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INGA HIIESALU

Belowground plant diversity and coexistence patterns in grassland ecosystems

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications that are referred to in the text by Roman numerals:

I **Pärtel M, Hiiesalu I, Öpik M, Wilson SD. 2012**. Below-ground plant species richness: new insights from DNA-based methods. *Functional Ecology* **26**: 775–782.

II **Hiiesalu I, Öpik M, Metsis M, Lilje L, Davison J, Vasar M, Moora M, Zobel M, Wilson SD, Pärtel M. 2012**. Plant species richness below-ground: higher richness and new patterns revealed by next generation sequencing. *Molecular Ecology* **21**: 2004–2016.

III **Hiiesalu I, Pärtel M, Davison J, Gerhold P, Lilje L, Metsis M, Moora M, Öpik M, Vasar M, Zobel M**. Primary productivity in natural grassland is related to the belowground diversity of plants and mycorrhizal fungi. Manuscript.

IV **Price JN, Hiiesalu I, Gerhold P, Pärtel M. 2012**. Small-scale grassland assembly patterns differ above and below the soil surface. *Ecology* **93**: 1290–1296.

The author contributed to developing the idea and experimental design (I, II, III, IV), molecular analysis (II, III, IV), data analysis (II, III), interpretation of the results and writing the papers (I, II, III, IV). The author was responsible for leading experimental design and data collection (II, III, IV), data analysis (II, III) and writing the papers (II, III).

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1. INTRODUCTION

Biodiversity patterns and functioning of ecosystems are central topics in both theoretical and experimental ecology (Huston, 1994). Our current understanding about plant species diversity and coexistence is almost entirely founded upon empirical studies of aboveground vegetation. However, the majority of biomass production occurs belowground in many widespread ecosystems; 50–90% in grassland, steppe, tundra and desert (Stanton, 1988; Jackson et al., 1997). This belowground component of vegetation contributes importantly to biodiversity and ecosystem processes, but it is unclear whether the current understanding of these processes based on aboveground communities also hold true for the large belowground portion.

Studies of plant belowground communities were previously inhibited by methodological constraints: generally the roots and rhizomes of different species are morphologically indistinguishable. Thus, previous methods have included laborious and time-consuming excavation of root systems in order to trace their linkage to aboveground parts (Wildova, 2004). New DNA-based techniques allow identification of roots and rhizomes in field samples (Frank et al., 2010; Kesanakurti et al., 2011; Jones et al., 2011), although certain methodological challenges remain. Challenges include the ability of particular marker regions to discriminate between taxa, the effectiveness of primers in amplifying a range of taxa and the correspondence between taxon biomass and sequence read abundance (**I**). Once these challenges are met, and as studies measuring belowground richness and abundance start to accumulate, major differences in above- and belowground community patterns are likely to emerge, especially in vegetation types where belowground productivity dominates. We expect this new information to have a great impact on our understanding of mechanisms governing coexistence of plant species and their interactions with organisms from other trophic levels (e.g. bacteria, fungi).

There are several lines of indirect evidence that support the notion that belowground richness exceeds that aboveground. First, most perennial plants have belowground storage organs and meristems that allow short- or long-term dormancy for up to decades without producing aboveground shoots (Klimesova & Klimes, 2007; Reintal et al., 2010). Second, roots and rhizomes tend to be laterally more wide-spread than aboveground plant parts (Schenk & Jackson, 2002) resulting in greater belowground overlap with other individuals and species. Third, the diverse nature of the soil environment including its variety of heterogeneous soil resources (Hutchings & John, 2004) and the abundance of soil symbiotic micro-organisms (Bever et al., 2010) may lead to higher richness belowground. Fourthly, relatively more symmetric belowground competition for nutrients compared with asymmetric aboveground competition for light (Weiner, 1990) might allow more species to coexist belowground.

Thus, roots, rhizomes and belowground meristems can survive during unfavourable environmental conditions, seasons and years in the absence of

aboveground shoots, in a state called vegetative dormancy (Shefferson et al., 2005). Shoots may be missing in one year but present in another, resulting in >30 % of turnover in aboveground richness between years (Pärtel & Zobel, 1995; Wilson & Tilman, 2002). Consequently, the average aboveground species richness within years stays the same, but the cumulative number of species observed in an area over several consecutive years increases – a phenomenon referred to as the 'Carousel Model' (van der Maarel & Sykes, 1993). Originally this was explained by short longevity of plant individuals (van der Maarel & Sykes, 1993), but many species persist belowground and produce aboveground shoots only during some years (Wilson & Tilman, 2002). Missing species could be detected through repeated aboveground inventories over many consecutive years, but this method could not separate real changes in species composition from the temporary absence of dormant species. An advantage of belowground measurements is that a relatively short-term single-year study can detect all members of the community. It could be assumed that differences in above- and belowground richness are greatest at the plant neighborhood scale measured. However, belowground richness may still exceed aboveground at community scale, if the process influencing dormancy act at that scale.

The belowground parts of most terrestrial plants form tight associations with arbuscular mycorrhizal fungi (AMF), which play a key role in plant nutrient uptake and have been linked both to plant diversity and primary production (van der Heijden et al., 1998; Maherali & Klironomos, 2007). However, most studies report results from manipulated experiments and our knowledge about plant-AMF diversity relationships and how the interaction between trophic level relates to plant productivity in natural ecosystems is very limited. I know of one such study from a natural plant community which found a positive relationship between AMF spore richness and aboveground plant richness (Landis et al., 2004). As spore identification can underestimate taxa that do not establish in a pot culture or rarely sporulate (Sanders, 2004), this relationship needs to be confirmed based on identification of AM taxa directly from roots using molecular methods.

Previous knowledge about how above- and belowground richness vary with increasing sample size is very limited. One of the most commonly observed relationships in ecology is that species richness increases with increasing sample size (Williamson, 2003). However, DNA-based methods are likely to reveal new information about species-diversity relationships. It can be assumed, that the rate of increase in richness with sample area is greater belowground compared with aboveground, because belowground species richness is a much more complete measure of plant species actually present in a community.

Belowground and aboveground plant richness may also respond differently to environmental gradients. The unimodal relationship between aboveground plant richness and habitat productivity (often measured as soil fertility) is among the most well-known patterns in temperate herbaceous communities (Grime, 1979). At very low soil fertility, both above- and belowground richness

should be relatively low due to the small size of the species pool (Zobel & Pärtel, 2008), which includes the few species that are able to survive harsh conditions. As soil fertility increases the species pool may be larger, but eventually competition for light starts to reduce aboveground richness. In fertile habitats asymmetric light competition is the main cause of competitive exclusion (Weiner, 1990). This means that larger plants gain a disproportionate share of the limiting resource (light), thereby increasing size differences which potentially results in exclusion of smaller plants. It can be hypothesized however that belowground richness is less affected by competitive exclusion resulting from increased soil fertility. In contrast to competition for light, soil resource competition is size-symmetric, and thus less likely to cause competitive exclusion belowground (Cahill & Casper, 2000).

Previous studies have shown that high biodiversity is important in maintaining the functions of grassland communities (Naeem et al., 1994; Tilman et al., 1996). The positive effect of biodiversity on primary productivity can be explained by niche complementarity, whereby plant communities with high diversity, incorporating different functional groups, are able to access resources more completely and generate greater net primary productivity than less diverse communities. Although species diversity is proposed to be linked to plant primary productivity (Tilman, 1999), previous studies have not accounted for the diversity of roots and rhizomes. Biodiversity can also be characterized using measures of phylogenetic diversity, which reflects the variety of different evolutionary lineages present in a community (Faith, 1992). The effect of phylogenetic diversity on primary productivity can be stronger than that of traditional species diversity of plants (Tilman et al., 1997; Cadotte et al., 2009; Flynn et al., 2011), and AM fungi (Maherali & Klironomos, 2007) because a greater variety of evolutionary lineages and traits could allow more complete access to available resources, thus contributing to higher biomass.

Above- and belowground plant communities may differ in the processes that govern species assembly. Plant community assembly rules can be viewed as biotic or abiotic processes by which species from the regional species pool are filtered to the local community (Keddy, 1992). Assembly rules are typically studied by inferring mechanisms from observed patterns of community composition, assuming that various processes leave different imprints. Non-random patterns are usually interpreted as evidence for deterministic assembly processes (biotic or abiotic processes), whereas random patterns are attributed to stochastic or dispersal-based assembly processes. A recent review found limited evidence for deterministic assembly rules (Götzenberger et al., 2012). Almost all studies on plant community assembly rules have been conducted using only aboveground data, due to the methodological difficulties associated with identifying belowground plant parts. However, belowground communities might provide new insights into assembly processes because they encompass all species coexisting in a community. One way in which assembly rules might differ above- and belowground relates to the relative symmetry of competitive

interactions. Aboveground communities are usually shaped by asymmetric competition, whereas belowground competition is size symmetric (Weiner, 1990). These interactions should leave different imprints on community composition. To date, there are only two studies on belowground assembly rules, reporting mixed results (Frank et al., 2010; Kesanakurti et al., 2011). These studies, however, did not directly compare above- and belowground communities.

The following main research hypothesis of the thesis were:

- 454 sequencing technique is suitable for measuring belowground plant richness and abundance from bulk root samples (**II**)
- Belowground plant richness exceeds aboveground at various spatial scales (**I**, **II**)
- AMF diversity (taxon and phylogenetic diversity, and phylogenetic dispersion) is positively related to the respective plant diversity measures and is more strongly related to belowground than to aboveground plant diversity measures (**III**)
- Above- and belowground plant richness respond differently to soil fertility (**I**, **II**)
- Total grassland primary productivity, including above- and belowground biomass, is positively related to both plant species and AMF taxon diversity (**III**)
- Patterns of plant community assembly differ above- and belowground, with biotic interactions playing more important role aboveground than belowground (**IV**)

2. MATERIALS AND METHODS

2.1. Study sites and sampling

Studies were conducted at two temperate grassland sites on different continents. The study site for paper **II** was a 2-ha diverse mesophytic grassland in south-eastern Estonia (Põlva County, 58˚06´N; 27˚04´E). Data collected for paper **II** was also used in paper **IV**. The soil at the study site is predominantly sandy with a pH (KCl) of 4.6–5.2. Average aboveground biomass is 325 g m^{-2}. The most common plant species at the site are *Galium boreale* L., *Geranium pratense* L., *Elymus repens* (L.) Gould, *Festuca rubra* L., *Knautia arvensis* (L.) Coult., and *Veronica chamaedrys* L. The grassland is mowed once per year and the hay removed. The study site for paper **III** was a ca 2-ha site near the northern edge of the Great Plains, at White Butte Recreational area (50° 28´ N, 104 °22´ W), 20 km east of Regina, Saskatchewan, Canada. Vegetation in the area is a combination of native mixed-grass prairie, dominated by *Stipa comata* Trin. & Rupr., *Carex eleocharis* L.H.Bailey and *Bouteloua gracilis* Lag. with patches of the shrub *Symphoricarpos occidentalis* Hook. (Pärtel & Wilson, 2002).

At both sites, sampling locations were arranged contiguously along ten randomly-placed 1-m long transects (separated from one another by at least 10 m), with ten samples per transect, resulting in 100 samples. Sample volumes (10 × 10 cm, 10 cm high) were identical above and below the soil at each location. Aboveground species richness was determined by identifying all vascular plant species in each sample. This included species that were rooted in samples, as well as species that occurred in the sample volumes but were rooted elsewhere (mean 0.5 species per sample). Belowground plant (papers **II, III**) and AMF (paper **III**) species richness was measured from roots in soil samples of the same dimensions as were used to measure aboveground richness (10 × 10 × 10 cm) and located directly below the corresponding aboveground samples. The litter layer was removed, roots were sieved from soil and dead roots were removed on the basis of color and physical appearance (Gregory, 2006). In paper **II**, soil fertility was determined by measuring total nitrogen (N) content (Kjeldahl method) adjacent to each transect. In paper **III**, primary productivity was measured by collecting the biomass of shoots and roots of each sample volume (0.001 m^3), biomass was dried and weighed. In both papers **II** and **III**, roots of each sample were crushed using liquid nitrogen, mixed, and a subsample was used for molecular analysis.

2.2. Molecular analysis

Belowground plant species (papers **II**, **III**) and AMF taxa (paper **III**) were identified using 454 pyrosequencing technique. Root subsamples were pulverized with steel beads and DNA was extracted. In papers **II** and **III**, plant chloroplast *trn*L (UAA) gene sequences were amplified using the primers *c* and

d (Taberlet et al., 1991). In paper **III**, Glomeromycota nuclear SSU rRNA gene sequences were amplified from the root DNA extracts of the same study using the primers NS31 and AML2 (Simon et al., 1992; Lee et al., 2008). In order to identify reads originating from different samples, a set of 8-base-pair bar-codes designed following Parameswaran et al. (2007). PCR was conducted in two steps: in the first PCR reaction PCR primers were linked to bar-codes and partial 454-sequencing adaptors A and B; in the second reaction the full 454-adaptors A and B served as PCR primers, completing the full 454-adaptor+bar-code+PCR primer. Resultant DNA mixes were subjected to sequencing on a Genome Sequencer FLX System, using Titanium Series reagents (Roche Applied Science) at GATC Biotech (Constanz, Germany).

In order to identify plant 454 sequences in papers **II** and **III**, a custom-made *trn*L(UAA) intron sequence reference database was compiled from three sources: (i) plants sampled at the study sites and sequenced using Sanger sequencing; and sequences from species occurring in the study systems or closely related taxa that were (ii) available in GenBank; or (iii) generated by the EcoChange Project (EU FP6 Integrated Project EcoChange). Plants collected from the study systems and its surroundings were identified and stored as vouchers.

In paper **II**, we tested the ability of 454 sequencing to detect the presence and abundance of plant species by preparing eight mixtures of roots with 2–5 species from a natural grassland site. The following species were used in the test mixtures: *Solidago missouriensis* Nutt., *Heterotheca villosa* (Pursh) Nutt. ex DC., *Artemisia frigida* Willd.**,** *Erysimum altum* (Ahti) Tzvelev and *Agropyron cristatum* (L.) Gaertn. We varied the proportion of biomass of added species (range: 10−90%) in order to determine whether sequencing could be used to measure species abundances in mixtures, potentially allowing the calculation of species diversity and evenness in addition to richness.

2.3. Bioinformatical analysis

Plant and AMF sequences were subjected to quality control prior to inclusion in subsequent analyses. Only samples that yielded at least six (paper **II**) or 10 (paper **III**) sequences were analysed further. Since the chloroplast *trn*L (UAA) intron sequence between *c* and *d* primers does not distinguish certain closely related species, we defined molecular operational taxonomic units (MOTUs) within our plant reference database by grouping species that exhibited sequence similarity of ≥ 97% using the BLASTclust algorithm. Plant 454 sequences were assigned to MOTUs by conducting a BLAST search (soft masking of DUST filter) against the plant reference database. A similar approach was used to assign AMF 454 sequences to MOTUs in paper **III**, where obtained 454 sequences were identified by conducting a BLAST search against the Maarj*AM* database of published Glomeromycota SSU rRNA gene sequences (http://maarjam.botany.ut.ee, Öpik et al., 2010) The Maarj*AM* database contains

representative sequences covering the NS31/AML2 amplicon from published environmental Glomeromycota sequence groups and known taxa.

2.4. Phylogenetic analysis

In paper **III**, we constructed phylogenies for the plant and AMF taxa found in the study site. The plant phylogeny was constructed using the Phylomatic web-interface (http://phylodiversity.net/phylomatic/), which is based on the Angiosperm Phylogeny Group APG III derived megatree (http://www.mobot.org/MOBOT/research/APweb/). For the AMF phylogeny we used SSU rRNA gene sequences from the Maarj*AM* database of Glomeromycota sequence records (Öpik et al., 2010, status April 2012). A phylogenetic tree containing a type (representative) sequence from all known VT was constructed using a Bayesian phylogenetic approach with BEAST (version 1.6.1, Drummond & Rambaut, 2007).

2.5. Statistical analysis

In paper **II**, we explored the ability of 454 sequencing to detect species presences in the known mixtures of roots. We quantified the correspondence between the composition of the known species mixtures and the molecularly-detected species in the mixtures. In order to test if 454 sequencing can quantify the relative abundance of species in the known mixtures, we compared the log-ratio transformed proportions of added roots for each species with the numbers of retrieved sequences.

In paper **II**, the relationship between aboveground richness and total belowground richness was determined by calculating the log of the ratio of aboveground richness to belowground additional richness, and relating this to the log of total belowground richness. Differences in above- and belowground richness were explored at two spatial scales. The plant neighborhood scale was investigated using species richness-area (volume) curves obtained by determining the richness in adjacent plots within each transect. Patterns of species occurrence at the community scale were additionally examined by producing species accumulation curves that calculated the cumulative number of species over an increasing number of transects (samples). Aboveground, belowground and additional belowground (i.e. those species only detected belowground) richness were related to soil total N content by constructing General Linear Mixed Models with a Gaussian spatial correlation structure.

In paper **III**, we used a variety of diversity measures and their quadratic values (to test for both linear and non-linear relationships) and related these to community biomass. The measures fell into three categories: plant aboveground diversity based on studying shoots, and both plant belowground diversity and AMF diversity from the roots. For each of these we calculated three diversity

indices: (1) species diversity (Shannon index, which is the logarithm of the effective number of species), (2) phylogenetic dispersion (MPD index) and (3) phylogenetic diversity (PD index). Firstly, we tested which of the plant diversity measures are good predictors of the corresponding AMF diversity measures. Secondly, we aimed to test which aspects of plant and AMF diversity are best related to above-, belowground and total plant biomass. All models were fit using Linear Mixed-Effects procedures, whereby spatial autocorrelation was accounted for by assigning transect as a random factor. The optimal models were chosen according to Akaike Information Criterion (AICc) and Akaike Weight (AW).

In paper **IV**, all analyses were conducted using above- and belowground species' presence-absence data from paper **II**. Species guilds were defined as grasses (Poaceae) or forbs (all other families). We compared variance in richness, guild proportionality and species co-occurrences (c-scores and checker index) in observed and randomized data-sets (2000 randomizations). Randomizations were spatially constrained, i.e. randomization was applied only within each transect of 10 samples. The significance of deviations between observed and randomized data-sets were defined using the Monte Carlo method. Species pairwise associations were compared taking into account spatial configuration using Generalized Estimating Equations (GEE) for binary data. We also conducted a Fisher exact test to determine if there was a non-random pattern in the number of positive or negative interactions within and between our guilds, i.e. grasses – grasses, grasses – forbs, forbs – forbs.

3. RESULTS

3.1. Suitability of 454 sequencing for detecting presence and abundance of plants belowground

Mixtures with known species composition showed a significant correlation between added and observed species presences (**II**). Two species (*Solidago* group and *Artemisia* spp.) were used in most mixtures and this allowed us to compare relative sequence abundance with relative biomass. We found a good correspondence between the proportions of added biomass in the root mixtures and the numbers of retrieved sequences, indicating that 454 sequencing can provide quantitative data on species abundances, allowing the calculation of species diversity and evenness in addition to richness.

3.2. Difference in above- and belowground richness at various spatial scales

In total we detected 29 and 16 plant species (MOTUs) from the natural grassland sites in Estonia (**II**) and Canada (**III**), respectively. The relationship between aboveground richness and total belowground species richness was significantly non-linear (Fig. 3, in **II**). Thus, the increase in total belowground richness was initially associated with an increase in aboveground richness, but average aboveground richness reached an asymptote at about seven species when total belowground richness exceeded 10 species. In addition, total belowground richness exceeded aboveground richness at all scales investigated. At the smallest sampled scale (0.001 m^3), differences in above- and total belowground richness were least pronounced – total belowground richness was on average 1.4 (in **II**) and 1.5 (in **III**) times higher than aboveground. At the plant neighborhood scale (0.001 m^3 to 0.008 m^3), total belowground richness was, on average, 1.8 times higher than aboveground richness (Fig. 4, in **II**). Total belowground richness also exceeded aboveground richness at the community scale, as indicated by the pattern of species accumulation from 1 to 10 transects (Fig. 5, in **II**).

3.3. Relationships between plant and AMF diversity measures

In total we detected 70 AMF virtual taxa from a natural prairie site in Canada (**III).** In paper **III,** we examined which plant species diversity and phylogenetic diversity measures are related to the respective AMF diversity measures. The best predictor of AMF taxon diversity and phylogenetic diversity was belowground plant species diversity and phylogenetic diversity. Both relationships were positive and linear (Fig 2a and b, Table 1 in **III**).

3.4. Difference in above- and belowground diversity measures along ecological gradients

In paper **II**, we examined the effect of soil total N content on species richness above- and belowground. Aboveground richness decreased significantly with increasing soil total N (Fig. 6, in **II**). In contrast, additional belowground richness increased with soil N, while total belowground richness did not change along a gradient of soil N (Fig. 6, in **II**). In paper **III**, we looked at how total plant biomass production is related to plant and AMF diversity measures. Total plant biomass was best explained by a model combining belowground plant diversity, belowground plant phylogenetic dispersion and root AMF taxon diversity (Fig 5 a–c, Table 2 in **III**). Total plant biomass was positively linearly related to belowground plant richness and positively non-linearly related to belowground plant phylogenetic dispersion. In contrast, total biomass was negatively non-linearly related to AMF taxon diversity.

3.5. Difference in above- and belowground plant community assembly rules

We studied above- and belowground plant community assembly rules by comparing variance in plant species richness and species co-occurrences (c-scores and checker index) in observed and randomized data-sets (paper **IV**). Aboveground plant species richness was significantly less variable than expected at random, whereas belowground plant data showed a tendency towards greater variance in richness than expected. Species co-occurrence tests revealed that aboveground species were significantly segregated based on c-scores. However, this was not significant based on the checker index, except when species were constrained by their belowground presence. Pairwise comparisons based on the presence and absence of all species pairs revealed many positive and negative species associations (i.e. aggregation and segregation, respectively) above- and belowground (Fig. 1, in **IV**). More species aggregation (14 species pairs) than segregation (7 species pairs) was recorded belowground, whereas aboveground similar numbers of species pairs were significantly segregated and aggregated (10 and 8, respectively). However, the c-scores suggest that the aboveground community is characterised by segregation, so these species pairs must be frequent enough to drive this pattern.

4. DISCUSSION

We found that many more plant species coexist within a limited area than are detected using conventional aboveground methods. Above- and belowground plant species diversity measures responded differently to environmental gradients. Investigation of community assembly rules revealed contrasting processes governing the assembly of above- and belowground plant communities.

We investigated the suitability of 454 sequencing for detecting the presence and abundance of plant species belowground (**II**). Analysis of samples containing known root mixtures indicated that 454 sequencing has the potential to produce quantitative estimates of belowground plant species richness from environmental samples, as long as certain limits are recognized. Difficulties with taxon recovery and species resolution (ca 20% of the molecular taxonomic units grouped two or more closely related species) remain as constraints of the chloroplast *trn*L(UAA) intron marker as used in paper **II**. However, it is now possible to acquire 454 sequence read length of up to 1000 bp that would improve the species resolution of *trn*L(UAA) intron considerably by increasing the usable length of the amplicon and thus the number of variable sites per sequence. The method can also be used to study root-inhabiting biota (bacteria, fungi, invertebrates) using the same samples as for plant identification but with the application of appropriate taxon-specific primers, as done in paper **III**.

At the plant neighborhood scale, the non-linear pattern between above- and belowground richness indicates saturation of the aboveground community (Cornell & Lawton, 1992; Srivastava et al., 2012), even as belowground richness continues to increase (**II**). Further, higher total belowground richness compared to aboveground richness, suggests that traditional measures of aboveground plant richness greatly underestimate the number of coexisting species at small scales. Greater belowground richness was also apparent at the community scale: we did not detect any convergence of cumulative species richness with increasing scale over the 10 transects in the 2-ha Estonian study site (**II**). In paper **I**, we hypothesized possible biological mechanisms that might contribute to a higher richness of plants belowground. Virtually all grassland plant species found aboveground have roots or rhizomes in nearby soil, but the converse is not necessarily true: aboveground shoots might not be present at every location where there are roots or rhizomes belowground. A number of processes may lead to an absence of aboveground shoots. For example, clonal plants can become temporarily “invisible” to the aboveground observer while persisting as rhizome networks with few aboveground shoots (Wildova et al., 2007). Thus, high clonal mobility might enhance coexistence belowground (Zobel et al., 2010). Also, roots and rhizomes are generally more persistent than shoots, and can survive during unfavorable periods (e.g. winter, heavy grazing), while some species can be dormant for up to decades (Klimesova & Klimes, 2007; Reintal et al., 2010). Further, the soil environment contains heterogeneous

resources and is rich in micro-organisms that interact with plant roots and influence plant species coexistence (Bever et al., 2010).

In total we detected 70 AM fungal taxa at the studied Canadian prairie site (**III**). This places the AMF richness for the site among the highest recorded in a natural plant community. Very few studies have used bulk root samples for AMF identification (Heinemeyer & Fitter, 2004; Dumbrell et al., 2011); more commonly roots of individual plants are sampled (cf. Öpik et al., 2010). Dumbrell et al. (2011) used a similar approach by pyrosequencing bulk root samples from a limestone grassland in the UK and also detected 70 AMF taxa. However, Dumbrell et al. (2011) sampled 11 times through the year detecting some taxa in cool or warm season only, whereas we sampled in summer only. We found that AMF diversity was positively associated with plant diversity (**III**), and that belowground plant diversity was a better predictor of AMF diversity than was aboveground plant diversity. Previous experimental work has reported positive (van der Heijden et al., 1998, Maherali & Klironomos, 2007), negative (Hartnett & Wilson, 1999; O'Connor et al., 2002) or no relationship (Waldrop et al., 2006) between plant diversity and AMF community diversity. We know of one study from a natural study system (oak savanna) which reported a positive relationship between AMF spore richness and aboveground plant richness at small sampling scales (Landis et al., 2004). We found that AMF phylogenetic diversity increased with increasing belowground plant phylogenetic diversity (**III**), which is predictable on the basis of the species diversity results, since species richness and phylogenetic diversity are likely to be correlated (Cadotte et al., 2009). Recent studies on the structure of symbiotic interactions show that there can be reciprocal specialization between plants and AMF at the level of ecological groupings (Öpik & Moora, 2012), which might result in a positive relationship between the phylogenetic diversity of both trophic groups.

Due to inherent differences in the way plants live and interact above- and belowground we hypothesized that above- and belowground plant richness might behave differently along a soil fertility gradient (**I**). Indeed, aboveground richness decreased significantly with increasing soil total N, while additional belowground richness increased with soil N (**II**). Total belowground richness did not change along a gradient of soil N (**II**). These results support the idea that aboveground exclusion of species in fertile soils is probably caused by asymmetric light competition where tall plants gain a disproportionate advantage over small ones (Zobel, 1992). Roots, however, preferentially grow into fertile patches (Hodge, 2004), which may result in symmetric root competition since all plants are relatively equal in their ability to acquire soil resources (Weiner, 1990; Cahill & Casper, 2000). Many perennial species can stay dormant belowground until environmental conditions are favorable again (Shefferson et al., 2005). In this way plant species may be buffered against local extinction in fertile soils. Total belowground richness did not change along the soil fertility gradient because aboveground richness decreased but additional

belowground richness increased, causing the overall relationship to remain neutral.

The relatively low biomass values measured at the Canadian prairie site (**III**) indicated that we observed the left hand-side of the unimodal diversity-productivity relationship, where higher diversity increases primary productivity. We addressed the question of how total plant primary productivity (the sum of above- and belowground plant biomass) is related to various plant aboveground, belowground and AMF diversity measures (**III**). Total primary productivity was best explained by a combination of three factors – AMF and belowground plant diversity, and belowground plant phylogenetic dispersion (**III**). This result indicates the importance of belowground processes, often overlooked in diversity-productivity studies, in determining ecosystem primary productivity. The decline in total productivity with increasing AMF diversity is a result that contradicts earlier studies that report a promoting effect of AMF diversity on total plant biomass (Tilman et al., 2001; Tilman et al., 2006). However, negative growth responses of plants to AMF are common (Klironomos, 2003), for example for a range of prairie plant species (Wilson & Hartnett, 1998). The positive linear relationship between total primary productivity and belowground plant diversity reflect the pattern reported previously for aboveground biomass (Tilman, 1999; Tilman et al., 2006). However, belowground plant species diversity can be considered the more complete measure of plant community diversity, as it includes species that were absent aboveground at the time of sampling (**II, III**). Total primary productivity first decreased and then increased with belowground plant phylogenetic dispersion (**III**). It is possible, that closely related species (low phylogenetic dispersion) were dominant species with high biomass values, while distantly related species have different competitive abilities driving competitive exclusion (Mayfield & Levine, 2010). However, since competition is not an important process in shaping belowground communities (**IV**) the complementarity effect of high phylogenetic dispersion may have outweighed an effect of competition.

We hypothesized that patterns of plant assembly differ above- and belowground (**IV**) based on the differences between the aboveground and soil environments reviewed in paper **I**. Aboveground, we found more support for biotic assembly processes, as demonstrated by lower variance in species richness than expected at random, and species segregation (**IV**), consistent with other aboveground studies (see Götzenberger et al., 2012, for a review). Aboveground assembly appears to be driven mainly by biotic processes, presumably asymmetric light competition. Hence, biotic filters operate strongly to determine species presence aboveground. Belowground, we found more support for assembly governed by abiotic and stochastic processes, as demonstrated by greater variance in richness and less species segregation than expected and random species association patterns, consistent with Frank et al. (2010). The soil environment is more variable than the aboveground environment, including gradients of different macro- and micro-nutrients, and chemical

and physical conditions (e.g. pH, soil particle size). This diversity of resources produces large variability in micro-environmental conditions, thereby promoting belowground coexistence, compared to the main aboveground resource of light. The results in papers **II** and **IV** suggest that increased species coexistence belowground is partly because competitive exclusion is not occurring at the same spatial or temporal scale as it occurs aboveground. Biotic assembly processes aboveground were further demonstrated by more negative plant species pairwise associations (**IV**), most likely driven by competition for light . The negative species associations were driven by a few species that were abundant in the grassland community. Belowground, the majority of pairwise associations were positive and no associations were found aboveground (**IV**). Positive associations belowground can be due to facilitation. For example, roots can increase the availability of resources for other species (Callaway, 1995). Positive associations may also reflect root behavioural ecology, as roots can detect the presence of self and non-self roots, with the response being either stimulation of root growth or avoidance (Semchenko et al., 2007; de Kroon, 2007).

5. CONCLUSIONS

We found that up to two times more plant species coexist within a limited area than are detected using conventional aboveground methods, and plant richness is not proportionally related above- and belowground. Greater total belowground richness compared to aboveground richness can be detected at the plant neighborhood scale as well as at the community scale, suggesting that some species are dormant at the time of aboveground sampling. The results of this thesis indicate, that using 454 sequencing to study roots from the natural communities can shed new light on plant biodiversity.

454 sequencing can also be used to study root-inhabiting arbuscular mycorrhizal fungi using the same root samples for plant identification but with the application of appropriate taxon-specific primers. So far, the relationship between plant and AMF community diversity in natural ecosystems is largely unexplored. We detected remarkably high AMF taxon diversity from a natural prairie site and related this to plant diversity measures (species diversity, and phylogenetic). The results revealed that AMF diversity measures increased linearly with increasing plant diversity measures, and that belowground plant diversity measures are better predictors of AMF diversity measures than are aboveground plant diversity measures.

Above- and belowground plant species diversity measures respond differently to environmental gradients. Similar to other grassland studies, aboveground richness declines with increasing soil fertility; in contrast, the number of species found only belowground increases significantly with fertility, suggesting that at high soil fertility, the rapid decline in aboveground plant richness attributed to light competition might not occur belowground for some time. Such a delay in the reduction of species richness provides a buffer period during which restoration of degraded sites could be successful.

We studied how primary productivity, most of which occurs belowground, is related to the species diversity and phylogenetic diversity of both plants and AMF. Our results showed that belowground diversity measures are strongly linked to total primary productivity in a natural grassland ecosystem. Primary productivity was higher with high species diversity of plant roots and rhizomes, especially if they are from different phylogenetic lineages. In contrast, productivity declined when the diversity of arbuscular mycorrhizal fungi increased, suggesting that less plant biomass is produced in the presence of diverse fungal communities. A challenge for future research is to identify the underlying mechanisms and causes that shape the diversity-productivity relationship in natural communities.

Investigating the plant community assembly patterns of aboveground plant shoots and belowground roots and rhizomes in a natural community revealed different assembly in the belowground and aboveground communities; there is more evidence for abiotic and stochastic processes and less support for biotic processes belowground. Future studies examining the processes underlying

these observed patterns are needed to better understand plant community assembly above- and belowground.

Incorporating belowground plant diversity together with the diversity of other trophic levels into future studies is likely to reveal new patterns that can refine predictions of vegetation responses to biodiversity threats and may stimulate a reassessment of ecological theory.

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SUMMARY IN ESTONIAN

Taimede maa-aluse mitmekesisuse ja kooseksisteerimise väikeseskaalalised seaduspärad niiduökosüsteemides

Teadmised liigilisest mitmekesisusest ja liikide kooseksisteerimisest põhinevad suures osas empiirilistel töödel, mis käsitlevad taimekoosluste maapealset osa. Samas on teada, et paljudes laialtlevinud ökosüsteemides, nagu erinevad rohumaad, stepid, tundrad ja kõrbed, võib 50–90% taimsest biomassist olla paigutunud maa alla. Maa-alune osa on väga oluline taimekoosluste liigirikkuse ja talitlemise seisukohast, kuid on teadmata, kas seaduspärad, mis on tuvastatud taimekoosluste maapealse osa uurimisel, kehtivad ka maa all. Taimekoosluste maa-alust osa on vähe uuritud, kuna varasemad meetodid ei võimaldanud morfoloogiliselt väga sarnaseid juuri ja risoome liikideks määrata. Uued DNA-põhised meetodid võimaldavad taimede maa-aluseid osi identifitseerida, kuigi see on endiselt tehniliselt keerukas. Taimeökoloogia lähituleviku üheks eesmärgiks võibki pidada maa-aluse taimekoosluse toimimise ja seaduspärade uurimist ning saadud tulemuste võrdlemist maapealsete osade uurimisel leitud teadmistega. Tõenäoliselt avalduvad erinevused maapealse ja maa-aluse taimekoosluse seaduspärades just neis taimekooslustes, kus rohkem biomassi paigutub maa-alla (niitudel ja rohumaadel).

On võimalik, et väikesel skaalal esineb maa all rohkem taimeliike, kui võiks eeldada ainult maapealse liigirikkuse määramise põhjal. Selleks on mitmeid põhjuseid. Esiteks, paljud mitmeaastased taimeliigid moodustavad maa-aluseid säilitusorganeid ja meristeeme, mis võimaldavad lühi- või pikaajalist puhkestaadiumis viibimist ilma maapealsete osade moodustamiseta. Samuti on juurte ja risoomide horisontaalne ulatus tunduvalt suurem kui taimede maapealsete osade oma, põhjustades suuremat kattuvust teiste taimeindiviidide ja -liikidega maa all. Teiseks, maa-alused ressursid ja taimedega sümbioosis elavad mikroorganismid võivad toetada maa all liikide tihedamat kooseksisteerimist võrreldes sama suure ruumiühikuga maa peal. Kolmandaks, maa-alust konkurentsi peetakse sümmeetriliseks taimede suuruse suhtes ning vastupidiselt maapealsele konkurentsile, mida peetakse asümmeetriliseks, ei pruugi maa-alune konkurents põhjustada taimede konkurentset väljatõrjumist. Maa-alune liigirikkus moodustub proovis juurdunud maapealsetest liikidest ja nendest liikidest, mida leitakse lisaks maa alt tänu juurte määramisele molekulaarsete meetoditega.

Üks ulatuslikumalt kirjeldatud ökoloogilisi seaduspärasid on liigirikkusepindala suhe ehk liigirikkuse kasvu seos uuritava ala suurusega. Siiani ei olnud teada, kas ja kuidas antud seos erineb maapealse ja maa-aluse taimede liigirikkuse vahel, kuid uued DNA-põhised meetodid aitavad sellele küsimusele peagi vastuse leida. Võib eeldada, et maa-alune liigirikkus kasvab suhteliselt kiiremini kui maapealne, kuna väikesel alal maa all esineb suurem osa kogu koosluse liigirikkusest võrreldes maapealse liigirikkusega.

Juured ja risoomid on tihedalt seotud sümbiootiliste arbuskulaarmükoriisa (AM) seentega, kes mängivad olulist rolli taimede toitainete omastamises. Varem on seostatud AM seeni taimede mitmekesisuse ja biomassi produktsiooniga, kuid meie teadmised AM seente ja taimede vahelisest interaktsioonist ja selle mõjust biomassi produktsioonile looduslikes ökosüsteemides on olnud puudulikud.

Võib eeldada, et maapealne ja maa-alune taimede liigirikkus erineb ka selle poolest, kuidas nad piki ökoloogilisi gradiente varieeruvad. Üks tuntumaid ökoloogilisi seoseid on unimodaalne seos liigirikkuse ja produktiivsuse vahel. Madala produktiivsuse tingimustes peaks nii maa-alune kui ka maapealne liigirikkus olema madal, kuna vaid vähesed liigid suudavad selliseid tingimusi taluda. Kõrge produktiivsuse juures on maapealne liigirikkus aga madal suurenenud valguskonkurentsi tõttu, mille käigus tõrjutakse väiksemad liigid domineerivate liikide poolt välja. Võib aga eeldada, et konkurentne väljatõrjumine ei oma maa all nii suurt mõju, kuna konkurents mullaressursside üle ei anna suurematele liikidele ebaproportsionaalseid eeliseid.

Varasemad uuringud on leidnud, et suur liigiline mitmekesisus on oluline säilitamaks taimekoosluste pikaajalist toimimist ja stabiilsust. Seda seletatakse niši komplementaarsuse teooria abil, mille kohaselt suurema mitmekesisusega taimekooslustes esineb rohkem erinevaid funktsionaalseid tunnuseid. Mitmekesisemates kooslustes suudavad taimed kasutada kasvukohas leiduvaid ressursse palju efektiivsemalt kui liigivaestes kooslustes ja seeläbi suureneb ka biomassi produktsioon. Vähe on teada, kuidas taimede mitmekesisus mõjutab biomassi produktsiooni ja AM seente mitmekesisust.

Maapealsed ja maa-alused taimekooslused võivad erineda ka selle poolest, millised faktorid on mõjutanud nende koosluste liikidega komplekteerimist. Neid faktoreid nimetatakse koosluse kokkupaneku reegliteks ning need võivad olla abiootilised või biootilised protsessid, mis filtreerivad liike regionaalsest liigifondist vaadeldavasse kooslusesse. Koosluse kokkupaneku reegleid on seni enamasti uuritud tuginedes andmetele taimekoosluste maapealsest osast, aga sarnaselt elurikkusele võib eeldada, et maa-all on need reeglid erinevad.

Käesoleva töö põhilised hüpoteesid olid: 1) 454 sekveneerimine on sobilik juurte liigirikkuse ja rohkuse määramiseks maa-alustest proovidest (**II**); 2) taimede liigirikkus maa peal ja maa all on erinev (**I**, **II**); 3) AM seente mitmekesisus on positiivses seoses taimede liigilise ja funktsionaalse mitmekesisusega, sealjuures on AM seened tugevamalt seotud maa-aluse taimede mitmekesisuse parameetritega (**III**); 4) maapealne ja maa-alune taimede liigirikkus on mulla viljakusega erinevalt seotud (**I, II**); 5) kogu koosluse biomassi produktsioon (maapealse ja maa-aluse biomassi summa) on positiivselt seotud taimede ja AM seente mitmekesisuse parameetritega (**III**); 6) koosluse kokkupaneku reeglid erinevad maapealses ja maa-aluses taimekoosluses, sealjuures on biootilised protsessid olulisemad maa peal ja abiootilised ning juhuslikud protsessid olulisemad maa all (**IV**).

Testisime 454 sekveneerimise võimet määrata juureproovidest taimeliigid ja nende ohtrused. Selleks koostasime proovid, milles segasime kokku teadaolevate taimeliikide juured erinevates vahekordades. Leidsime hea korrelatsiooni testproovidesse teadlikult pandud liigirikkuse ja taimeliikide ohtruse vahel, mis kinnitab 454 sekveneerimise sobilikkust maa-aluse taimekoosluse uurimisel.

Et vastata küsimustele, kas taimede liigirikkus erineb maa peal ja all, kogusime taimede liigirikkuse andmeid pool-looduslikult niidult Lõuna-Eestis, Ahja vallas. Maapealsed liigid määrasime tavapärase morfoloogiliste tunnuste vaatluse abil ja maa-alused liigid määrasime juureproovidest uue põlvkonna 454 sekveneerimise abil. Leidsime, et maa-alune taimede liigirikkus oli keskmiselt ligi kaks korda suurem kui samas skaalas maa peal (**II**). Erinevus säilis ka kogu koosluse skaalal. Antud tulemused viitavad sellele, et vaadeldes ainult koosluse maapealset osa, näeme kõigest "jäämäe tippu", kuna tegelik liikide kooseksisteerimine leiab aset maa all. Suurem liigirikkus maa all võib olla tingitud mitmete bioloogiliste mehhanismide poolt (**I**). Näiteks võivad klonaalsed taimed moodustada maa all laiaulatuslikke risoomide võrgustikke, samas võivad nad maapealseid osi moodustada ainult siin-seal või mõnel aastal üldse mitte.

Uurimaks AM seente ja taimede mitmekesisuse eri parameetrite vahelisi seoseid kogusime proove Kanada looduslikust preeriakooslusest. Taimeliigid maa peal ja maa all määrasime nagu töös **II**, kuid identifitseerisime juureproovidest ka AM seenetaksonid, kasutades antud seenerühmale spetsiifilisi markereid. Määrasime ka taimeliikide ja seenetaksonite fülogeneetilise mitmekesisuse. Leidsime, et AM seente taksonite mitmekesisus ja fülogeneetiline mitmekesisus kasvab taimede liigilise ja funktsionaalse mitmekesisuse kasvades, ning sealjuures on AM seente mitmekesisuse parameetrid tugevamini seotud just maa-aluste taimede mitmekesisuse parameetritega (**III**). Hiljutised uuringud on näidanud, et taimed ja nende AM sümbiondid on evolutsiooni käigus vastastikku spetsialiseerunud, mis võib viia funktsionaalsete tunnuste mitmekesisuse kasvule mõlemas organismirühmas.

Taimede liigirikkus maa peal ja maa all erines ka piki mullaviljakuse gradienti, nagu näitasid andmed Ahja niidult (**II**). Leidsime sarnaselt varasemate töödega, et maapealne liigirikkus langeb mullaviljakuse kasvades, kuid uudne aspekt on, et maa-aluste liikide arv proovis kasvas mullaviljakuse kasvades. Need tulemused toetavad teooriat, mille kohaselt suurenenud mullaviljakuse tingimustes saavad suurekasvulised liigid ebaproportsionaalselt suure osa valgusressursist põhjustades teiste liikide väljatõrjumist. Juurekonkurentsis aga ei saa suuremad liigid sellist eelist, kuna toitained on kättesaadavad kõigist suundadest ja seega ei pruugi konkurentne väljatõrjumine olla maa all oluline faktor. Suurenenud mullaviljakuse tingimustes võivad taimed minna üle puhkeseisundisse, mille jooksul nad ei moodusta maapealseid osi, kuid suudavad teatud aja vältel maa all eksisteerida ning uuesti maa peale ilmuda, kui valgustingimused on paranenud.

Mõõtsime Kanada preeria alalt kogu koosluse biomassi (maapealsete ja maa-aluste proovide biomassi summa) ning seostasime need väärtused koosluses

esinevate maapealsete, maa-aluste taimede ning AM seente mitmekesisuse parameetritega (**III**). Leidsime, et kogu koosluse biomassi kirjeldavad kõige paremini kolm parameetri: maa-alune taimede liigiline mitmekesisus ja fülogeneetiline dispersioon ning AM seente taksonite mitmekesisus (**III**). Antud tulemused näitavad, et primaarproduktsioon on suurem kui juurte ja risoomide liigiline mitmekesisus on suur, eriti juhul, kui maa-alused liigid on fülogeneetiliselt kaugelt seotud. Vastupidiselt eeltoodud positiivsetele seostele, AM seente taksonite mitmekesisuse kasvades primaarproduktsioon väheneb.

Sarnaselt elurikkusele selgus ka, et maapealne ja maa-alune taimekooslus on kokku pandud erinevate protsesside tagajärjel (**IV**), tingituna maapealsete ja maa-aluste keskkonnatingimuste erinevusest (**I**). Analüüsides Ahja niidu maapealse ja maa-aluse taimekoosluse andmestikku (**II)**, leidsime, et maapealsete liikide kooseksisteerimine on pigem määratud biootiliste interaktsioonide poolt, nagu näiteks valguskonkurents ja sellest johtuv liikide väljatõrjumine, samas kui maa-aluse koosluse kokkupanekut mõjutavad suuresti abiootilised ja stohhastilised protsessid (erinevad toitainete gradiendid, mulla pH, jm mulla keemilis-füüsikalised omadused) (**IV**). **IV** ja **II** töö tulemused toetavad teooriat, mille kohaselt on maa all liikide kooseksisteerimine pikaajaliselt stabiilsem, kuna liikidevaheline konkurents on väiksem.

Kokkuvõtteks toovad selle doktoritöö tulemused esimest korda esile taimekoosluste maa-aluse komponendi (sh eri troofilistel tasemetel) olulisuse liikide kooseksisteerimise ja ökosüsteemi protsesside uurimisel. Molekulaarsete meetodite kasutuselevõtt võimaldab avastada uusi liigirikkuse ja koosluste kokkupaneku seaduspärasid otse looduslikest kooslustest, mis võivad muuta senikehtinud ökoloogilisi teooriaid.

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***

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PUBLICATIONS

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List of Publications:

Pärtel, M., **Hiiesalu, I**., Öpik, M. & Wilson, S.D. (2012) Belowground plant species richness: new insights from DNA-based methods. Functional Ecology 26: 775–782

Laanisto, L., Tamme, R., **Hiiesalu, I.**, Szava-Kovats, R., Gazol, A., Pärtel, M. Microfragmentation consept explains non-positice environmental heterogeneity-diversity relationships. Oecologia DOI: 10.1007/s00442-012-2398-5.

Price, J.N., **Hiiesalu, I.**, Gerhold, P., Pärtel, M. (2012) Small-scale grassland assembly patterns differ above and below the soil surface. Ecology 93(6) 1290–1296

Hiiesalu, I., Öpik, M., Metsis, M., Lilje, L., Davison, J., Vasar, M., Moora, M., Zobel, M., Wilson, S.D. & Pärtel, M. (2012) Plant species richness

belowground: higher richness and new patterns revealed by next-generation sequencing. Molecular Ecology 21: 2004–2016

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(4), 796–801.

Conference presentations:

Hiiesalu, I., Pärtel, M., Davison, J., Moora, M., Öpik, M., Zobel, M., Wilson, S.D. "Belowground diversity of plants and arbuscular mycorrhizal fungi determine ecosystem productivity". Oral presentation. 23–28 July 2012. 55th Annual meeting of the International Association for Vegetation Science, in Mokpo, South-Korea.

Hiiesalu, I., Price, J.N., Gerhold, P., Pärtel, M. "Do aboveground assembly rules apply belowground?" Oral presentation. 21–25 Nov 2011, 36. Ecological Society of Australia, Tasmania, Australia.

Hiiesalu I., Öpik, M., Metsis, M., Davison, J., Vasar, M., Moora, M., Zobel, M., Wilson, SD., Pärtel, M. "Root sequencing doubles small-scale plant richness measures and alters diversity patterns." Oral presentation. 20–24 June 2011, 54th Annual meeting of the International Association for Vegetation Science in Lyon, France.

Hiiesalu, I., M. Öpik, M. Metsis, J. Davison, M. Moora, M. Zobel, S.D. Wilson. and M. Pärtel. "Small-scale vegetation diversity patterns belowground: concept and methods". Oral presentation 18–23 April 2010. 53rd Annual meeting of the International Association for Vegetation Science in Ensenada, Mexico.

Hiiesalu, I., Tamme, R., Helm, A., Pärtel, M. "Soil heterogeneity and plant diversity in habitat change between grassland and forest". Poster. 30 May–4 June 2009. 52nd. Annual meeting of the International Association for Vegetation Science in Crete, Greece.

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Väikeseskaalalised taimede liigirikkuse mustrid niiduökosüsteemides. Maa-aluse ja maapealse liigirikkuse ja liikide kooseksisteerimise mustrite võrdlused ning seosed koosluse parameetritega. Liigirikkuse seosed mulla väikeseskaalalise heterogeensusega.

Publikatsioonide loetelu:

Pärtel, M., **Hiiesalu, I**., Öpik, M. & Wilson, S.D. (2012) Belowground plant species richness: new insights from DNA-based methods. Functional Ecology 26: 775–782

Laanisto, L., Tamme, R., **Hiiesalu, I.**, Szava-Kovats, R., Gazol, A., Pärtel, M. Microfragmentation consept explains non-positice environmental heterogeneity-diversity relationships. Oecologia DOI: 10.1007/s00442-012-2398-5.

Price, J.N., **Hiiesalu, I.**, Gerhold, P., Pärtel, M. (2012) Small-scale grassland assembly patterns differ above and below the soil surface. Ecology 93(6) 1290–1296

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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(4), 796–801.

Konverentsi ettekanded:

Hiiesalu, I., Pärtel, M., Davison, J., Moora, M., Öpik, M., Zobel, M., Wilson, S.D. "Belowground diversity of plants and arbuscular mycorrhizal fungi determine ecosystem productivity". Suuline ettekanne. 23–28 Juuli 2012. 55. Rahvusvahelise Taimkatte Assotsiatsiooni Aastakonverents. Mokpo, Lõuna-Korea.

Hiiesalu, I., Price, J.N., Gerhold, P., Pärtel, M. "Do aboveground assembly rules apply belowground?" Suuline ettekanne. 21–25 November 2011, 36. Austraalia Ökoloogiaühingu konverents, Tasmaania, Austraalia.

Hiiesalu I., Öpik, M., Metsis, M., Davison, J., Vasar, M., Moora, M., Zobel, M., Wilson, SD., Pärtel, M. "Root sequencing doubles small-scale plant richness measures and alters diversity patterns." Suuline ettekanne. 20–24 Juuni 2011, 54. Rahvusvahelise Taimkatte Assotsiatsiooni Aastakonverents. Lyon, Prantsusmaa.

Hiiesalu, I., M. Öpik, M. Metsis, J. Davison, M. Moora, M. Zobel, S.D. Wilson. and M. Pärtel. "Small-scale vegetation diversity patterns below-ground: concept and methods". Oral talk 18–23 April 2010. 53. Rahvusvahelise Taimkatte Assotsiatsiooni Aastakonverents. Ensenada, Mehhiko.

Hiiesalu, I., Tamme, R., Helm, A., Pärtel, M. "Soil heterogeneity and plant diversity in habitat change between grassland and forest". Poster. 30 May–4 Juuni 2009. 52. Rahvusvahelise Taimkatte Assotsiatsiooni Aastakonverents. Kreeta, Kreeka.

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Olin 2011. a Tartus peetud doktorantide konverentsi "Next generation insights into geosciences and ecology" üks peakorraldaja.

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