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The relationship between small-scale environmental heterogeneity and plant species diversity

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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

I. Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R. & Pärtel, M. 2010. Environmental heterogeneity, species diversity and coexistence at different spatial scales. *Journal of Vegetation Science* 21: 796–801.
II. Laanisto, L., Tamme, R., Hiiesalu, I., Szava-Kovats, R., Gazol, A. & Pärtel, M. 2013. Microfragmentation concept explains non-positive environmental heterogeneity-diversity relationships. *Oecologia* 171: 217–226.
III. Gazol, A., Tamme, R., Price, J.N., Hiiesalu, I., Laanisto, L. & Pärtel, M. 2013. A negative heterogeneity–diversity relationship found in experimental grassland communities. *Oecologia* 173: 545–555.
IV. Price, J.N, Gazol, A., Tamme, R., Hiiesalu, I. & Pärtel, M. 2014. The functional assembly of experimental grasslands in relation to fertility and resource heterogeneity. *Functional Ecology* 28: 509–519.
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Author's contribution to the publications:

I. had the main responsibility in developing the idea, data collection and analysis as well as manuscript preparation
II. participated in developing the idea and manuscript preparation
III. participated in conducting the experiment, data collection and manuscript preparation
IV. participated in conducting the experiment, data collection and manuscript preparation
V. participated in conducting the experiment and data collection, had the main responsibility in data analysis and manuscript preparation

1. INTRODUCTION

1.1. Theoretical background

Understanding species diversity patterns and coexistence mechanisms is a central topic in ecology (Begon et al. 2009), and has important implications for biodiversity conservation (Margules & Pressey 2000) – in preventing local species loss (Krauss et al. 2010) or global extinctions (Dirzo & Raven 2003). Many mechanisms have been proposed to explain species coexistence, among them, environmental heterogeneity is considered one of the main factors in maintaining species richness in terrestrial plant communities (Tilman & Pacala 1993; Wilson 2011). Environmental heterogeneity is traditionally viewed as a way for species to avoid competitive exclusion by allowing niche differentiation and coexistence of functionally different species (Ricklefs 1977; Shmida & Wilson 1985; Tilman & Pacala 1993; Silvertown 2004; Wilson 2011; Adler et al. 2013). However, the generality of the positive heterogeneity-diversity relationship (hereafter HDR) has been questioned, as several experiments and observational field studies have also found non-significant or negative effects of heterogeneity on plant species diversity (reviewed in Lundholm 2009, see also Eilts et al. 2011; Costanza et al. 2011; Rose & Malanson 2012; Gazol et al. 2012).

Empirical evidence for environmental heterogeneity promoting coexistence comes mostly from studies where heterogeneity is measured at relatively large spatial scales (Stein et al. 2014). Large-scale heterogeneity is expressed as gradients in environmental conditions (e.g. climate, soil, topography, habitat type), and explains turnover in species composition among communities (Wilson 2000). For species coexistence within communities, small-scale heterogeneity due to patchy resource distribution is more important (Wilson 2000; Hutchings et al. 2003). Small-scale resource patchiness impacts directly on plant individuals and species interactions, and is expected to structure communities (Hutchings et al. 2003). Observational and experimental studies at small spatial scales often report non-positive HDRs (e.g. Maestre & Reynolds 2007; Reynolds et al. 2007; Eilts et al. 2011; Rose & Malanson 2012; Gazol et al. 2012). However, compared to large-scale analyses, studies on small-scale HDRs in plant communities are scarce (Lundholm 2009) and the precise mechanisms by which small-scale heterogeneity affects species diversity are not yet clear.

In natural conditions, environmental heterogeneity occurs at different spatial scales (Ettema & Wardle 2002), and coexisting species vary in their sizes (Schenk & Jackson 2002; Hutchings et al. 2003). The effect of small-scale environmental heterogeneity on community structure is predicted to vary depending on whether patchiness occurs at scales larger or smaller than plant individuals (Hutchings et al. 2003). The relative scale of heterogeneity determines whether individuals view the surrounding environment as homo-

geneous (patches larger) or encounter patchiness in resource distribution (patches smaller). Based on the relative size of plants and patches, three predictions can be made for small-scale HDRs.

Environmental heterogeneity occurring at larger scales than plant individuals can promote species coexistence, based on the idea of niche differentiation with species preferring different patch types (Silvertown 2004). Individuals and populations occupy homogeneous patches within heterogeneous conditions and are not affected by heterogeneity. The patches can be considered as sub-communities (Hutchings et al. 2003) that are made of functionally different species depending on their preference for patch type (Questad & Foster 2008; Adler et al. 2013). There is evidence for positive small-scale HDRs in plant communities (Lundholm 2009), but while it is intuitive that niche differentiation should be reflected in functional differences between coexisting species, very few studies have examined this based on traits (Adler et al. 2013).

If patches are still larger than plant individuals, but too small to support viable populations, heterogeneity can have a negative or neutral effect on species diversity (Kadmon & Allouche 2007; Costanza et al. 2011). Within a fixed area, increasing heterogeneity by adding new patch types inevitably results in a decreased area of each patch and isolation of the same patch types. Even if the total area of each patch type remains constant, increasing heterogeneity means fragmentation of patches. Species that prefer a specific patch type, are negatively affected by heterogeneity since it can decrease population size, restrict dispersal between isolated patches and increase extinction rates within subcommunities (Saunders et al. 1991). This process is analogous to habitat fragmentation at the landscape level (e.g. Helm et al. 2006; Krauss et al. 2010). Empirical evidence for this idea at local scales comes from animal studies, for example Tews et al. (2004) reviewed HDRs for animals and found that while habitat heterogeneity provides niche differentiation for some animal groups, it leads to habitat fragmentation for others. Further studies are needed to test this idea and its applicability in plant communities.

Environmental heterogeneity occurring at smaller scales, enabling plant individuals to forage among patches, can reduce species diversity by altering competitive interactions in a community (Hutchings et al. 2003). Many experimental studies have shown that plant species differ in their ability to forage for resources in heterogeneous conditions (reviewed in Hodge 2004; Kembel & Cahill 2005). If some species in a community are better able to forage for resources and outcompete others, the HDR can be negative (Hutchings et al. 2003; Reynolds et al. 2007; Rajaniemi 2010; Eilts et al. 2011). Moreover, communities should be characterised by functionally similar species, since traits associated with good foraging ability are favoured. There is some experimental evidence that species with more effective root foraging behaviour (Fransen et al. 2001; Rajaniemi 2010), or clonal species with extensive rhizomes (Reynolds et al. 2007; Eilts et al. 2011) are advantaged in heterogeneous soils. However, only a few experimental studies have considered how coexisting species differ

in their responses to heterogeneity in plant communities (Wijesinghe et al. 2005; Maestre & Reynolds 2007; Reynolds et al. 2007; Rajaniemi 2010; Eilts et al. 2011). It has been suggested that if all species can forage through the patches, small-scale heterogeneity has no effect on species diversity, as plants are influenced by surrounding average conditions (Tilman & Pacala 1993; Stevens & Carson 2002). However, both resource heterogeneity and availability can impact on plant individuals and community structure in a non-additive way (Maestre & Reynolds 2007).

In natural conditions, species of various sizes coexist, and perceive or respond to heterogeneity in different ways. Therefore, multiple simultaneously occurring mechanisms can determine the HDR in plant communities.

1.2. Objectives of the thesis

The purpose of this thesis was to shed further light on the heterogeneity-diversity relationship (HDR) at small spatial scales and explain the mechanisms behind a negative HDR. We used a meta-analytical approach to study the relationship between spatial scale and the HDR (**I)** and hypothesized that the HDR is positive at larger spatial scales, but negative HDRs become more common when heterogeneity occurs as small-scale patchiness in environmental conditions. We defined mechanisms behind a negative HDR at small spatial scales in paper **I**. Depending on the relative scale of plant individuals and patchiness in environmental conditions, we hypothesized that heterogeneity can decrease species diversity by restricting dispersal between patches (patches larger than plant individuals) or intensifying competitive interactions (patches smaller than plant individuals). We then used a model simulation (**II**) and a greenhouse experiment (**III**, **IV**, **V**) to test these ideas.

The main aims of the thesis were:

1. to describe the small-scale HDR using meta-analytical (**I**), modelling (**II**) and experimental approaches (**III**)
2. to explore the trend of the HDR at different spatial scales of heterogeneity (**I**)
3. to assess the role of dispersal and local stochastic extinctions in HDRs (**I**, **II**, **III**)
4. to assess the role of competition in HDRs (**I**, **III**, **IV**, **V**)
5. to identify characteristics and traits that enable species to take advantage of heterogeneous conditions (**II**, **IV**, **V**)

2. MATERIALS AND METHODS

2.1. Meta-analytical approach

In paper **I**, we used a dataset of previously published experimental and observational heterogeneity studies in plant communities from Lundholm (2009) to examine the heterogeneity-diversity relationship (HDR) at varying spatial scales. To quantify the HDR, we used the standardized difference in mean diversity (between homogeneous and heterogeneous treatments) as the effect size for experimental studies, and Fisher's *Z* (estimated from the correlation coefficient or *P* and *t* values) for observational studies. We used spatial grain as our scale of heterogeneity. This was equal to the patch size in experimental studies, and to average distance between environmental measurements in observational studies. Grain size was $\log_{10}$-transformed for the analyses.

Studies often reported several measures of diversity and heterogeneity. Since these can be correlated and bias statistical tests, we included a single measure of the HDR from distinct treatments (experimental studies) or sites (observational studies). If a study included multiple sites or treatments with varying configurations of heterogeneity, several data points were included. We used the following selection criteria to decide which observations to include from multiple measurements: (1) if studies reported more than one measure of species diversity we selected 'total species richness' (from a few case studies we used 'mean compositional diversity', 'Simpson's diversity index' and 'area–species richness slope' instead); (2) when species diversity was measured at different spatial scales, we included the smallest scale as this was most likely to correspond to the scale at which heterogeneity was measured; (3) of the environmental variables, we selected those measuring heterogeneity of soil topography or soil nutrient content.

We included 23 data points from nine experimental studies, and 46 data points from 29 observational studies in the analyses (Appendix S1 in **I**). In the meta-regression analysis, we excluded observational studies where data for grain size were not available, thus, 35 data points from 19 case studies were included.

We checked both experimental and observational studies for publication bias using funnel plots and Begg and Mazumdar's rank correlation test (Borenstein et al. 2009). We then applied meta-regressions with mixed effects (unrestricted maximum likelihood model) between the HDR and spatial scale of heterogeneity (Borenstein et al. 2009). All analyses were performed separately for experimental and observational studies using Comprehensive Meta-Analysis v.2 (Biostat Inc., USA).

2.2. Modelling approach

In paper **II**, we used the freeware simulation model CAPS, designed to examine multiple processes driving spatial patterns of abundance and diversity of sessile species in heterogeneous landscapes (Plotnick & Gardner 2002; Gardner & Engelhardt 2008). To run a simulation of species dynamics within CAPS, it is necessary to create a habitat map, define species' habitat preferences as well as dispersal and fecundity parameters, and describe a disturbance regime.

For the habitat map, we created 100 × 100-node lattice landscapes combined of two habitat types in a chessboard pattern (see Fig. 1 in **II**). Each node of the lattice represented a homogeneous habitat site of a sufficient size to support a single individual. Different sized patches of habitat type were used to model heterogeneity at various spatial scales, but the overall area of each habitat type was kept constant. We used the following patch sizes: 50 × 50 nodes, 25 × 25 nodes, 10 × 10 nodes, 5 × 5 nodes, 2 × 2 nodes, and 1 × 1 nodes. The probability, that one of the adjacent nodes represented another habitat type, increased with decreasing patch size (0.08%, 0.32%, 2%, 8%, 50%, 100%, respectively). We also varied the temporal scale, using simulation steps of 500, 1000, 3000, 5000 and 10000 units (e.g. years). Each simulation time step represented an independent simulation.

The species pool for all datasets contained 30 species. At the beginning of a simulation, every node was filled with a random individual, but all 30 species were presented in equal probability. Species in the CAPS simulation model can be assigned with different values of habitat preference (niche breadth), relative fecundity and dispersal ability. We kept fecundity constant for all species in each run of the model. Dispersal distance was always one node length *per* each time step and landscapes had wrapped boundaries allowing dispersal 'over the edge' (to eliminate edge effects). We varied species' habitat preferences in four scenarios (scenario 1, 2, 3, 4) and two frameworks (categorical, continuous; see Table 1 in **II**):

- Scenario 1 – only specialists, with 15 species preferring habitat A and the other 15 species preferring habitat B. For categorical species preferences, habitat A species could not survive in habitat B and *vice versa*; for continuous species preferences, habitat A species could also survive (their fitness was 1 out of 9) in habitat B and *vice versa*.
- Scenario 2 – mostly specialists, with 10 species preferring habitat A, 10 species habitat B, and 10 species equally capable of living in both habitat types. For categorical species preferences, habitat A species could not survive in habitat B and *vice versa*, while generalists were equally capable of living in both habitats; for continuous species preferences, habitat A species could also survive (their fitness was 1 out of 9) in habitat B and *vice versa*. Generalist species fitness for both habitats was 8, which was slightly lower than specialist species whose fitness in the preferred habitat was 9.

- Scenario 3 – mostly generalists. This scenario was similar to scenario 2, but contained 20 generalist species, and 5 species preferring habitat A and 5 species preferring habitat B.
- Scenario 4 – only generalists, with all 30 species equally capable of living in both habitats. We only included a categorical framework for this scenario since the continuous framework would have been in essence identical to the categorical framework.

In addition to environmental heterogeneity and species preferences to certain habitats, community diversity was also regulated by random disturbance, which removed 10% of the population at each time step. The empty node was then occupied by the descendant of the species from a neighbouring node that exhibited the best fitness for the habitat type. Only a single individual could occupy each node in the landscape at any point in time. For each unique set of variables (scale of heterogeneity, time, and type of community), we performed ten simulations that differed only by the random initial species distribution. The outcome richness in every set of variables was the average of those ten simulations. Diversity was expressed as Simpson's Reciprocal Index, which has been commonly used in comparable HDR studies (e.g. Lundholm 2009; Smith & Lundholm 2012).

2.3. Experimental approach

2.3.1. Experimental design and sampling

For papers **III**, **IV** and **V**, we conducted a mesocosm greenhouse experiment at the University of Tartu, Estonia between the 15th February and 11th June 2011. The experiment consisted of five treatments (each replicated ten times) including three homogeneous treatments of different levels of fertility (low, medium and high), and two heterogeneous treatments (small- or large-scale patches, see Fig. 1 in **III**).

We used 50 galvanized steel square boxes (25 × 25 × 20 cm) and different combinations of commercial sand and black soil (*Biolan Must Muld*®; N = 100 mg/l; P = 200 m/l; K = 400 mg/l) for growing medium. The low fertility treatment (Low) was created using a 1:4 mixture of soil and sand, the medium fertility treatment (Med) consisted of a 1:1 mixture of soil and sand, and the high fertility treatment (High) was a 4:1 mixture of soil and sand. The small- and large-scale heterogeneity treatments (HetS and HetL, respectively) were created using checkerboard combinations of Low and High treatment mixtures. HetS treatment consisted of 16 6.25 × 6.25 cm patches, while HetS treatment was made of four 12.5 × 12.5 cm patches. The two heterogeneous treatments had the same overall fertility as treatment Med, but varied in their spatial configuration. Quadrats were filled to 5 cm depth with gravel in order to ensure water drainage, and then filled with the respective sand and soil

mixtures. We used a partition separating each quadrat before adding growing medium, but this was removed to allow root growth among soil patches.

We obtained seeds of 15 Northern European grassland species (see Table 2 in **III**) from a commercial supplier (B & T World Seeds, Paguignan C.P. 34210, Aigues-Vives, France). The chosen species resembled a diverse community in terms of plant traits and are known to commonly co-occur in seminatural grasslands (Pärtel et al. 1999). For each replicate box, we ensured at least 32 seeds of each species. To include microbial communities, we mixed 0.5 l of sieved natural grassland soil with the seeds prior spreading the mixture uniformly on top of the growing medium.

For the first 15 days, the boxes were covered with a plastic sheet and watered every other day to aid germination. Growing conditions were full light (18 h light), air temperature 17 °C, relative air humidity 75%, and photosynthetically active radiation 7.98 MJ m^{-2} day^{-1}. Light conditions for each box were measured every 2 weeks after germination until 15 May, with a LI-190SA quantum sensor and LI-250A light meter (LI-COR Biosciences, USA). As a measure of relative photosynthetic active radiation (below/above vegetation), we took four measurements below and one above the vegetation layer in each box. To minimize position effects in the greenhouse, the boxes were rearranged weekly. We randomly selected four quadrats in each box (200 quadrats in total) for subsequent sampling. In the heterogeneous treatments, two of both the low and high fertility quadrats were included. We recorded shoot number for each species in these quadrats every two weeks following germination.

After the experiment had run for 105 days and communities had reached their peak productivity, we recorded species' presence and harvested the aboveground biomass in all quadrats in each box. In the four preselected quadrats, the biomass was collected separately for each species (data used in paper **V**). Additionally, we sampled root biomass in two randomly selected quadrats in each box (in heterogeneous treatments, we ensured that one low fertility and one high fertility quadrat are included). To obtain the root samples, the entire block of soil and roots was removed from the box, and the quadrats were cut and separated from each other. Hence, the soil samples contained the roots of both species rooted in the quadrat and those foraging from neighboring quadrats. Soil samples were air-dried, and roots were carefully separated from the soil. Shoot and root biomass was oven dried at 80 °C for 24 h and weighed (precision = 0.01 g).

For trait measurements in paper **IV**, we obtained plant material of 10 individuals per species from each experimental treatment. In the heterogeneous treatments, 10 individuals were selected from both low and high fertility patches. In some cases, less than 10 individuals were available, and we excluded species from the analysis if less than 5 individuals were found. Following the protocols of Cornelissen et al. (2003), we measured specific leaf area (SLA, the ratio of leaf area to dry weight, mm^2 mg^{-1}), leaf size (mm^2) and plant height (mm). Leaf area was measured as the one-sided projected surface

area from leaf scans using Image-J (Rasband 2014). Leaves were oven-dried at 80 °C for 24 h, and weighed. Plant height was measured to the highest photosynthetically active tissue.

2.3.2. Data analysis

Using data from the mesocosm experiment, we examined how soil resource heterogeneity impacts on taxonomic (**III**) and functional diversity (**IV**), community biomass (**III**), niche overlap (**IV**), and species-specific responses (**V**). We performed analyses at the community (experimental box) and patch level. For the community-level analyses, we used data from all the treatments (HetS, HetL, Low, Med, High) and compared the heterogeneous treatments to each homogeneous treatment following our *a priori* hypotheses specific to each study. In the patch-level analyses, we compared low or high fertility patches within heterogeneous treatments to the homogeneous low or high fertility treatment (respectively) in all of the studies (**III**, **IV**, **V**).

In paper **III**, we used data from all the quadrats to calculate plant diversity, shoot and root biomass, as well as root:shoot biomass ratio. To measure plant diversity, we calculated the inverse of Simpson's dominance index using the number of shoots of each species as a measure of abundance. In the community-level analyses, we used generalized linear models to test the effect of the treatments on the community variables. We then compared both of the heterogeneous treatments to the Med treatment. Additionally, we compared the HetL treatment to the Low and High treatments. In the patch-level analyses, we used mixed-effect models with box identity as a random factor (Zuur et al. 2009), except in the root biomass analysis (since only one sample of low or high fertility quadrat was included *per* box). We included a fixed variance structure among groups to account for the different number of samples (i.e. heterogeneous treatments had half the number of low- or high fertility quadrats than Low or High treatment). The data was tested for homogeneity of variances and normal distribution, and we used Gaussian models with identity link functions in all of the analyses.

To test if there is an indirect effect of soil resource heterogeneity on diversity due to an increase in light competition, we used structural equation modelling (SEM) in paper **III**. To construct our theoretical model, we included plant diversity, shoot biomass, and relative light conditions (measured 21 days before harvesting) of the three treatments that varied in the spatial configuration of resources but had the same overall fertility (i.e. Med, HetL and HetS). The treatments were represented in the model as a composite variable with two dummy indicators, accounting for all three treatments. We hypothesized that heterogeneity can directly impact on species diversity and shoot biomass (competition for soil resources), but also affect diversity indirectly via shoot biomass → relative light availability (light competition) pathway. To assess the overall fit of the model, we used the X^2 statistic and its associated probability

and the root mean square error of approximation (RMSEA) and its associated probability.

To describe the functional composition of the experimental communities in paper **IV**, we used community weighted mean (CWM) trait values (Garnier et al. 2004; Lavorel et al. 2008). CWMs were calculated separately for three traits – SLA, leaf size and plant height, using the following equation (Lavorel et al. 2007):

$$CWM = \sum_{i=1}^{n} p_i trait_i$$

where p_i is the relative abundance of species i, $trait_i$ is the mean trait value of species i, and n is the number of species in an experimental community. Mean trait values were the average of the 10 individuals measured in each treatment for the homogeneous treatments and average of 20 individuals measured in the heterogeneity treatments. Relative abundance for each species was calculated using the number of shoots per box. In addition, CWMs were calculated separately for the low- and high-fertility patches in the heterogeneity treatments, using the average of 10 individuals measured in each patch type ($trait_i$). Mean trait values of leaf size and plant height were log-transformed prior to the calculations of the CWM values.

We further examined functional community assembly in paper **IV**, comparing niche overlap in functional traits among co-existing species to that expected if species are randomly distributed in a community. We used the kernel function method by Mouillot et al. (2005). The estimation of the community-level niche overlap is based on the following three steps (see Mouillot et al. 2005; Mason et al. 2011 for more details):

1. Calculation of the niche space occupied by the population of each species. Using a kernel function, a bell-shaped density distribution is calculated around every trait measurement. Adding together all the distributions for each measurement gives the niche space occupied by the species for a particular functional trait. We calculated the niche overlap of SLA, leaf size and plant height using the measurements of the 10 individuals of each species per treatment. For community-level analysis, 10 measurements were randomly selected from the original 20 measurements in the heterogeneous treatments to keep the number of samples equal.
2. Calculation of niche overlap between each pair of species. Niche overlap is calculated by considering the niche space occupied by both species. The value of the index is 0 when there is no niche overlap and 1 when the two species occupy exactly the same trait space.
3. Calculation of community-level niche overlap. For each trait, community niche overlap is calculated by considering the niche overlap between each pair of species and the proportional abundance of each species in the

community. We calculated the mean niche overlap at the box scale and shoot number was used as a proportional abundance for each species.

For the randomly assembled communities, we simulated the community niche overlap values of SLA, leaf size and plant height by randomizing (10000 permutations) the proportional abundance of the species within the experimental communities (Mason et al. 2011). The mean niche overlap for each trait was calculated as for observed communities (explained above), therefore, the differences between the observed and the simulated niche overlap is attributed to species abundances. Finally, we used the standardized effect size (SES, Gotelli & McCabe 2002) to compare niche overlap in observed communities to that expected by chance:

$$SES = \frac{Obs - Exp}{\sigma_{Exp}}$$

where *Obs* is the observed community-level niche overlap for a trait in each box, *Exp* is the mean value of niche overlap in randomizations and σ_{Exp} its standard deviation.

In paper **IV**, we used one-way ANOVA to compare CWM and SES values for SLA, leaf size and plant height among the treatments, and Tukey's post hoc test for multiple comparisons. In the community-level analyses, we made all pairwise comparisons. In addition to comparing low- or high-fertility patches within heterogeneous treatments to the respective homogeneous treatment in the patch-level analyses, we also compared patches of different fertility level to each other. We also examined the relationship between SES in niche overlap and aboveground biomass using linear regression.

For the species-specific analyses in paper **V**, we used average aboveground biomass data *per* quadrat from the nine most abundant species in the experiment (*Antennaria dioica*, *Briza media*, *Centaurea jacea*, *Cirsium acaule*, *Festuca rubra*, *Hypericum perforatum*, *Plantago media*, *Primula veris*, *Prunella vulgaris*, *Trifolium montanum*, hereafter referred to by genus name) and excluded six species that were in very low numbers in all of the experimental treatments by the time of biomass sampling (*Erophila verna*) or throughout the duration of the experiment (*Anthyllis vulneraria*, *Filipendula vulgaris*, *Galium verum*, *Primula veris*, *Viola rupestris*). Note that species-specific biomass data was collected from four quadrats *per* box (see above). To account for species' survival, we assigned a biomass of 0 to a species that had germinated in the quadrat, but did not survive until the final sampling. All statistical analyses were performed for the nine species separately and we included data from quadrats and boxes where the species under study had established. We tested for homogeneity of variance across treatments using Levene's test (Zar 1999) and $\log_{10}(x+1)$-transformed the data to meet the assumption of normality. We

used simple models with treatment as a fixed factor in the community-level analysis and mixed-effects models with box identity as a random factor in the patch-level analysis. We also included a constant variance function structure to account for the different number of quadrats within treatments (Zuur et al. 2009). We used ANOVA to test the overall effect of treatment on species' responses. We used one-way ANOVA with Welch correction (Zar 1999) for *Antennaria* in the community-level analysis since the data failed to meet the assumptions of homogeneity of variance, and included a heteroskedasticity-consistent covariance matrix estimation for comparisons (Herberich et al. 2010).

Analyses were performed in the R environment (R Core Team 2014). We used the nlme package for fitting the mixed-effects models (Pinheiro et al. 2014) and the multcomp package (Hothorn et al. 2008) for multiple comparisons (**III**, **V**). CWMs (**IV**) were calculated using the *funcomp* function in the FD package (Laliberté & Shipley 2011). Niche overlap (**IV**) was calculated using the function provided by Mouillot et al. (2005), available online (http://www.ecosym.univ-montp2.fr/software/nicheoverlap.R). We used the car package (Fox & Weisberg 2011) for performing Levene's test for homogeneity of variance and the *vcovHC* function from the sandwich package (Zeileis 2004; Zeileis 2006) to include a heteroskedasticity-consistent covariance matrix estimation where necessary (**V**). SEM (**III**) was performed using the IBM SPSS Amos version 19 (Arbuckle 2010).

3. RESULTS

3.1. Heterogeneity-diversity relationship at different spatial scales

We found no evidence for publication bias in experimental (Fig. 1 in Appendix S2 in **I**) or observational heterogeneity-diversity (HDR) studies (Fig. 2 in Appendix S2 in **I**). We found a significant positive effect of grain size on the HDR in experimental (Fig. 1a in **I**) and observational studies (Fig. 1b in **I**). A negative HDR was more common at smaller grain sizes.

3.2. Evidence for a negative heterogeneity-diversity relationship in modeled communities

We found that the relationship between small-scale environmental heterogeneity and species diversity was non-positive in our modeled communities. However, the trend of the HDR depended on the species' characteristics in the community. Communities with only specialist species (Scenario 1) showed mostly unimodal relationships (Fig. 2 in **II**). When a few generalist species were present (Scenario 2), the HDR was mostly negative (Fig. 3 in **II**). In generalist-dominated communities (Scenario 3), heterogeneity had a neutral or negative effect on diversity (Fig. 4 in **II**). In communities with only generalists (Scenario 4), heterogeneity had no effect on diversity (Fig. 5 in **II**).

The HDR also differed depending on the time scale considered and whether a categorical or continuous framework was used (see Online Resource 3 in **II** for more details):

- Scenario 1 – only specialists. For shorter time scales, diversity remains higher and more stable with changing heterogeneity, especially in the continuous framework. Species diversity in the categorical framework almost falls to zero after a peak in medium patch sizes (10 × 10 and 5 × 5 nodes, Fig. 2 in **II**).
- Scenario 2 – mainly specialists. In simulations with 20 specialist and 10 generalist species, the effect of heterogeneity on diversity is negative with shorter time scales and more neutral when using longer time steps. In categorical frameworks, specialists tend to disappear in almost all communities and only generalists survive and attain a stable diversity plateau at smaller patch sizes. In continuous frameworks, species diversity shows a slight peak at 25 × 25 patch size, but then decreases and reaches a plateau by 5 × 5 patch size (Fig. 3 in **II**).
- Scenario 3 – mainly generalists. Overall dynamics are similar to Scenario 2, but since there are more generalist species, the effect of heterogeneity on diversity is more neutral. There is some variation in the continuous frame-

work, with a slight peak in diversity around 25 × 25 and 10 × 10 patch size (Fig. 4 in **II**).

- Scenario 4 – only generalists. There is no effect of heterogeneity on diversity, but diversity depends on the time scale (Fig. 5 in **II**).

3.3. Evidence for a negative heterogeneity-diversity relationship in experimental grassland communities

We found a significant effect of heterogeneity on species diversity, root and shoot biomass as well as their ratio at the community and patch level. In the community-level analysis, plant diversity was lower in the HetS treatment compared to the homogeneous treatment of the same overall fertility, but not for the HetL treatment (Fig. 2a, Table 3 in **III**). Additionally, the HetL treatment did not differ from Low or High treatments (Fig. 2a, Table 3 in **III**). Shoot and root biomass in both HetL and HetS treatments was significantly higher than in Med although the overall fertility was the same (Fig. 2b, c; Table 3 in **III**). Shoot and root biomass in HetL was higher than in treatment Low and lower than in treatment High following an increase in fertility (Fig. 2b, c; Table 3 in **III**). In the patch-level analysis, we found that low fertility quadrats in HetS had lower diversity, but higher shoot and root biomass than quadrats in treatment Low (Fig. 3, Table 4 in **III**). In the HetL treatment, only shoot biomass was significantly higher in low-fertility quadrats in heterogeneous conditions compared to the low fertility homogeneous treatment. There were no differences in diversity or biomass between high fertility quadrats in HetS or HetL and the High treatment.

Results from SEM further indicated that soil resource heterogeneity directly increased shoot biomass, but only had an indirect negative effect on diversity *via* shoot biomass → relative light availability pathway (Fig. 4 in **III**). The model showed a good fit ($X^2 = 2.11$, $P = 0.72$; RMSEA = 0.001, $P = 0.74$) and accounted for 29% of the variation in diversity, 37% in shoot biomass and 80% in relative light. Full details of the SEM results are found in Online Resource 3 in **III**.

3.4. Trait responses to soil resource heterogeneity

We found significant differences in the community weighted mean trait values as well as niche overlap between the treatments (Fig. 2, 3; Appendix S1 in **IV)**. In the community-level analyses, we found that CWM in SLA differed among the fertility treatments, with highest SLA in the medium-fertility treatments (Fig. 2a, Appendix S1 in **IV**). The HetS treatment had lower SLA than the Med treatment, but HetL did not differ from Med. Leaf size and plant height showed

similar patterns and increased with fertility (Fig. 2c, e; Appendix S1 in **IV**). In both heterogeneous treatments, leaves were larger and plants taller than in the homogeneous Med treatment and did not differ significantly from the High treatment.

For SLA, there was greater niche overlap in Low and Med than in the High treatment, and both heterogeneous treatments differed from all homogeneous treatments (Fig. 3a, Appendix S1 in **IV**). Niche overlap in leaf size was significantly greater in High compared to the Low and Med treatments, but heterogeneous treatments only differed from the homogeneous low-fertility treatment (niche overlap was greater in heterogeneous treatments; Fig. 3c, Appendix S1 in **IV**). For plant height, we found that niche overlap was lower in treatment Low compared to all other treatments, and only HetL showed significant differences from Med and High treatment (greater niche overlap in HetL; Fig. 3e, Appendix S1 in **IV**).

In the patch-level analysis, low- and high-fertility patches had significantly different CWM values in SLA and leaf area, with greater SLA in low-fertility patches (Fig. 2b, Appendix S2 in **IV**), and higher leaf area in high-fertility patches (Fig. 2d, Appendix S2 in **IV**). However, CWM values in plant height did not differ between low- and high-fertility patches (Fig. 2f, Appendix S2 in **IV**). We found that CWM values in all traits (SLA, leaf area, plant height) increased with reducing patch size in the Low treatment compared to patches of low-fertility (Low – HetL or Low – HetS; Table 2, Appendix S2 in **IV**). SLA was slightly lower in the high-fertility patches in HetS compared to the High treatment.

Niche overlap in SLA differed significantly between low- and high-fertility patches in heterogeneous conditions (Fig. 3b, Appendix S2 in **IV**), and niche overlap decreased with reducing the patch size in low-fertility patches (Table 3, Appendix S2 in **IV**). In high-fertility patches, niche overlap was greatest in HetS. For leaf area, niche overlap differed between patches of different fertility only in HetS treatment (Fig. 3d, Appendix S2 in **IV**). In low-fertility patches, niche overlap was greatest in HetL treatment, but there were no differences in high-fertility patches (Table 3, Appendix S2 in **IV**). Niche overlap in plant height did not differ significantly between low- and high-fertility patches (Fig. 3f, Appendix S2 in **IV**), but was greater in low-fertility patches within HetL and HetS compared to Low treatment (Table 3, Appendix S2 in **IV**). In high-fertility patches, niche overlap in plant height was significantly greater in HetS compared to High treatment.

We found that SES niche overlap in SLA decreased with increasing productivity, while niche overlap in leaf area and plant height increased (Fig. 4 in **IV**). Hence, in environments with greater light competition, species were more similar in leaf area and plant height, but not in SLA.

3.5. Species-specific responses to soil resource heterogeneity

In the species-specific analyses, we found that five out of the nine analysed species responded to soil heterogeneity at the community level, but this response varied between species and depended on the spatial pattern of heterogeneity (Fig. 1, Table 2 in **V**). *Festuca* had higher aboveground biomass in the HetS treatment compared to the Med treatment (of the same overall fertility), whereas *Antennaria* had significantly lower biomass in both heterogeneous treatments. *Festuca* and *Plantago* showed a strong positive response to patchy resource availability at both spatial scales of heterogeneity, compared to the Low treatment. *Briza* had marginally higher aboveground biomass in HetS and HetL compared to the Low treatment and *Trifolium* had marginally lower biomass in the HetL. *Festuca* was the only species negatively affected by heterogeneity (HetL) compared to the High treatment. Aboveground biomass did not differ between HetS and High treatments for any of the species despite the heterogeneous treatment having lower overall fertility.

In the patch-level analyses, we found that *Briza*, *Festuca* and *Plantago* increased their aboveground biomass within the low fertility patches in both HetS and HetL compared to the Low treatment (Fig. 2, Table 3 in **V**). Additionally, *Prunella* produced more aboveground biomass in the low fertility patches in the HetL compared to the Low treatment. *Antennaria* showed a contrasting pattern, with less aboveground biomass in the low fertility patches in both heterogeneous treatments than in homogeneous low fertility conditions, while *Trifolium* had lower aboveground biomass only in the HetL treatment. *Antennaria* and *Cirsium* were the only species that showed differences in the high fertility conditions, and produced significantly more aboveground biomass in the high fertility patches in the HetS or HetL treatment, respectively, compared to the homogeneous High treatment.

4. DISCUSSION

4.1. Negative heterogeneity-diversity relationship at small spatial scales

We found no evidence for a universal positive heterogeneity-diversity relationship (HDR) in plant communities (**I**) and negative HDRs were more common at small spatial scales (**I, II, III**). In a recent meta-analysis of HDRs across different taxa, Stein et al. (2014) further support our findings by showing that the HDR is positively related to the spatial scale of heterogeneity.

Our results show that classical niche differentiation theory alone cannot account for the varying effects of small-scale soil heterogeneity on community structure, and alternative concepts are needed to account for negative HDRs. The varying trends in the HDR have usually been attributed to confounding factors, most often to resource availability (Lundholm 2009). If heterogeneity occurs at very small spatial scales, all plants can equally forage among the different quality patches and may not respond to heterogeneity *per se,* but to the average surrounding conditions (**I**, Tilman & Pacala 1993). However, results from previous modelling and experimental studies suggest that heterogeneity can have a direct effect on diversity (**I**). In paper **I**, we summarised the findings and ideas from previous small-scale HDR studies to propose two concepts that explain negative HDRs.

If the scale of heterogeneity is larger than individual plant size and species prefer different patch types, increasing environmental heterogeneity can have a negative effect on population dynamics (e.g. dispersal, survival) and lead to a decrease in species diversity. In a fixed area, adding new patch types inevitably decreases the area of each patch (Kadmon & Allouche 2007) or increases isolation among different patches even if the total area of each patch type remains constant. We proposed the term microfragmentation in paper **I** and defined it in paper **II** as follows: *microfragmentation is a community influencing process of changing habitat into a more heterogeneous environment that can have negative effects on diversity through habitat loss and subsequent isolation*.

If the scale of heterogeneity is smaller than individual plant size, heterogeneity can decrease species diversity if some species in a community exhibit strategies that allow them to tolerate or benefit from the patchy resource distribution and gain a competitive advantage in plant communities. In paper **I**, we state this idea as *heterogeneity as a separate niche axis: species differ in their ability to tolerate or benefit from heterogeneous conditions and this impacts on competitive interactions and community structure*.

We used model simulation and a greenhouse experiment to explicitly test the concepts of microfragmentation (**II**, **III**) and heterogeneity as a separate niche axis (**III**, **IV**, **V**), and the results are discussed below.

4.2. Microfragmentation

We found strong evidence for microfragmentation in the model simulation (**II**), where the HDR was often negative but the strength and trend of the relationship depended on other factors (community structure and time-scale). We also found some evidence for microfragmentation in the experimental communities, where patch size was designed to be larger than most plant individuals (12.5 × 12.5 cm), and heterogeneity impacted on species-specific (**V**) and trait responses (**IV**) but we did not find a negative HDR (**III**).

The premise of microfragmentation (and niche theory) is that species sort into different patch types in heterogeneous conditions and patches act as subcommunities (Hutchings et al. 2003). In the model simulation (**II**), we varied species' habitat preferences and included different combinations of habitat-specialists and generalists. We found that the HDR can be negative, unimodal, or neutral depending on the community structure, and whether specialist or generalist species are dominant. In the greenhouse experiment (**III**, **IV**, **V**), all species grew in both patch types, but there were species that were more productive in the high fertility treatment compared to the low fertility homogeneous treatment and *vice versa* (**V**). The differences in plant trait values and niche overlap between homogeneous treatments suggested that patches in heterogeneous conditions should act as distinct subcommunities. Indeed, low- and high-fertility patches differed in their leaf trait values (area and SLA), and niche overlap in SLA. Moreover, heterogeneous conditions were more diverse (less niche overlap) in terms of SLA (**IV**). These results suggest that species had preferences for soil type, but the effects did not scale up to affect species diversity patterns (**III**).

Microfragmentation causes a negative HDR mainly by restricting dispersal between patches. Smaller and more isolated habitat patches support smaller populations with higher vulnerability to stochastic events. Dispersal between habitat patches would allow population dynamics to occur and promote species' persistence in the community (Palmer 1992; Seabloom et al. 2005). In the model simulation (**II**), individuals could disperse only to neighbouring nodes. This simulates short-distance dispersal in herbaceous plant communities where gaps are usually occupied by nearby species that are capable of colonizing very quickly, mainly by clonal dispersal (Otsus & Zobel 2002). Small-scale heterogeneity is expected to have a stronger effect on short-distance dispersal, whereas large-distance dispersal would occur as in homogeneous conditions. Similarly, dispersal in the experiment (**III**) could only occur by clonality since the experiment lasted for one growing season. Failure to find strong evidence for a negative HDR in the experimental community can also be attributed to the short time-scale since the negative HDR becomes more evident in longer time frames (**II**).

Fahrig et al. (2011) emphasized the importance of distinguishing between the effects of compositional heterogeneity (number of patch types) and configura-

tional heterogeneity (spatial arrangement of patch types) on species diversity. Increase in the compositional heterogeneity almost always has a positive effect on species diversity by increasing available niche space (Silvertown 2004) and the community species pool (Zobel et al. 1998; Rose & Malanson 2012), whereas increasing the configurational heterogeneity can have a negative effect on diversity (Palmer 1992; Kadmon & Allouche 2007). Therefore, compositional and configurational heterogeneity can have opposite effects on species diversity and can balance each other out, so different trends of the HDR are not distinguishable (Smith & Lundholm 2012). In the model simulation (**II**), we used two habitat types and varied only their spatial configuration. Hence, we were able to show that species diversity is reduced with decreasing the spatial scale of environmental heterogeneity, even if the number of patch types remains constant. In their analytical models, Kadmon & Allouche (2007) as well as Smith & Lundholm (2012) reported unimodal or negative HDRs even without partitioning the compositional and configurational heterogeneity and suggested that whereas heterogeneity provides more habitat niches for more species, it simultaneously reduces diversity due to a decrease in the area of each habitat type.

In natural conditions, environmental heterogeneity entails both compositional and configurational heterogeneity, and differentiating between them is difficult. In a greenhouse experiment (**III**), we tested microfragmentation in a more natural setting and compared the heterogeneous treatment with larger patch size to homogeneous low or high fertility (same fertility as individual patches in heterogeneous conditions). Therefore, heterogeneity entailed an addition of a new patch type, as well as a decrease in the size, and increase in the isolation of each patch. In this case, we did not find strong evidence for microfragmentation, and species diversity in the heterogeneous treatment did not differ from any of the homogeneous treatments. In a recent observational study, Redon et al. (2014) used forest habitat maps to determine environmental heterogeneity within landscapes and studied its effect on understory species richness. They found a unimodal HDR and suggested that landscape heterogeneity has a positive effect on diversity if it increases the number of habitat patches, but only if the patches are large enough to maintain viable specialist species populations.

The earlier analytical models of the HDRs by Kadmon & Allouche (2007) were criticized by Hortal et al. (2009) who questioned the applicability of the model to natural systems since only habitat specialists were considered. By varying the habitat requirements of the model species, we were able to show that negative HDRs can be encountered whenever there are specialist species among generalist (**II**), but even with only including generalists, we failed to find a positive HDR. Specialist species exhibited much stronger responses to environmental heterogeneity than generalists. This is not surprising since the populations of generalist species that survive in different conditions and are more successful colonisers are expected to better cope with heterogeneous

environments (Tews et al. 2004; Hortal et al. 2009). In nature, both specialist and generalist species co-occur (Cramer & Willig 2005), and depending on the community structure different responses to heterogeneity can be expected.

4.3. Heterogeneity as a separate niche axis

Using a greenhouse mesocosm experiment, we found support for the idea of heterogeneity as a separate niche axis, since the heterogeneous treatment with small patches (6.25 × 6.25 cm) decreased species diversity compared to the homogeneous treatment with the same overall fertility (**III**). Moreover, plants in heterogeneous conditions were more similar in terms of plant height and leaf area (**IV**). The negative HDR found in the experimental communities was due to a tall grass *Festuca* gaining a disproportionate advantage and excluding a small forb *Antennaria* in competition (**V**). Similar results have been reported in previous experimental studies (e.g. Baer et al. 2004; Reynolds et al. 2007; Eilts et al. 2011), where soil resource heterogeneity promoted the dominance of rhizomatous or clonal species and decreased species richness. In our experiment, the species that showed positive responses to soil resource heterogeneity (*Festuca*, *Plantago*, *Briza*) were also the ones that dominated the communities in terms of aboveground biomass (see Table 1 in **V**) and had higher plant height and leaf size (see Table 1 in **IV**). In contrast, species that were disadvantaged in heterogeneous conditions, *Antennaria* and *Trifolium*, were characterised by being subordinates in all of the treatments (see Table 1 in **V**) and *Antennaria* was also one of the smallest plants in our experimental communities (see Table 1 in **IV**). The mechanisms that allow some species to benefit from soil resource heterogeneity are related to root foraging (Hutchings et al. 2003). Although we did not measure root foraging directly, plant size (both shoot and root biomass) is found to be correlated with root foraging scale in grassland species (Rajaniemi & Reynolds 2004), suggesting that plant aboveground biomass is a good indicator of species' root responses as well as its competitive ability (Grime 1973). Therefore, species that showed positive biomass responses to heterogeneity most likely had an advantage in locating roots in resource-rich patches and depleting them from resources, leading to asymmetric belowground competition (Schwinning & Weiner 1998).

Resource-rich patches in heterogeneous conditions are expected to become hotspots for species interactions since many species compete for resources in a smaller area than in equivalent homogeneous conditions (Hutchings et al. 2003), whereas low-fertility patches are predicted to act as safe sites from intense competition, benefitting subordinate species in the long-term (Fransen & de Kroon 2001; Day, Hutchings, & John 2003a; Day, Hutchings, & John 2003b; Hutchings et al. 2003). However, if some species can rapidly access resource-rich patches belowground and grow taller, smaller species may be excluded from low-fertility patches due to light competition (Wilson 2000;

Hutchings et al. 2003; Lamb et al. 2009). The high-fertility patches in heterogeneous treatments did not differ from the high-fertility homogeneous treatment in terms of species composition (**III**, **V**), community biomass (**III**), functional diversity or mean trait values (**IV**), suggesting that competitive interactions were similar in heterogeneous and homogeneous treatments. However, we found that low-fertility patches were characterized by more intense light competition in heterogeneous conditions. Soil heterogeneity had an indirect negative effect on species diversity (**III**) by increasing aboveground biomass of larger dominant species (*Briza*, *Festuca*, *Plantago*) and decreasing light availability for subordinates (*Antennaria* and *Trifolium*, **V**). Moreover, in environments with higher community productivity, species were more similar in leaf area and plant height indicating a more intense competition for light (**IV**).

Although we expected the concept of heterogeneity as a separate niche axis to apply for the heterogeneous treatment with smaller patch sizes (6.25 × 6.25 cm), we found some evidence for heterogeneity altering competitive interactions also in the heterogeneous treatment with larger patch sizes (12.5 × 12.5 cm). Heterogeneous conditions with larger patch size were more productive in terms of community biomass (**III**), and showed similar functional composition (**IV**) and species-specific responses (**V**) to the heterogeneous treatment with smaller patch size. These results indicate that even with the larger patch size some species were able to rapidly access patchily distributed resources causing changes in some aspects of plant community structure.

5. CONCLUSIONS

Environmental heterogeneity is a common feature in natural habitats and occurs at different spatial scales. Large-scale heterogeneity promotes the coexistence of different plant communities, whereas small-scale heterogeneity directly impacts on plant populations and individuals, and has varying effects on community structure.

The results of this thesis shed further light on the small-scale heterogeneity-diversity relationship (HDR), and describe negative HDRs in observed (**I**), experimental (**I**, **III**) and modeled plant communities (**II**). In a meta-analysis of previously published heterogeneity-diversity studies we found that negative HDRs are more common at smaller spatial scales (**I**). Moreover, in a model simulation (**II**) and greenhouse experiment (**III**), we detected negative or neutral small-scale HDRs.

We compiled evidence from previous model simulations and heterogeneity experiments, and defined two clear mechanisms by which small-scale heterogeneity can have a direct negative effect on species coexistence (**I**). Depending on the relative spatial scale of heterogeneity and plant individuals, we proposed the ideas of heterogeneity as (1) microfragmentation – a community influencing process of changing habitat into a more heterogeneous environment that can have negative effects on diversity through habitat loss and subsequent isolation, or (2) separate niche axis – species differ in their ability to tolerate or benefit from heterogeneous conditions and this impacts on competitive interactions and community structure.

Microfragmentation explained the results from our model simulation (**II**) where varying sets of species were modeled at different scales of heterogeneity (different patch sizes). Our results show that environmental heterogeneity can reduce community diversity, by restricting dispersal and increasing local extinctions. We did not find strong evidence for microfragmentation in the greenhouse experiment, as species diversity in the heterogeneous treatment (where patch size was designed to be larger than most plants) did not differ from homogeneous treatments (**III**). However, patches within heterogeneous treatments differed from each other in terms of leaf trait values (**IV**), and species' preference for soil type (**V**).

The idea that environmental heterogeneity decreases diversity through competitive exclusion was supported in the greenhouse experiment (**III**, **IV**, **V**). Species diversity (**III**) and functional trait diversity (**IV**) were lower in the heterogeneous treatment (where patch size was designed to be smaller than most plants) compared to homogeneous conditions. Environmental heterogeneity benefitted some species, but some were excluded in competition (**IV**, **V**).

Environmental heterogeneity had varying impacts on different species in a community. Heterogeneity as microfragmentation affected more strongly specialist than generalist species (**II**). If foraging between patches was possible,

heterogeneity benefitted larger dominant species, but smaller subordinates were disadvantaged (**IV**, **V**).

The varying effects of environmental heterogeneity on plant communities has received little attention in plant ecology, yet ubiquitous small-scale heterogeneity can have important impacts on different aspects of community structure. Since plant growth, dispersal, survival, species interactions and species composition in heterogeneous conditions may not be comparable to those found in a homogeneous environment, considering small-scale heterogeneity in future ecological studies is important. Moreover, as heterogeneous conditions do not necessarily support higher species diversity, understanding the mechanisms behind a negative HDR can help to predict future changes in plant communities and aid conservation decisions.

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SUMMARY IN ESTONIAN

Keskkonna heterogeensuse ja taimede mitmekesisuse seos väikesel ruumiskaalal

Elusloodus mitmekesisuse hoidmine on üks olulisemaid eesmärke looduskaitses ning liikide kooseksisteerimist mõjutavate tegurite väljaselgitamine on paelunud ökolooge läbi aegade. Ruumiline varieerumine keskkonnatingimustes ehk keskkonna heterogeensus on üks neist teguritest, mis üldlevinud arusaama järgi suurendab liigilist mitmekesisust looduses. Seda positiivset heterogeensuse-mitmekesisuse seost seletatakse enamasti nišiteooria abil – keskkonna heterogeensus lubab paljudel erinevate nõudlustega liikidel leida oma nišš või koht koosluses, soodustades nii liikide kooseksisteerimist. Keskkonna heterogeensus on eriti oluline taimekooslustes, mis on eluta keskkonna poolt enim mõjutatud, kuid mitmed eksperimendid ja vaatlused looduses on näidanud, et heterogeenses keskkonnas taimede liigiline mitmekesisus hoopis väheneb.

Milliseks kujuneb heterogeensuse-mitmekesisuse seos taimekoosluses, sõltub eelkõige heterogeensuse ruumiskaalast. Kui heterogeensus esineb suures ruumiskaalas keskkonnatingimuste (nt. kliima, muld, topograafia) gradiendina ning ala koosneb erinevatest elupaikadest, siis leiab alalt ka palju erinevaid taimeliike. Koosluste sees on taime jaoks olulised keskkonnatingimused ja -ressursid laiguliselt jaotunud ka väikesel skaalal. Selline väikeseskaalaline heterogeensus, näiteks mulla toitainete või valgustingimuste jaotuses, on taimekooslustes tavaline nähtus. Väikeseskaalaline heterogeensus mõjutab taimepopulatsioone, liikidevahelisi suhteid ja isendite kasvu ning võib seeläbi koosluse liigilist mitmekesisust nii suurendada kui ka vähendada. Väikeseskaalalise heterogeensuse mõju taimekooslustele on aga siiani vähe uuritud.

Olenevalt heterogeensuse ruumiskaalast ja taimeisendite mõõtmetest, võib keskkonna heterogeensus avaldada mitmekesisusele mõju kolmel viisil: (1) vastavalt nišiteooriale soodustab keskkonna heterogeensus taimede mitmekesisust, kui heterogeensust moodustavad laigud on suuremad kui isendid ja erinevad liigid eelistavad erinevaid keskkonnalaike; (2) sarnaselt maastikuskaalal toimuvale elupaikade killustumisele võib keskkonna heterogeensus vähendada liigilist mitmekesisust, kui laigud muutuvad väiksemaks ja üksteisest rohkem eraldatuks (kuid on siiski suuremad kui taimeisendid), vähendades populatsioonide elujõulisust ja piirates levimist; (3) keskkonna heterogeensus võib vähendada taimede mitmekesisust, kui heterogeensus esineb väga väikesel skaalal selliselt, et taimeisendite juured või maapealsed võsud ulatuvad läbi erinevate keskkonnalaikude ning osad taimeliigid saavad sellistes tingimustes paremini hakkama ja võidavad liikidevahelises konkurentsis.

Võrreldes suureskaalaliste uurimustöödega on heterogeensuse-mitmekesisuse seost väikesel skaalal siiani vähe uuritud ning negatiivse seose selgitamine pälvinud vähe tähelepanu. Käesolevas töös näitan väikeseskaalalise keskkonna heterogeensuse olulisust taimekooslustes. Töö peamised eesmärgid olid:

1. kirjeldada heterogeensuse-mitmekesisuse seost, kasutades varasemate tööde meta-analüüsi (**I**) ning andmeid simulatsioonimudelist (**II**) ja kasvuhoonekatsest (**III**);
2. uurida, kuidas heterogeensuse-mitmekesisuse seos sõltub ruumiskaalast (**I**);
3. uurida, kuidas heterogeensus mõjutab levimist ja seeläbi heterogeensuse-mitmekesisuse seost (**I**, **II**, **III**);
4. uurida, kuidas heterogeensus mõjutab liikidevahelist konkurentsi ja seeläbi heterogeensuse-mitmekesisuse seost (**I**, **III**, **IV**, **V**);
5. välja selgitada, milliste tunnustega liigid on heterogeensetes tingimustes eelistatud (**II**, **IV**, **V**).

Kõik väitekirja kaasatud tööde tulemused näitasid, et keskkonna väikeseskaalalisel heterogeensusel on oluline mõju taimekooslustele (**I**, **II**, **III**, **IV**, **V**) ning enamasti on väikeseskaalalise heterogeensuse ja taimede mitmekesisuse seos negatiivne (**I**, **II**, **III**).

Kasutades varasemate eksperimentide ja vaatluste uurimistulemusi meta-analüüsis, leidsime, et negatiivne heterogeensuse-mitmekesisuse seos on tõenäolisem just väikesel ruumiskaalal (**I**). Töös **I** defineerisime kaks selgitust negatiivsele heterogeensuse-mitmekesisuse seosele. Nagu eespool kirjeldatud, mõjub keskkonna heterogeensus pigem levimisele ja taimepopulatsioonide püsimisele või liikidevahelistele suhetele olenevalt sellest, kas heterogeensust moodustavad keskkonnalaigud on taimeisenditest suuremad või väiksemad. Kui keskkonna laigulisus esineb suuremal skaalal kui taimeisendid, siis võib heterogeensus avaldada mitmekesisusele negatiivset mõju, vähendades populatsioonide elujõulisust ja taimede levimist. Me selgitame sellist negatiivset heterogeensuse-mitmekesisuse seost *mikrofragmenteerumisega,* mis tähendab, et *keskkonna heterogeensusega kaasneb elupaigalaikude vähenemine ja üksteisest eraldumine, mis avaldab kooslustele negatiivset mõju*. Kui aga keskkonnalaigud on taimeisenditest väiksemad, võib heterogeensus vähendada taimede mitmekesisust, mõjutades liikidevahelise konkurentsi. Sellisel juhul on *heterogeensus kui eraldi nišitelg – kuna taimeliigid taluvad väikeseskaalalist heterogeensust erinevalt, mõjutab see liikidevahelist konkurentsi ja koosluste struktuuri*. Järgnevalt kasutasime simulatsioonimudelit (**II**) ning kasvuhoonekatset (**III**, **IV**, **V**), et testida heterogeensuse kui mikrofragmenteerumise ja eraldi nišitelje ideid.

Simulatsioonimudeli abil näitasime, et keskkonna tingimuste järk-järguline fragmenteerumine (heterogeensuse suurenemine) enamasti vähendas liigirikkust, sest levimine oli piiratud (**II**). Heterogeensuse-mitmekesisuse seos sõltus ka teistest mudelis seatud tingimustest (nt. koosluste algne liigiline koosseis, simulatsiooni ajaline pikkus), kuid ei olnud kunagi positiivne. Kasvuhoonekatse tulemused näitasid, et mõned liigid tõepoolest eelistasid üht mullakeskkonda teisele (**V**) ja samuti erinesid taimed eri tüüpi mullalaikudes mõningate tunnuste poolest (**IV**) nagu mikrofragmenteerumise (ja nišiteooria) puhul eelduseks. Samas, taimeliikide mitmekesisus ei erinenud heterogeense ja

homogeense mullatöötluse vahel, kuigi heterogeenne keskkond koosnes sellise mõõtmetega laikudest, mis eelduste kohaselt olid suuremad kui taimeisendid.

Tulemused kasvuhoonekatsest andsid kinnitust ka heterogeensuse kui eraldi nišitelje ideele (**III**, **IV**, **V**). Võrreldes homogeensete tingimustega, oli nii taimeliikide (**III**) kui ka taimetunnuste (**IV**) mitmekesisus väiksem heterogeenses keskkonnas, kus mullalaigud olid taimeisendi mõõtmetest väiksemad. Mõned liigid said heterogeenses keskkonnas paremini hakkama kui teised (**V**). Näiteks kõrreline *Festuca rubra* kasvas paremini just heterogeenses keskkonnas, aga (meie katses) väikesekasvuline rohund *Antennaria dioica* peaaegu kadus kooslusest. Varem on arvatud, et selline väikeseskaalaline heterogeensus mullatingimustes vähendab liigirikkust eelkõige läbi juurekonkurentsi, sest taimeliigid võitlevad toitainete pärast toitainerikastes mullalaikudes. Meie töös selgus, et konkurents võib toimuda ka valguse pärast. Liigid, mis läbivad kiiresti erinevaid mullalaike jõudmaks toitainerikaste tingimusteni, kasvavad suuremaks terves koosluses (nii toitainerikastes kui ka toitainevaestes laikudes; **IV**, **V**). Seega vähendavad need liigid valguse kättesaadavust samuti terves koosluses ja toitainevaesed mullalaigud ei paku väiksematele liikidele isegi ajutist varjupaika konkurentsi eest (**III**, **IV**, **V**).

Kuna taimekooslustes kasvavad koos erinevate tunnustega liigid, siis ei mõjuta keskkonna heterogeensus kõiki liike ka päris ühtmoodi. Kui heterogeensust moodustavad keskkonnalaigud on taimeisenditest suuremad, siis mõjutab heterogeensus pigem elupaigaspetsialiste, kuid mitte selliseid liike, mis on võimelised igal pool kasvama (**II**). Kui keskkonnalaigud on taimeisenditest väiksemad, soodustab heterogeensus suurekasvulisi ja konkurentsivõimelisi taimeliike, kuid vähendab väikeste ja konkurentsis allajäävate liikide ellujäämisvõimalust (**IV**, **V**).

Kuigi keskkonna väikeseskaalaline heterogeensus on seni vähe tähelepanu pälvinud, on see looduses pigem reegel kui erand ja mõjutab otseselt taimepopulatsioone ja -isendeid (**I**). Käesoleva töö tulemused kinnitasid, et väikeseskaalaline heterogeensus avaldab taimede mitmekesisusele enamasti negatiivset mõju (**I**, **II**, **III**), kuid erinevate tunnustega liigid reageerivad heterogeensusele erinevalt (**II**, **IV**, **V**). Keskkonna väikeseskaalalise heterogeensuse mõju taimekooslustele peaks arvesse võtma ka looduskaitseliste otsuste tegemisel – vastupidiselt üldlevinud arusaamale ei taga heterogeensus alati koosluste elurikkust.

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2012, 2013, 2014	Maateaduste ja ökoloogia doktorikooli välissõidutoetused
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