

KADRI KOOREM

The influence of abiotic and biotic
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patterns and regeneration
in boreonemoral forest



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LIST OF ORIGINAL PUBLICATIONS

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

- I. **Koorem K, Gazol A, Öpik M, Moora M, Saks Ü, Sõber V, Uibopuu A, Zobel M.** Microbes are more sensitive to small-scale variation in soil nutrient content than plants. Manuscript.
- II. **Koorem K, Saks Ü, Sõber V, Uibopuu A, Öpik M, Zobel M, Moora M. 2012.** Effects of arbuscular mycorrhiza on community composition and seedling recruitment in temperate forest understory. *Basic and Applied Ecology* <http://dx.doi.org/10.1016/j.baae.2012.09.008>
- III. **Koorem K, Price JN, Moora M. 2011.** Species-specific effects of woody litter on seedling emergence and growth of herbaceous plants. *PLoS ONE* **6(10)**: e26505.
- IV. **Koorem K, Moora M. 2010.** Positive association between understory species richness and a dominant shrub species (*Corylus avellana*) in a boreone-moral spruce forest. *Forest Ecology and Management* **260**: 1407–1413.

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The author's contribution to the papers:

	I	II	III	IV
Designing the experiments	*	*	*	*
Data collection	*	*	*	*
Analysing the results		*	*	*
Manuscript preparation	*	*	*	*

I. INTRODUCTION

Forest is a climax community type in many parts of the world (Honnay et al. 2005), meaning that under natural conditions a considerable proportion of the Earth's land surface would be covered with forest. Humans have had a striking, mostly negative influence on vegetation and, in general, the increasing abundance of human populations over time has resulted in a decrease in forest cover (Pongratz et al. 2008). However, during the 20th century, a relatively large proportion of agricultural land was abandoned in some parts of the world (e.g. in north-western Europe and north-eastern North America), which led to the development of forests in those areas (Flinn & Vellend 2005, Hermy & Verheyen 2007). Forests that grow on formerly cultivated areas (frequently referred to as "recent forests") differ from those that have never been cleared for other land uses ("ancient forests") in certain abiotic characteristics including soil nutrient content (Honnay et al. 2002, Baeten et al. 2009) and soil physical structure (Honnay et al. 2002). Ancient forests have also been found to exhibit higher species richness compared to recent forests, especially among herbaceous species (Sciama et al. 2009). This difference is important, as understorey can contain more than 90% of forest plant species even though it represents less than 1% of forest biomass (Gilliam 2007). Ancient forests can therefore be considered as important "hot spots" for measuring forest quality and preserving species richness (Hermy & Verheyen 2007). Thus, it is crucial to understand forest understorey dynamics.

In addition to species richness, understorey plant community composition has been shown to differ between ancient and recent forests (Verheyen et al. 2003). Hermy et al. (1999) composed a list of plant species typical of forests — so called ancient forest species — and highlighted several characteristics distinguishing those species from plant species frequently colonising recent forests. Ancient forest species are usually shade or semi-shade and stress tolerant (Hermy et al. 1999), whereas recent forests are frequently colonised by species that require high light and nutrient levels (Honnay et al. 2002). Species colonising recent forests are also highly competitive (Baeten et al. 2009) and can therefore suppress the colonisation of ancient forest species (Honnay et al. 2002), which leads to the deficiency of typical forest species in those ecosystems (Hermy & Verheyen 2007). In addition, ancient forest species are poorly represented in the seed bank of forests that are dominated by early-successional species (Decocq et al. 2004). Although regeneration from seed in perennial plant communities is relatively infrequent in general (Eriksson & Fröborg 1996, Ehrlén & Eriksson 2000), ancient forest species are known to have particularly low colonisation capacity (Hermy et al. 1999). Successful regeneration, however, is key in shaping the species composition and diversity of local plant communities (Dickson & Foster 2008). The list and characteristics of ancient forest species described above is based on European broadleaved forests (Hermy et al. 1999), but the features of forest species identified by Hermy et al. (1999) also seem to apply to other forest types. Nevertheless, plant

species listed as ancient forest species (Hermy et al. 1999) are not necessarily specialised to forests in general. The term forest specialist plant species is therefore used in this study to refer to the habitat preferences of the species in Estonia (Paal 1997). To ensure the existence of sustainable understories in forests in general, it is essential to improve existing knowledge about the factors that determine the regeneration success of plant species characteristic to the habitat.

Plants can perceive their close surrounding, but when abiotic and/or biotic factors vary in scales considerably greater or smaller than plant individuals, plants are not necessarily capable of distinguishing the variation (Day et al. 2003a). This highlights the need to understand the effects of abiotic and biotic factors on plants at the small scales relevant to plant individuals. Indeed, abiotic factors including resource levels (e.g. soil nutrients) play important roles in determining the growth of individual plants (e.g. Hodge 2004) and the development of plant communities (e.g. Gough et al. 2000). Several studies conducted in artificial conditions have demonstrated that small-scale heterogeneity of soil resources (i.e. the patch of soil nutrients that can be reached by the roots of a plant individual) can be important in determining plant productivity, since plants can concentrate their root biomass into zones of high nutrient content (Hutchings & Wijesinghe 1997, Day et al. 2003a,b). High nutrient content can lead to intensified competition, which can in turn reduce regeneration success (Gustafsson & Ehrlén 2003, Verheyen & Hermy 2004). However, there is still little information available about the role of nutrient variation in determining small-scale plant biomass and regeneration success in stable natural ecosystems.

Biotic factors also play a critical role in the development of plant communities. For example, arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) colonise the roots of most terrestrial plants and facilitate mineral nutrient uptake from soil in exchange for plant-assimilated carbon (Smith & Read 2008). The presence of AM can be especially crucial for seedlings, as they can acquire carbon and nutrients through a common mycelial network, making them more resistant to competition and unfavourable environmental conditions (Moora & Zobel 2010). Despite the wide occurrence of the symbiosis, the growth of different plant species is not equally influenced by the presence of AM fungi (Uibopuu et al. 2009, 2012). Recent studies have demonstrated that the abundance of AM fungi in soil is not uniform (Mummey & Rillig 2008, Spence et al. 2011). However, remarkably little is known about how the abundance of AM fungi affects plant biomass and species composition in natural ecosystems.

The effects of abiotic and biotic factors on plant communities can be interdependent and therefore especially difficult to estimate. For example, the effect on vegetation of AM fungi can depend on limiting nutrient (Hoeksema et al. 2010), host plant species (O'Connor et al. 2002), habitat type and the intensity of herbivory (Ruotsalainen & Eskelinen 2011). Even less is known about the role of multitrophic interactions in determining seedling establishment

(Hermy & Verheyen 2007), although there are reasons to suspect that it may be of major importance. For example, it is known that the role of AM fungi in seedling establishment is species-specific and depends on particular environmental conditions (reviewed by van der Heijden & Horton 2009 and Moora & Zobel 2010): AM may be crucial for seedlings in unfertile conditions and detrimental in fertile conditions. Moreover, current evidence concerning the dependence of seedling establishment on AM and biotic/abiotic factors is limited to experimental rather than natural systems.

All of the factors that influence the growth of herbaceous species in forest ecosystems are to a greater or lesser extent influenced by the overstorey. The overstorey can affect the abiotic environment by altering soil characteristics (Binkley & Giardina 1998), soil pH (Wulf & Naaf 2009, Mölder et al. 2009) and water availability (Barbier et al. 2008a). Similarly, woody species in the overstorey can modify the effect of biotic factors; for example by changing the composition of mycorrhizal fungi (Lang et al. 2011, Wu et al. 2012). A considerable proportion of the overstorey effect is mediated by litter (Janisova et al. 2007). Plant litter can intercept light and rain, change the surface structure and act as a mechanical barrier for seeds, seedlings and shoots (Facelli & Pickett 1991a,b). It can also influence the chemical properties and pH of the soil, nutrient availability and the diversity of fungi and other soil organisms (Facelli & Pickett 1991a, Sayer 2006). Litter has thus been shown to play an important role in structuring understorey communities (Xiong & Nilsson 1999, Rodriguez-Calcerrada et al. 2011).

Germination and establishment are key stages in plant community assembly (Grubb 1977), and they are particularly sensitive to the effects of litter (Xiong & Nilsson 1999). The effects of litter are highly complex, depending on several factors including the life-stage of the seedling (e.g. emerging or establishing), and the type and amount of litter (reviewed by Xiong & Nilsson 1999). Litter has been shown to inhibit emergence (Xiong & Nilsson 1999, Kostel-Hughes et al. 2005) through alteration of the physical environment (e.g. by reducing light availability), mechanical effects (e.g. creating a barrier to seedling emergence), and changes to the chemical environment (e.g. changing soil pH) (Facelli & Pickett 1991a). However, litter can also modify environmental conditions to have positive effects on seedling growth by maintaining soil moisture, moderating soil temperature, providing nutrients during decomposition, and reducing inter-specific competition (Facelli & Pickett 1991a, Xiong & Nilsson 1999, Jögar & Moora 2008). Hence, plant litter can have differential effects on plant performance at different life stages (e.g. at emergence and seedling growth, see Xiong & Nilsson 1999). Nevertheless, relatively little is known about the effects of litter on plants at different life stages in the same study system.

By modifying the abiotic and/or biotic factors described above, the overstorey has been shown to influence several aspects of the understorey, including cover, species composition, and diversity (e.g. Sydes & Grime 1981, Saetre 1999, Augusto et al. 2003, van Oijen et al. 2005, Barbier et al. 2008b, Wulf & Naaf 2009). Understorey characteristics vary among forests, e.g.

species richness under hardwoods is often higher compared to conifers (Barbier et al. 2008b). However, it has been shown that variation in understorey characteristics in relation to canopy species also exists within single sites (Wallrup et al. 2006). In addition to the tree species in the canopy, shrub species in the sub-canopy can have a significant effect on the understorey (e.g. Godefroid et al. 2005). However, knowledge about the effect of different tree and especially shrub species is still sparse.

The aims of this doctoral thesis were:

- to address the role of soil nutrients and AM fungi in determining plant community above- and belowground biomass (**I**, **II**) and composition (**II**).
- to study the role of AM fungi on regeneration by seeds and its dependence on soil fertility (**II**).
- to address the effect of overstorey litter type and amount on herbaceous species regeneration from seed (**III**).
- to determine whether variation in small-scale understorey species richness is related to variation in woody species, and to investigate the mechanisms potentially driving the relationship (**IV**).

2. MATERIALS AND METHODS

2.1. Study system

The study system is located in Koeru, central Estonia (58°58'N; 26°03'E), within a flat landscape consisting of a mosaic of cultivated arable areas and forest. The climate in the area is transitional between maritime and continental. Mean annual precipitation is 700–750 mm. The mean annual air temperature in the region is 4.3–6.5 °C, ranging between –7.4 °C in January and 17.0 °C in July (Jaagus 1999). The study site is a forest of a *Hepatica* site type (Lõhmus 2004). The soil is a calcaric cambisol, and soil conditions are uniform throughout the study area (Zobel et al. 2007). *Picea abies* (L.) Karst. (Norway spruce, hereafter spruce) is the dominant tree species, with individuals of *Acer platanoides* L., *Fraxinus excelsior* L. and *Pinus sylvestris* L. also present. *Corylus avellana* L. (Common hazel, hereafter hazel) dominates in the subcanopy of old stands, while individuals of *Lonicera xylosteum* L. dominate in the shrub layer. Hazel is a shrub, but can grow to a height of 8–10 m and therefore resembles a small subcanopy tree in old growth stands (Wesolowski & Rowinski 2006). Genets of hazel can reach several hundred years in age; genets with a diameter of 1 m are approximately 100 years old (Norden & Paltto 2001). The age of the oldest hazel shrubs in the Koeru study area is likely to be more than 100 years. The understorey is herb rich, with *Oxalis acetosella* L. the dominant species.

The Koeru forest area has not undergone arable cultivation: the study area is classified as forest on the oldest map available (1828). Therefore it classifies as an ancient forest *sensu* Hermy et al. 1999. The forest has however been managed, and clearcutting has taken place in patches of approximately 1–2 ha. However, part of the forest contains a mature stand with different age classes, where the oldest spruces are 130–140 years old.

Although spruce trees in boreonemoral forests are known to be colonised by numerous ectomycorrhizal species (Korkama et al. 2006), high numbers of AM fungi have been recorded in this study system (Õpik et al. 2008). It has also been shown that AM communities in plant roots differ between plant species at the study site – plant species that are characteristic of forest harbour more AM fungal species in their roots than habitat generalist plant species (Õpik et al. 2009).

2.2. Experimental design and data collection

To address the role of soil nutrients and the abundance of AM fungi on plant biomass descriptive (I) and manipulative (II) studies were conducted. Samples were collected with a soil core (15 cm diameter and 10 cm deep) in the middle (I) and at the end of growing season (II). All soil cores (147 in I and 240 in II) were transported to the laboratory where shoots and roots of herbaceous and woody plant species were distinguished. All plant biomass was then dried to a

constant weight at 70 °C and weighed. Soil samples were analysed for organic C%, N%, P and K content (mg/kg). In Paper **II**, soil nutrient content was either enhanced by applying fertilizer, decreased by applying sugar or left unchanged during the two growing seasons prior to the collection of samples. In Paper **I**, the abundance of AM fungi in soil was estimated using ester-linked fatty acid (ELFA) analysis, specifically fatty acid 16:1 ω 5c (Graham et al. 1995). In addition, the abundance of fungi other than AM was estimated using fatty acid 18:2 ω 6,9 (Frostegård & Bååth 1996). In Paper **II**, the abundance of AM fungi was manipulated by adding fungicide during two growing seasons before the collection of samples. AM fungal abundance was assessed by measuring the percentage of AM fungal colonisation in plant roots.

To estimate the role of AM fungi and soil fertility on regeneration success, the cumulative number of naturally emerged seedlings of *O. acetosella* were recorded in all experimental units during one growing season (**II**). In addition, seeds of *Prunella vulgaris* were added to 40 experimental plots (10 per soil fertility and AM fungal activity treatment combination), and the cumulative number of emerged *P. vulgaris* seedlings was recorded on those plots during one vegetation period (**II**). Three seedlings of each species that were distant from one another were chosen and allowed to grow until the end of the growing season when the samples were harvested; the rest of the seedlings were weeded after recording. To estimate the role of AM fungi and soil fertility on seedling growth, the shoot- and root biomass of seedlings were separated, dried to a constant weight and weighed (**II**).

To study the effect of overstorey litter on seedling emergence and growth, a full factorial greenhouse study was established (**III**). The effects of litter amount (shallow, deep and leachate) and type (spruce, hazel and spruce + hazel, hereafter mixed) were tested on three common plant species, also found in the understorey of boreonemoral forests (*Geum rivale* L., *Hypericum maculatum* Crantz, *P. vulgaris*). Pots (1 dm³ volume, see Fig. 1 in **III**) were prepared by mixing field soil and sand (ratio 4:1). Soil was collected from the study system to preserve the natural abundance and composition of soil organisms. Freshly senesced, undecomposed leaves of hazel were collected in autumn 2008 and stored at –20 °C until use. Branches of spruce were cut in autumn 2008; fallen needles were collected afterwards and stored at –20 °C. Litter of hazel was cut to smaller pieces (2 cm²) to provide an even coverage of the pots and to enable litter mixtures to be formed.

Litter was applied to pots in a layer 4 mm deep (hereafter shallow litter) or 12 mm deep (hereafter deep litter). For the mixture treatment, equal amounts of spruce and hazel litter were combined and then applied to the pots. To distinguish the physical and chemical effects of litter, a litter leachate treatment was used. Leachate was extracted by collecting 12 mm (the same as the deep litter treatment) of spruce, hazel and mixed litter and placing it in mesh bags (15 bags, one per pot), which were kept in water (15 x 100 ml) for 48 h before the first application. Leachate (100 ml/pot) was then applied to pots every two days, when the other pots received the same amount of tap water. Water was

continually added to the mesh bags to simulate natural decomposition rates under field conditions. An additional 15 control pots, which received no litter, were included for each plant species.

Ten seeds were sown in each pot on the soil surface and were either covered with litter or left uncovered (controls). The number of emerged seedlings in each experimental unit was recorded at regular intervals during 65 days. In each pot the three individuals most distant from each other were selected after 26 days and retained; the other seedlings were removed from the pot to avoid intraspecific competition. Selected seedlings of each species were harvested after 65 days (at the end of the experiment), dried at 70 °C to a constant weight and weighed (III).

To estimate whether forest understorey composition and biomass varies in relation to the identity of the closest woody species, a descriptive study was conducted (IV). Three microsite types were distinguished in the understorey: 1. under spruce trees, 2. under hazel shrubs, and 3. in forest gaps (all hereafter referred to as microsites). Vascular plant species richness and percent cover of vascular plants and bryophytes was estimated in 60 plots — 30 each for microsite types 1 and 2. In addition, data from 30 plots (1 x 1 m) described in Moora et al. (2007) from the same sampling area with no tree cover were used (i.e. representing microsite type 3). The standing biomass of bryophytes and herbaceous and woody plants was harvested from a 50 x 100 cm area in half the plots (15 each under spruce and hazel). Biomass was dried to a constant weight at 70 °C and weighed.

To explore potential variation in abiotic conditions in relation to the closest woody species, light, soil and litter conditions were recorded (IV). The thickness of the litter layer was measured and litter samples were collected. Topsoil (1–10 cm) samples were collected and analysed for P, K, Mg, Ca content mg/kg, % of N and organic matter and pH_{KCl} .

2.3. Data analysis

The ratio between AM fungi and other fungi was calculated to estimate the relative importance of AM fungi for herbaceous plants (I). Generalized Linear Mixed Models (GLMM) were used to determine the role of soil nutrients, AM fungi and the ratio between AM fungi and other fungi in explaining the above- and belowground biomass of herbaceous plants at small scales.

The effect of experimental treatments (fertilizer and sugar addition; fungicide addition) and their interaction on soil parameters, root AM fungal colonisation (%) and seedling shoot and root dry weight (g) was estimated using Two-way Analysis of Variance (ANOVA). The effect of experimental treatments on the cumulative number of seedlings was estimated using Generalized Linear Models (GLM) for Poisson distributed data, with soil fertility (three levels) and mycorrhizal status (two levels) serving as fixed factors. Fisher's LSD post hoc multiple comparisons test was applied with a significance level of 0.05 in order

to estimate the significance of differences between treatments. Biomass and percentage of AM fungal colonisation data were log- and arcsine transformed, respectively, prior to statistical analysis (II).

Seedling responses to the litter treatments were estimated by calculating logarithmic (log) response ratios (III). Log response ratios were calculated as: In emergence or biomass of treated plant/average emergence or biomass of control plants. As the log response ratio cannot be calculated for pots without emerged seedlings, these were excluded from analysis, and therefore replication was reduced for some treatments (Table 1 in III). The effect of litter was considered significant when the 95% confidence interval of the ratio did not overlap with zero (i.e. treated values were different from the control). Three-way ANOVA with Tukey's HSD test was used to compare the log response ratio of seedling emergence and biomass of three understorey species under the different litter treatments (litter amounts: shallow, deep, leachate and litter types: spruce, hazel, mixed; see III).

One-way ANOVA with Tukey's HSD test was used to compare understorey species richness, cover and biomass in the three microsite types associated with woody species or gaps (IV). Indicator species analysis (Dufrenoy & Legendre 1997) was used to detect characteristic species associated with each of the microsites. Non-parametric analysis (Mann-Whitney U-test) was used to test for differences in litter layer depth and topsoil chemical content under spruce and hazel, since these data failed to meet the assumptions of parametric tests (IV).

3. RESULTS

3.1. The effect of soil nutrients and AM fungi on plant community above- and belowground biomass and composition

Small-scale aboveground biomass of herbaceous plants increased when soil fertility was experimentally enhanced (II), while it showed mixed responses to the abundance of AM fungi. The aboveground biomass of herbaceous plants increased both in relation to the ratio of AM fungi: other fungi in natural conditions (I) – and to the suppression of the abundance of AM fungi in experimental conditions (Fig. 1E in II). The belowground biomass of herbaceous plants was not affected by natural (I) or experimental (Fig. 1D in II) variation in soil nutrient content or abundance of AM fungi.

Understorey plant community composition was not directly influenced by the experimental manipulation of soil fertility and AM fungal abundance (II). However, the effect of AM fungi seemed to depend on the level of soil fertility, as there was a marginally significant difference between plant communities with natural and suppressed AM abundance in conditions of enhanced soil fertility (II). In addition, the vegetative growth of one of the most abundant species, *Luzula pilosa* (L.) Willd., increased with the suppression of AM fungi (Fig. 2A in II). Another abundant plant species, *Veronica chamaedrys* L., showed a corresponding decrease in vegetative growth in response to the suppression of AM fungi (Fig. 2B in II).

3.2. The role of AM on herbaceous species regeneration by seeds and its dependence on soil fertility level

The number of naturally occurring *O. acetosella* seedlings showed no response to the manipulated abundance of AM fungi or soil fertility (II). Suppression of AM fungi decreased the number of emerging *P. vulgaris* seedlings, while the level of soil fertility had no significant effect (II).

Aboveground biomass of *O. acetosella* seedlings was significantly higher in conditions with experimentally decreased soil fertility when the abundance of AM fungi was unaffected, compared to conditions with decreased soil fertility and suppressed abundance of AM fungi (II). Aboveground biomass of *P. vulgaris* was not affected by the experimental treatments (II).

3.3. The effect of litter type and amount on herbaceous species regeneration by seeds

Seedling emergence responded differently to all litter amount and type treatments (Table 2, Fig. 2A in **III**). However, the influence of litter amount was clearly dependent on litter type (Table 2, Fig. 2A in **III**). Spruce litter had a negative effect on emergence; and the effect was greatest in deep litter conditions. Mixed litter also tended to inhibit emergence, but a significant effect appeared only in the deep litter treatment. Seedling emergence in the shallow hazel litter treatments did not significantly differ from the control (95% confidence intervals overlapping 0-line), and there was no difference with changing litter depth (Table 2, Fig. 2A in **III**). Similarly, the effect of spruce leachate was strongly negative, whereas hazel and mixed litter leachate had milder suppressive effects (Table 2, Fig. 2A in **III**). The ability of understorey species to tolerate litter differed between species (Table 2, Fig. 3A, B, C in **III**).

Seedling biomass also responded differently to all litter amount and type treatments (Table 2, Fig. 2B in **III**). As was observed in the emergence data, the influence of litter amount was dependent on litter type (Table 2, Fig. 2B in **III**). The effect of shallow hazel litter did not significantly affect biomass, but the effect was significantly positive for deep litter (Table 2, Fig. 2B in **III**). Mixed litter had a significantly positive effect on biomass that increased with depth, whereas the effect of spruce litter was neutral for both depths (Table 2, Fig. 2B in **III**). Leachate continued to have negative effect for biomass acquisition: the effect was strongest for spruce, intermediate for mixed and weakest for hazel (Fig. 2B in **III**). The effect of litter amount and type differed between the understorey study species (Table 2, Fig. 3D, E, F in **III**).

3.4. The association between woody species and patterns of understorey vegetation

Understorey species richness was twice as high under hazel compared to spruce and intermediate in gaps (Table 1 in **IV**). In addition, a considerable number of species found under hazel never occurred under spruce, and several understorey species were significantly associated with hazel (Table 2 in **IV**). The biomass of herbaceous species was also greater under hazel compared to spruce (Table 1 in **IV**).

Litter layer depth differed under hazel and spruce, being approximately three times thicker under the latter (Tables 1 and 3 in **IV**). Topsoil P and K concentration also differed under hazel and spruce, with both higher under spruce (Table 3 in **IV**). Light conditions under hazel and spruce canopies did not differ (Table 1 in **IV**).

4. DISCUSSION

4.1. The effect of soil nutrient content and abundance of AM fungi on the understorey

4.1.1. Above- and belowground biomass and community composition

The aboveground biomass of herbaceous species in the understorey responded to variation in abiotic and biotic factors (**I**, **II**, **IV**). This reflects the light limitation of understorey plants in forest ecosystems, as suggested by earlier studies (Svenning & Skov 2002, Hardtle et al. 2005, Moora et al. 2007). Indeed, increased soil nutrient availability brought about higher aboveground biomass (**II**) as has been shown in numerous previous studies (e.g. Manninen et al. 2011, Marshall et al. 2011). Similarly, a greater proportion of AM fungi in comparison to other fungi led to an increase in aboveground biomass (**I**), as has been reported earlier (e.g. Bennett & Bever 2007). At the same time, an increase in aboveground biomass also followed the suppression of AM fungal activity (**II**). Rather than reflecting AM fungal activity, this result could be a consequence of plants being released from fungi other than AM (e.g. pathogenic fungi, Maron et al. 2011), as the fungicide used was not selective to AM fungi (Welc et al. 2010). Improved growing conditions enabled plants to invest more resources into competition for light. As light reaching to the understorey is similar despite the variation in overstorey species (**IV**), one might expect that main light competition occurs among understorey plants in which higher aboveground biomass can give a remarkable advantage.

The results of this study demonstrated that small-scale variation in soil nutrient content does not affect understorey belowground biomass (**I**, **II**). Several greenhouse studies have showed increased belowground biomass with high nutrient content (Hutchings & Wijesinghe 1997, Day et al. 2003a,b). Those contrasting results suggest that the cost of root growth may outweigh the benefits coming from higher nutrient content in an old and relatively stable natural ecosystem where soil conditions are quite uniform (Zobel et al. 2007). In addition, the strong growth response to nutrient content observed in experimental conditions (Hutchings & Wijesinghe 1997, Day et al. 2003a,b) may reflect the lack of mycorrhizal fungi in those artificial systems. Herbaceous plants in natural ecosystems such as boreonemoral forests are predominantly arbuscular mycorrhizal (AM) (Öpik et al. 2008, Uibopuu et al. 2012). Therefore they can acquire a high proportion of nutrients from soil via AM fungi when soil nutrient content is low, and there may be no need for plants to invest in higher root growth in nutrient rich patches. No significant effect of AM fungal abundance on belowground plant biomass was recorded either (**I**, **II**). Thus it seems that in stable ecosystems, a higher proportion of plant nutrition occurs through AM fungi in case of low soil fertility and *vice versa*, resulting in uniformly distributed belowground biomass (**I**, **II**).

Suppression of AM fungi led to differences in the plant communities growing under enhanced soil fertility (II), which may reflect the loss of the beneficial effect of AM symbiosis for plants in fertile soil (van der Heijden & Horton 2009). Some plant species may suffer more than others from mycorrhizal growth depression in fertile conditions, as they are unable to discard the symbiotic interaction that is no longer beneficial (Johnson et al. 1997). Changes in the abundance of such species might lead to differences in plant community composition, although establishing the presence of such a mechanism requires further study. Alternatively, it is possible that direct nutrient uptake via plant roots was lower in plants with natural as compared to suppressed AM fungi, but that mycorrhizal nutrient uptake did not compensate for the difference, resulting in higher biomass of plants with suppressed AM fungi. This pattern coincides with reported negative growth responses of mycorrhizal plants with a functional fungal nutrient uptake pathway compared to non-mycorrhizal plants without it (Grace et al. 2009). A third non-exclusive explanation could be that without potentially suppressed pathogenic fungi in the fungicide treatment, the less mycorrhiza-responsive plants were able to gain a greater benefit from the increased soil nutrient content, having been released from pathogen suppression (Maron et al. 2011). The variety of plausible mechanisms that could generate the observed results is indicative of the complexity of interpreting mycorrhizal roles in natural communities (Smith & Smith 2012).

4.1.2. Regeneration success: seedling number and biomass

The results of this study show that the effects of abiotic and biotic factors on regeneration success differ between species and seedling development stages (II). The emergence of *O. acetosella* was unaffected by experimental manipulations of soil fertility and AM fungal activity, but subsequent growth was enhanced by the natural activity of AM fungi when soil fertility was decreased (II). Under conditions of low soil fertility, seedlings experience less shoot competition than in fertile conditions, where plants allocate more biomass aboveground (Bazzaz 2004, II). At the same time, seedlings growing in low soil fertility conditions may experience greater nutrient stress, and AM symbiosis can improve nutrition for many plant species (van der Heijden & Horton 2009). Suppression of AM fungi under conditions of low soil fertility may therefore result in inhibited seedling growth. In contrast to the behaviour of *O. acetosella*, emergence of *P. vulgaris* was positively influenced by the natural abundance of AM fungi, but the subsequent growth of these seedlings showed no significant response to experimental manipulations (II). This shows that the growth of seedlings of this plant species does not depend on the presence of AM fungi even when soil fertility is low. *O. acetosella* is a plant species that is specialised to forests and has been shown to harbour a high number of AM fungi in its roots when growing in this study area (Öpik et al. 2009, Davison et al. 2011). In contrast, *P. vulgaris* is considered to be a habitat generalist, and habitat generalists in this study area tend to harbour lower numbers of AM fungi in

their roots than habitat specialists (Öpik et al. 2009, Davison et al. 2011). It seems that the observed differences in the emergence success and seedling growth (II) may reflect ecological characteristics: plant species that are specialised to the habitat are more directly influenced by local biotic and abiotic factors than habitat generalist species.

4.2. The effect of litter on seed emergence and seedling growth

As woody species are considerably larger than herbaceous species, they also produce more litter, which can influence understorey vegetation. Indeed, it is known that seedlings of only a few species are able to penetrate thick litter layers in forests (Graae & Heskjaer 1997). However, the current study revealed that litter depth *per se* does not determine emergence success in several common forest herbs; rather, its effect is dependent on litter type (III). The negative effect of spruce litter on seedling emergence increased with litter layer depth (III), suggesting that the negative effect of spruce occurs partly through physical interference (Facelli & Pickett 1991a). The effect of hazel litter did not have any influence on emergence, regardless of depth (Fig. 2A in III). Effects of litter type on seedling emergence have previously been attributed to differences in litter structure (Sydes & Grime 1981, Quested & Eriksson 2006, Donath & Eckstein 2008, 2010). Donath and Eckstein (2008) suggested that emergence from below oak litter may be easier compared to grass litter, which forms dense mats on the ground, because seedlings may displace oak leaves during emergence. Spruce needle litter also forms dense mats, whereas hazel leaves stay loose on the ground and rapidly lose mass, which might explain the differential effects of litter type found in this study (III). Chemical effects of litter are expected to be mostly negative (Facelli & Pickett 1991a). Indeed, both hazel and spruce leachate suppressed seedling emergence (III), although the observed effect was relatively mild, supporting the importance of the physical structure of litter. Litter in natural habitats is rarely monospecific (Facelli & Pickett 1991a), and inclusion of hazel litter with spruce litter reduced the negative effect of spruce litter and enabled a higher number of understorey species to emerge (III), possibly by preventing the formation of dense spruce mats and mitigating chemical inhibition.

Seedling emergence is expected to be more susceptible than subsequent growth stages to the effects of litter (Xiong & Nilsson 1999). Indeed, contrasting with the mostly negative effects on seedling emergence, the effect of litter on seedling growth ranged from neutral to positive, whereas leachate of both spruce and hazel litter suppressed seedling growth (III). The positive effect of hazel litter on seedling growth, which increased with depth (III), could be the result of more stable temperature and/or moisture conditions compared to bare ground (Facelli & Pickett 1991a, Eckstein & Donath 2005, Donath & Eckstein 2010) and/or faster decomposition rates of deciduous litter releasing

nutrients for seedling growth (Cornwell et al. 2008). The neutral effect of spruce litter suggests that spruce litter structure does not create better conditions for growth compared to bare ground. It is also possible that positive and negative effects are balanced out, i.e. the positive effects are reduced by chemical inhibition, resulting in a net neutral effect. When spruce litter is mixed with hazel, it has a positive effect on seedling growth (**III**) which results in enhanced understorey productivity (**IV**). Observed pattern might be largely attributable to the positive effect of hazel litter; but it may also reflect accelerated decomposition rates of spruce litter in mixtures, as it has been reported that deciduous litter decomposes faster than evergreen litter (Saetre 1999, Mohr et al. 2005).

4.3. The association between woody species and herbaceous species in the understorey

Sparsely located deciduous overstorey trees have been shown to have a positive effect on understorey species richness in coniferous forest (Wallrup et al. 2006). By contrast, shrubs have been shown to have a negative effect on understorey richness in temperate zones, possibly through the negative effect of additional shading (Godefroid et al. 2005). Our study revealed a significant positive association between the abundance of several herbaceous species and dominant subcanopy species (**IV**). The presence of a deciduous subcanopy may therefore be one of the key factors explaining the presence of understorey species characteristic of forests and the species rich herb layer in boreonemoral spruce forests.

High understorey species richness and biomass under hazel (**IV**) probably reflect the microsite changes generated by the species (Tirado & Pugnaire 2005, Cavieres & Badano 2009), which may be more favorable for understorey species than those under spruce canopy. Changes in local environment can occur through altered abiotic factors. Indeed, hazel litter has been shown to increase soil nutrient content (Mohr et al. 2005). However, soil nutrient content was not higher under hazel compared to spruce (**IV**), which reflects the modest role of soil nutrients in structuring the understorey in the current study system (**I, II**). Hazel litter can also have a direct effect on the understorey, as it is more favorable to seed emergence and seedling growth than spruce litter (**III**). In addition, hazel can influence the understorey by impeding the formation of a thick litter layer (**IV**), as thick litter layers are generally known to suppress the development of understorey species (Xiong & Nilsson 1999, **III**).

Woody species can also affect the understorey through direct and indirect changes in biotic factors. For example, the easily decomposable litter of herbaceous species and deciduous hazel can increase the abundance of macrofauna (Vos et al. 2011, Slade & Riutta 2012) and elevate nutrient circulation through increased decomposition processes. In addition, woody species can affect the abundance of soil microbes like mycorrhizal fungi (Klironomos et al. 1999, Saetre & Bååth 2000, Bach et al. 2010). The proportion of ectomycorrhizal and AM fungi can have a strong effect on the understorey (**I**), and the abundance of

soil microbes can be influenced by woody species (Saetre & Bååth 2000). Spruce and hazel both live in symbiosis with ectomycorrhizal fungi (e.g. Tedersoo et al. 2008, Weden et al. 2009), whereas the majority of herbaceous species in the understorey live in symbiosis with AM fungi (Öpik et al. 2008). Mycorrhizal fungi can be influenced by the effects of litter, and the presence of litter from ectomycorrhizal species is known to increase the colonisation of ectomycorrhizal fungi and decrease the colonisation of AM fungi (Becklin et al. 2012). The abundance of AM fungi has been shown to increase with the number of plant species (De Deyn et al. 2011, Spence et al. 2011). Therefore it is conceivable that microsites under spruce canopy, which have a thick litter layer (IV), are unfavorable for understorey growth due to the high abundance of ectomycorrhizal fungi. On the other hand, microsites under hazel, which have a shallower litter layer and a higher number and biomass of vascular plant species (IV), might be expected to contain a higher abundance of AM fungi and present more favorable conditions for the growth of understorey species.

The number of plants specialised to forest habitat is known to decrease with habitat fragmentation (Jamoneau et al. 2012); hence, changes in land use can clearly affect understorey plant communities. Similarly, AM fungal colonisation of host plants and the composition of AM fungal communities have been shown to vary between sites with different land use history (Boerner et al. 1996, Uibopuu et al. 2009, Davison et al. 2011). Plants also seem to exhibit preferences between different AM fungal partners (Moora et al. 2004a,b, Uibopuu et al. 2009). As the growth of a forest specialist plant species was enhanced by AM fungi (II), a lack of suitable symbiotic fungi could be an important factor limiting the establishment of forest specialist plant species, especially in conditions with low nutrient availability. Future studies could aim to verify this suggestion and to disentangle the effects of different abiotic and biotic factors – including different litter types, light conditions and the presence of woody species — on this symbiotic relationship.

5. CONCLUSIONS

The results of the thesis demonstrate that the effects on forest understorey plant communities of several abiotic and biotic factors are interdependent and also depend on the vegetation parameter considered (**I**, **II**, **III**, **IV**). Small-scale variation in soil nutrient content and abundance of arbuscular mycorrhizal (AM) fungi play modest roles in determining belowground biomass (**I**, **II**). Soil nutrients are easily accessible for plant roots when their concentration is high, and fungal symbionts seem to play a larger role in nutrient transport when soil nutrient conditions are poor, hence providing an equally good nutrient supply for plants. However, soil nutrient content and the abundance of AM fungi had a significant effect on the aboveground biomass of understorey plants (**I**, **II**). As forest understorey is frequently light limited, improved nutrition conditions can result in changes in aboveground biomass.

An effect of AM fungi on understorey community composition was apparent only in conditions of enhanced soil fertility (**II**), which is indicative of the complexity of interpreting mycorrhizal roles in natural communities. The results of this study highlight the importance of data collected in natural conditions to improve existing knowledge about factors like the presence of AM fungi on plant communities.

Regeneration by seeds is strongly influenced by different factors: soil fertility, abundance of AM fungi, presence and type of litter layer (**II**, **III**). Germination and growth responses may be plant ecological group- rather than species-specific (**II**). Seedling growth of a forest specialist plant species, which harbours a high diversity of AM fungi in its roots, was enhanced by AM fungi under low soil fertility. In comparison, a habitat generalist plant, which has been shown to live in symbiosis with a relatively lower number of AM fungi, did not benefit from the presence of AM fungi in any conditions.

Overstorey species influence the small-scale pattern of the understorey, and herbaceous species richness and biomass was considerably higher under hazel compared to spruce (**IV**). The effect of the overstorey might occur through the pattern of litter accumulation on the forest floor – the litter layer was three times thicker under spruce compared to hazel (**IV**). This could have a crucial influence on the emergence success and seedling growth of understorey species (**III**).

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SUMMARY IN ESTONIAN

Abiootiliste ja biootiliste tegurite väikeseskaalalise varieerumise mõju metsa alustaimestiku struktuurile ja koosseisule

Suurel osal maismaast on mets kliimaskoosluseks, mis tähendab, et looduslike tingimuste juures oleks suur osa Maa pinnast metsaga kaetud. Inimtegevuse tagajärjel on aga metsade pindala aja jooksul dramaatiliselt vähenenud. Üha arenev tehnoloogia ning loodusliku mitmekesisuse väärtustamine võimaldab mitmel pool maailmas tänapäeval haritava maa pindala vähendada, luues seeläbi võimaluse metsade pindala suurenemiseks. Varasemalt haritud aladele kasvama hakanud metsad aga erinevad tihtipeale vanadest looduslikest metsadest mitmete omaduste, näiteks rohttaimede liigirikkuse ning liigilise koosseisu poolest. Kui vanadele metsadele tüüpilisi taimeliike iseloomustab varjataluvus ning vähene levimisvõime, siis varasemalt haritud aladele kasvanud metsas domineerivad sageli valgus- ja toitainetenõudlikud taimed, mis on ka hea konkurentsivõimega ning pärsivad seetõttu tüüpiliste metsataimede kasvu. Metsa alustaimestiku liikide paljunemist ja kasvu mõjutavate tegurite mõistmine on seega oluline metsaökosüsteemi funktsioneerimise ning bioloogilise mitmekesisuse säilitamiseks, kuna alustaimestikus olevad liigid võivad moodustada rohkem kui 90% metsade liigirikkusest.

Taimed tajuvad eelkõige neid vahetult ümbritsevat keskkonda, mis tähendab, et kui ümbritseva keskkonna heterogeensuse skaala on oluliselt suurem või väiksem kui taimeindiviid, siis tajub taim keskkonda homogeensena. Seetõttu on oluline mõista, kuidas just erinevate abiootiliste ja biootiliste tegurite väikeseskaalaline varieeruvus üksikute taimede kasvu ning taimekoosluste kujunemist mõjutab. Abiootiliste tegurite nagu ressursside (näit. mullas olevate toitainete) tase mängib taimede kasvu määramisel vaieldamatult olulist rolli. On ka teada, et kui toitainete väikeseskaalaline jaotus mullas on heterogeenne (st. toitainete laigu suurus on umbkaudu võrdne taimeisendi juurestiku ulatusega), siis suudavad taimed neid laike eristada ning suunata oma juured toitainerikkasse laiku. Samas ei ole üheselt selge, kui oluline roll on väikeseskaalalisel toitainete heterogeensusel taimekoosluste mustrite kujundamisel. Lisaks mõjutavad taimede kasvu oluliselt ka biootilised tegurid nagu näiteks arbuskulaar-mükoriisete (AM) seente olemasolu. AM seened koloniseerivad enamiku maismaataimede juuri ning aitavad taimedel mullast toitaineid omastada, saades vastutasuks süsivesikuid. Seetõttu võib arvata, et AM seente olemasolu on eriti oluline väheviljakates mullaoludes kasvavatele taimedele, kuid tõendid selle kohta puuduvad.

Metsaökosüsteemis on kõik abiootilised ja biootilised tegurid vähemal või suuremal määral puude poolt mõjutatud. Üks oluline tegur, mille kaudu puud oma ümbritsevat keskkonda mõjutavad, on varis, mis võib omakorda mõjutada näiteks mulla keemilisi omadusi, aga ka mullaorganismide mitmekesisust. Puude lokaalset keskkonda kujundav mõju võib viia muutusteni alustaimestiku katvuses, liigilises koosseisus ning mitmekesisuses. Samas on vähe teada,

kuidas põõsad, mis on samuti puittaimed, alustaimestikku mõjutavad. Taimekoosluse arengu võtmeetappideks on idanemine ning idandite edukas ellujäämine. Need etapid on erinevatele abiootilistele ning biootilistele mõjuvustele väga vastuvõtlikud. Siiani on aga vähe teada, milline on metsa alustaimestiku liikide idanemise ja kasvamise edukus erinevate mullatingimuste, AM seente ohtruse ning varisekihi omaduste juures. Arvestades eelpool mainitud lünki meie teadmistes, valiti käesoleva doktoritöö mudelsüsteemiks Koerus asuv küps salukuusik, mille alustaimestiku ning AM seente koosluste kohta on juba olemas üsna põhjalikud teadmised.

Käesoleva väitekirja esimeseks eesmärgiks oli välja selgitada, kas väikese-skaalaline varieeruvus toitainete hulgas ja AM seente ohtruses mõjutavad ka alustaimestiku biomassi ja liigilist koosseisu. Selleks määrati väikestelt proovialadelt ($d=15$ cm) rohttaimede biomass, mulla toitainete sisadus ja AM seente ohtrus ja seda nii looduslikes (**I**) kui ka eksperimentaalsetes (**II**) tingimustes. Tulemused näitasid, et kuigi mulla toitainetesisaldus ja AM seente ohtrus varieerus, püsis rohttaimede juurte biomass muutumatuna (**I**, **II**). Sellest järeldub, et stabiilses ökosüsteemis, kus rohttaimed elavad sümbioosis AM seentega, on neil seentel suurem roll taimede toitainete hankimisel, kui toitainetesisaldus on madal, ja vastupidi. Taimedele on taolisel juhul tagatud lokaalselt võrdselt head toitumistingimused, hoolimata mulla toitainetesisaldusest – toitainete väiksemat sisaldust mullas kompenseerib AM sümbioos, mis aitab olemasolevat toitainetevaru efektiivsemalt omandada. Metsa alustaimestiku kasv on sageli aga mitte toitainete vaid valguse poolt piiratud ning igal võimalusel suunavad taimed rohkem ressursse võsude kasvaks, et nii valguskonkurentsis edukamad olla. Seda kinnitab ka antud töös leitud rohttaimede võsude biomassi suurenemine juhul, kui mullas olevaid toitaineid (**II**) või AM seeni oli ülejäänud seentega võrreldes ohtralt (**I**). Samas viis ka eksperimentaalne AM seente ohtruse pärssimine võsude biomassi suurenemiseni (**II**), mis näitab AM seente ja taimede suhete keerukust. Alustaimestiku liigilise koosseisu uurimine näitas, et AM seente mõju taimekooslusele sõltub mullaviljakusest (**II**). Loodusliku ning pärstitud AM seente ohtrusega kasvanud taimekooslused eristusid ainult viljakate mullatingimuste juures. Kirjeldatud muster võib tuleneda sellest, et kõrge toitainetesisalduse korral osutub osadele taimeliikidele kulukamaks varustada juurtes elavaid AM seeni süsinikuga, kui investeerida juurte kasvu ning nende kaudu toitaineid omastada. Seega võib viljakates tingimustes selliste taimeliikide ohtrus väheneda.

Käesoleva doktoritöö teiseks eesmärgiks oli selgitada, kuidas looduslik AM seente ohtrus mõjutab alustaimestiku taimeliikide idanemist ning idandite kasvu erineva mullaviljakuse juures (**II**). Selleks tõsteti ning langetati välieksperimendis mullaviljakust ning pärstiti fungitsiidiga AM seente ohtrust, mille järel jälgiti taimeliikide idanemist ja idandite kasvu. Tulemused näitasid, et vaatlusalustest liikidest ühe – hariliku jänese kapsa (*Oxalis acetosella*) – idanemine ei ole AM seente ohtruse poolt mõjutatud. Idandite kasv aga sõltus oluliselt mullaviljakuse ja AM seente ohtruse koosmõjust – madala mullaviljakuse korral olid idandid koos ohtra AM seenekooslusega kasvades suuremad, samas

kui viljakal mullal AM seente ohtrus idandite kasvu ei mõjutanud (II). Teine katseliik – harilik käbihein (*Prunella vulgaris*) – idanes paremini looduslikult ohtra AM seente kooslusega, kuid idandite kasv ei olnud AM seente arvukusest mõjutatud (II). Harilik jänesekapsas on tüüpiline metsataim, mis elab sümbioosis arvukate AM seentega. Harilik käbihein on seevastu laia ökoloogilise amplituudiga liik ning nagu näitavad varasemad uurimused, elavad sellised liigid sümbioosis tunduvalt väiksema arvu AM seenetaksonitega. Käesoleva töö tulemused viitavad sellele, et kasvukohale spetsialiseerunud taimeliikide idanemine ja kasv sõltub abiootilistest ja biootilistest teguritest suuremal määral kui laia ökoloogilise amplituudiga taimeliikide oma.

On teada, et ainult mõne taimeliigi idandid suudavad tungida läbi paksu varisekihi, mistõttu varisekihi omadused metsas kujundavad olulisel määral ka alustaimestiku liigilist koosseisu. Käesoleva töö kolmandaks eesmärgiks oli uurida hariliku kuuse (*Picea abies*) kui domineeriva puuliigi ja hariliku sarapuu (*Corylus avellana*) kui domineeriva põõsaliigi varise mõju rohttaimede idanemisele ja idandite kasvule (III). Selleks katsime eksperimentaalsetes tingimustes looduslikule mullale külvatud seemned erineva tüsedusega kuuse või sarapuu varisega. Selgus, et varise mõju sõltub lisaks tüsedusele väga olulisel määral ka varise tüübist – kuuse varise negatiivne mõju kasvas koos kihi tüsedusega, samas kui sarapuu varisel puudus oluline mõju isegi suure tüseduse korral (III). Ilmselt tulenevad erinevad mõjud variste erinevast struktuurist – kuuse varisest moodustub maapinnale tihe matt, samas kui sarapuu varis jääb maapinnale õhulise kihina ning kõduneb kiiresti. Idandite kasvule ei avaldanud kuuse varis, ka tüseda kihina, aga olulist mõju (III). Sarapuu varis seevastu suurendas idandite biomassi (III), kuna ilmselt olid selle varisekihi all stabiilsem temperatuur ja paremad niiskustingimused kui paljal maapinnal.

Neljandaks selgitas käesolev väitekiri, kas metsa alustaimestiku liikide esinemine ja arvukus on seotud lähima puittaimega (IV). Selleks registreeriti alustaimestiku liigirikkus, mulla toitainetesisaldus ja varisekihi tüsedus nii kuuse kui sarapuu lähistel. Tulemused näitasid puittaimede selget mõju alustaimestikule – sarapuude all leidis oluliselt rohkem taimeliike nii kõiki liike kui ka metsadele tüüpilisi taimeliike vaadates (IV). Lisaks liigirikkusele oli ka rohttaimede biomass sarapuu all oluliselt suurem kui kuuse all (IV). Vaadeldud erinevust saab selgitada puittaimede poolt avaldatava biootilise mõjuga (juurkonkurents) või nende poolt muudetud abiootiliste tingimustega. Mõõtmistest selgus, et mullaparametrid sarapuude all ei erine tingimustest kuuskede all, küll aga on sealne varisekiht ligi kolm korda õhem (IV). Sellest järeldub, et kuusikus, kus põõsarindes domineerib sarapuu, takistab viimane tiheda varisekihi moodustumist ning loob seeläbi rohttaimedele idanemiseks ning kasvuks soodsamaid tingimusi (III).

Käesolevas doktoritöös esitatud tulemused näitavad, et metsa alustaimestiku liigilist koosseisu ning sealsete liikide uuenemist mõjutab keeruline ökoloogiliste interaktsioonide kompleks, kus olulised on nii otsesed biootilised interaktsioonid (konkurents, sümbioos) kui ka organismide poolt mõjutatud

lokaalsed abiootilised tingimused. Käsitatud keerukate mõjude uurimine toob endaga kaasa parema arusaamise looduse dünaamikast, mida on võimalik kasutada ka looduskaitselistel eesmärkidel, näiteks vanadele metsadele iseloomuliku taimkatte taastamisel varasemalt kultiveeritud aladele kasvama hakanud metsades.

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- Koorem, K., Price, J.N. & Moora, M. 2011. Species-specific effects of woody litter on seedling emergence and growth of herbaceous plants. *PLoS ONE* 6(10): e26505.
- Koorem, K. & Moora, M. 2010. Positive association between understory species richness and a dominant shrub species (*Corylus avellana*) in a boreonemoral spruce forest. *Forest Ecology and Management* 260: 1407–1413.

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DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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