste madalat elurikkust ja kuidas kohalikud loodusolud ja inimõju mõjutavad levimispiirangu suurust.

Levimise uurimine on olnud teadlastele jaoks tõsine väljakutse, kuna loodusliku seemnelevi jälgimine on keerukas. Enamasti on levimispiirangut tuvastatud katseliselt seemnekülvamise abil. Sageli on seemnete lisamine ala liigirikust suurendanud, viidates sellele, et looduslikud taimekooslused pole liikidest küllastunud. Et paremini aru saada, millised ökoloogilised protsessid (levimine, konkurents, juhuslikud sündmused) piiravad kohalikku elurikkust, võime võrrelda vaadeldud elurikkuse ja puuduoleva (kuid elupaika sobiva ja ümbritsevas regioonis leiduvate liikide) ehk tumeda elurikkuse taimetunnuseid. Levimispiirangule viitab see, kui tumedasse elurikkusesse kuuluvate liikide seemnetoodang ja levimiskaugus on väiksem kui vaadeldud liikidel. Võrreldes vaadeldud ja tumeda elurikkuse suurust, saame hinnata ka koosluse täielikkust – kui suur osa kasvukohale sobilikust liigifondist on konkreetsel alal esindatud. Erinevalt liigirikusest võimaldab koosluse täielikkus võrrelda erinevaid alasid, elupaiku ja regioane suhtelisel skaalal, kuna võtab arvesse loodusliku varieeruvuse liigifondi suurustes.

Levimine on edukas vaid siis, kui seemned suudavad uutes kasvukohtades idaneda ja ellu jääda. Teooria kohaselt on liigirikad alad raskemini asustatavad, kuna kasvuks vajalikke ressursse ja vabu nišše on vähem. Samas on uuringute tulemused olnud väga varieeruvad: mõnikord on liigirikad kooslused paremini invadeeritavad, teinekord halvemini. Liigifondi ja tumeda elurikkuse kontseptsioonid võiksid paremini ennustada uute liikide invasioone, kuna erinevalt liigirikusest saab nende mõõdikute abil eristada levimis- ja asustamispiirangut. Ala suur liigifond tuleneb seal valitsevatest soodsatest ja mitmekesisest keskkonnatingimustest, mis pakub asustamisvõimalusi paljudele liikidele. Seetõttu võime erineva liigifondi suurusega alasid võrreldes leida invasiooniedukuse ja liigirikuse vahel positiivse seose biotilisest vastupanust olenemata. Koosluse täielikkuse mõõdik lubab aga hinnata biotiliste vastastikmõjude tugevust konkreetsel alal. Seega, biotiline vastupanuvõime uute liikide seemnete idanemisele

võiks suureneda koosluse täielikkusega (levimispiirangu osatähtsus on väiksem), samas kui seemnete asustamistõenäosus võiks olla kõrgem suurema liigifondiga aladel.

Käesolevas väitekirjas hindasime, milline on levimispiirangu osatähtsus taimede elurikkusmuutrite kujunemisel nii Kesk- ja Põhja-Euroopas kui ka kahes erinevas rohumaa ökosüsteemis – Läänemere regiooni kuivadel lubjarikastel niitudel ja Tartu piirkonna põllumajandusmaastike rohumaaaladel. Samuti uurisime liigifondi ja tumeda elurikkuse kontseptsioone kasutades, millest oleneb rohumaaaliikide invasiooniedukus. Tumeda elurikkuse leidmiseks analüüsisime taimealiikide koosesinemise mustreid ning levimispiirangu tuvastamiseks võrdlesime vaadeldud ja tumeda elurikkuse levimistunnuseid. Lisaks hindasime seemnelisamise katse abil 15 rohumaaaliigi invasiooniedukust. Väitekirjas andsime oma tulemustele tuginedes looduskaitsealisi soovitusi elurikkuse suurendamiseks meie põllumajandusmaastikes.

Töö peamisteks eesmärkides oli analüüsida:

- 1) mil määral põhjustab taimede vähenemine seemnetoodang ja piiratud levimiskaugus liikide puudumise sobivatest elupaikadest nii Kesk- ja Põhja-Euroopas kui ka regionaalsel tasandil kahes erinevas rohumaa ökosüsteemis;
- 2) kuidas levimispiirangu suurus Kesk- ja Põhja Euroopas sõltub kohalikest looduslikest tingimustest ja inimõjust (kliimast, maastiku heterogeensusest, rahvastiku arvust ja põllumajanduslikust tegevusest);
- 3) kuidas vaadeldud ja tumedasse elurikkuse kuuluvate rohumaaaliikide levimisvõimekus sõltub ümbritsevas maastikus olevast elupaiga pindalast;
- 4) mil määral sõltub levimispiirangu osatähtsus uuritud ruumiskaalast;
- 5) milliseid alasid asustavad rohumaaaliikide seemned paremini, ning kas koosluse täielikkus ja liigifond elurikkuse mõõdikuna aitavad liikide asustamisedukust paremini ennustada kui liigirikkus.

Tulemused näitasid, et paljud sobivad liigid olid elupaikadest puudu, teiste sõnadega, vaid osa sobilikust liigifondist oli aladel esindatud nii suures skaalas Kesk- ja Põhja Euroopas (I) kui ka kahes erinevas rohumaa ökosüsteemis (II, III). Võrreldes vaadeldud elurikkusega, oli tumeda elurikkuse liikidele üldjoontes omane väiksem seemnetoodang ning levimiskaugus (I–III). Seega piiras taimede kehv levimisvõime olulisel määral taimekoosluste liigilist täielikkust.

Levimispiirangu suurus sõltus Kesk- ja Põhja Euroopas nii looduslikest tingimustest kui ka inimõjust (I). Leidsime, et levimispiirangu osatähtsus oli väiksem tugeva keskkonnastressi puhul. Külma ja kuiva piirkondades mõjutas tõenäoliselt abiootiline stress taimede liigilise koosseisu kujunemist rohkem kui levimine. Soojadel ja niisketel aladel oli arvatavasti kohaliku taimestiku biotoiline vastupanu levimisest tähtsam. Varasemalt on rohumaaaladel leitud, et levimispiirang on suurim keskmise produktiivsusega aladel. Meie tulemused näitavad, et see seos kehtib ka Euroopa skaalas. Lisaks leidsime, et levimispiirangu osatähtsus oli väiksem tihedalt rahvastatud ja põllumajanduslikemas piirkondades (I). Seega on inimtegevus Euroopas pigem seemnelevile kaasa aidanud.

Hea levimisvõime aitab liikidel häiringutega paremini toime tulla, ent levimine ei pruugi olla alati parim strateegia. Oma töödes leidsime, et hea levimis-

võimega rohumaaliigid kuulusid suurema tõenäosusega tumedasse elurikkusesse nendes põllumajandusmaastikes, kus tänapäevaste või ajalooliste rohumaade osakaal oli väike (II, III). Hea levimisvõime ei tule seega killustunud maastikes kasuks, kuna kaugemale levides satuvad seemned enamasti kasvuks mittesobilikele aladele. Vältimaks heade levijate ja elurikkuse kadu, on seega väga oluline suurendada liigirikaste elupaikade pindala ja nende omavahelist sidusust tänapäevastes põllumajandusmaastikes.

Levimispiirangu osatähtsus taimede elurikkuse muustrite kujunemisel sõltus ka analüüsitud ruumiskaalast. Kogu uuritava Tartu piirkonna põllumajandusmaastike ulatuses leidsime, et hea levimisvõimega liigid asustasid paremini sobilikke elupaiku. Lisaks soodustas sobilike liikide saabumist suur rohumaade osakaal uurimisala naabruses (III). Levimispiirang oli aga vähetähtsam väiksemas ruumiskaalas, kus kohalikud keskkonnatingimused ja produktiivsus (konkurents) mõjutasid koosluse täielikkust. Seega sõltub erinevate ökoloogiliste protsesside mõju elurikkuse muustrite kujunemisele suuresti uuritud skaalast. Põllumajandusmaastikes tuleks liikide levimise soodustamiseks suurendada killustunud elupaikade sidusust. Domineerivaid taimi piiraks produktiivsetel aladel mõõdukas niitmine või karjatamine, mis ühtlasi aitaks kaasa ka seemnete levimisele.

Meie seemnelisamise katse näitas, et liigifondi ja koosluse täielikkuse mõõdikud suutsid invasioone liigirikkusest paremini ennustada (IV). Saime kinnitust, et seemned asustasid paremini suurema liigfondiga alasid, kus tõenäoliselt olid soodsamad kasvutingimused ja rohkem kasutamata nišše. Täielikumad alad olid jällegi raskemini invadeeritavad (IV). Seega, igasugused häiringud, mis vähendavad koosluste täielikkust võivad aidata kaasa ka soovimatute taimede, näiteks võõrliikide invasioonidele.

Ennustuse kohaselt muutub kliima suurematel lauskraadidel niiskemaks ja soojemaks, mis tõenäoliselt suurendab ka levimispiirangu osatähtsust Põhja-Euroopa hõredalt inimasustatud piirkondades (I). Kuigi mõõdukas põllumajanduslik tegevus üldiselt soosib seemnelevi (I), on elurikkus tänapäeva põllumajandusmaastike killustunud koosluses siiski vaid osaliselt realiseerunud (II, III). Taimede madal elurikkus kahandab tõenäoliselt ka kultuur(taimi) tolmelevate ja taimekahjureist toituvate selgrootute arvukust. Lisaks on vähetäielikud kooslused invasioonidele vastuvõtlikumad, mis võib soodustada võõrliikide levikut (IV). Kuna koosluste täielikkus on olulisel määral sõltuv levimisprotsessidest (II–III), on eriti oluline suurendada elurikaste koosluste pindala meie põllumajandusmaastikes. See soodustaks edukat seemnelevi ja aitaks vältida seemnete levimist kasvuks sobimatutele aladele. Ka mõõdukas karjatamine ja niitmine toetaks seemnelevi erinevate elupaikade vahel.

Käesolev väitekiri näitab, et elurikkuse mustreid tekitavatest protsessidest on võimalik paremini aru saada, kui arvestada ka kooslusest puuduolevate liikide ja nende tunnustega. Teades, milliste alade elurikkus on oodatust väiksem ja millised protsessid piiravad looduse mitmekesisust erinevates ökosüsteemides ja ruumiskaalades, saame teha ka paremaid looduskaitseotsuseid.

ACKNOWLEDGEMENTS

My deep gratitude goes to my supervisor Meelis Pärtel, who kindly agreed to become my supervisor in 2012. I thank him for his endless guidance, encouragement and support. I am very grateful that I had an opportunity to participate in various research projects, conferences and faraway expeditions. Our fabulous international Macroecology workgroup has not only taught me how to do research, but also helped to improve my social skills. I thank the previous and current members of Macroecology team – Krista, Liina, Argo, Marge, Madli, Tõnu, Jon, Rob, Antonio, Ignacio, Sabrina, Auréle, Carlos, Elisabeth, Aveliina, Tsipe, Robert, Ülle, Ene – and the people from neighbouring workgroups – Lena, Jaak-Albert, Inga, Kadri, Guille, Teele – for the fun times we had in and out of office. I thank my friend Riin for giving me such good scientific advice and for helping me to settle into the Macroecology workgroup and the Big Ecology Lab in Sydney, which I was visiting in 2015. I also thank my friend Liis for cheering me up so many times.

Last, but not least, I thank my family – my parents and brother for always supporting me. I thank Tanel for being so excited about my doctoral degree, despite the busy last months.

This research was supported by the Estonian Research Council (grants ETF9031, ETF8613, ETF9223, PUTJD15), by the institutional research funding IUT20–29 of the Estonian Ministry of Education and Research, and by the European Union through the European Regional Development Funds (Centre of Excellence FIBIR and EcolChange). The field trips that initiated the compilation of the dry calcareous grassland data were also financed by grants from the Swedish Inst. Visby Programme (01391/2005) and the Royal Swedish Academy of Agriculture and Forestry.

PUBLICATIONS

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- Riibak, K.**, Bennett, J.A., Kook, E., Reier, Ü., Tamme, R., Bueno C.G. & Pärtel, M. Plant dispersal limitation influencing observed and dark diversity in agricultural landscapes is stronger at larger spatial scales. *Submitted manuscript*.
- Riibak, K.**, Ronk, A., Kattge, J. & Pärtel, M. (2017). Dispersal limitation determines large-scale dark diversity in Central and Northern Europe. *Journal of Biogeography*, 44, 1770–1780.
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- Bennett, J.A., **Riibak, K.**, Kook, E., Reier, Ü, Tamme, R., Bueno, G.C. & Pärtel, M. (2016). Species pools, community completeness and invasion: disentangling diversity effects on the establishment of native and alien species. *Ecology Letters*, 19, 1496–1505.
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Riibak, K., Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Znamenskiy, S., Bengtsson, K., Rosén, E., Prentice, H.C. & Pärtel, M. 2015. Dark diversity in dry calcareous grasslands is determined by dispersal ability and stress-tolerance. *Ecography*, 38, 713–721.

Conference presentations:

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Riibak, K., Ronk, A., Pärtel, M. Dispersal and establishment limitation determine large-scale dark diversity in Central and Northern Europe.

– *Oral presentation* at the 58th IAVS Symposium, 2015, Brno, Czech Republic.

Riibak, K., Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Bengtsson, K., Rosén, E., Znamenskiy, S., Prentice, H.C., Pärtel, M. Dark diversity in dry calcareous grasslands is determined by dispersal limitation and stress-tolerance.

– *Oral presentation* at the 57th IAVS Symposium, 2014, Perth, Australia.

Riibak, K., Pärtel, M. Dark diversity in calcareous semi-natural grasslands: are absent species dispersal limited?

– *Poster presentation* at the 56th IAVS Symposium, 2013, Tartu, Estonia.

Riibak, K., Pärtel, M. Dark diversity in calcareous semi-natural grasslands: are absent species dispersal limited?

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- Riibak, K.**, Bennett, J.A., Kook, E., Reier, Ü., Tamme, R., Bueno C.G., Pärtel, M. Plant dispersal limitation influencing observed and dark diversity in agricultural landscapes is stronger at larger spatial scales. *Käsikiri*.
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– *Stendiettekanne* Rahvusvahelise Taimkatte Assotsiatsiooni (IAVS) 60. sümpoosionil. 2017, Palermo, Itaalia.

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– *Suuline ettekanne* 58. IAVS sümpoosionil. 2015, Brno, Tšehhi.

Riibak, K., Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Bengtsson, K., Rosén, E., Znamenskiy, S., Prentice, H.C., Pärtel, M. Dark diversity in dry calcareous grasslands is determined by dispersal limitation and stress-tolerance.

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Riibak, K., Pärtel, M. Dark diversity in calcareous semi-natural grasslands: are absent species dispersal limited?

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- Teadust populariseerivate töötubade läbiviimine Tartu ülikooli avatud uste päevadel (2016–...).
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