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Soil microbial communities in changing landscapes: spatiotemporal patterns in arbuscular mycorrhizal fungi

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Soil microbial communities in changing landscapes: spatiotemporal patterns in arbuscular mycorrhizal fungi

UNIVERSITY OF TARTU
Press

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

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LIST OF PUBLICATIONS

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

I) **Zárate Martínez O**, Hiiesalu I, Sepp S-K, Koorem K, Vasar M, Wipulasena AYAP, Liu S, Astover A, Öpik M, Pärtel M, Vahter T. 2024. Arbuscular mycorrhizal fungal diversity in agricultural fields is explained by the historical proximity to natural habitats. *Soil Biology and Biochemistry* 199: 109591

II) **Zárate Martínez O**, Degtjarenko P, Davison J, Helm A, Jõks M, Kõljalg U, Kook E, Mander Ü, Niinemets Ü, Öpik M, Vahter T, Vasar M, Võsaste M, Zobel M, Kohout P, Pärtel M. A century-long grassland legacy predicts arbuscular mycorrhizal fungal diversity in an urban landscape (Manuscript)

III) Riibak K, Noreika N, Helm A, Öpik M, Kook E, Kasari-Toussaint L, Jõks M, Paganeli B, **Zárate Martínez O**, Tullus H, Lutter R, Oja E, Saag A, Randlane T, Pärtel M. 2024. Plants, fungi, and carabid beetles in temperate forests: both observed and dark diversity depend on habitat availability in space and time. *Landscape Ecology* 39: 158.

IV) Pärtel M, Degtjarenko P, Davison J, Helm A, Jõks M, Kõljalg U, Kook E, Mander Ü, Niinemets Ü, Org E, Peet A, Tillmann V, Vasar M, Voor T, Võsaste M, **Zárate Martínez O**, Zobel M. 2026. Urban soil *Gammaproteobacteria* diversity, shaped by biodiverse land use, predicts a lower risk of developing allergy in children. *Urban Forestry & Urban Greening* 122: 129514.

Author's contributions to the publications:

	I	II	III	IV
Original idea	***	***	*	*
Study design	*	**	*	*
Data collection	***	**	*	*
Analysis and interpretation	***	***	**	**
Manuscript writing	***	***	*	*

minor contribution (*), moderate contribution (**), large contribution/leading role (***)

I. INTRODUCTION

1.1 Background

Human activities are transforming landscapes worldwide, with land-use change recognised as one of the dominant direct drivers of recent biodiversity loss (Jaureguiberry et al., 2022). The conversion and fragmentation of forests, grasslands, wetlands and other semi-natural habitats modify not only the amount of habitat available for organisms, but also the spatial arrangement of habitats, the movement of organisms among them and the environmental conditions experienced locally (Fahrig, 2003; Gámez-Virués et al., 2015; Mony et al., 2021). As a result, present-day communities are driven by both local conditions and the broader landscape context in which they occur.

However, biodiversity does not always respond immediately to landscape change. Local communities may continue to reflect former habitat configurations because extinctions, colonisation and community reassembly can occur slowly (Hanski and Ovaskainen, 2002; Lira et al., 2019). Therefore, contemporary local biodiversity reflects present-day environmental filtering, dispersal limitation, and historical landscape effects.

Soil microbial community assembly has traditionally been explained mainly by local environmental conditions, disturbance and biotic interactions. This emphasis partly reflects Baas-Becking's influential idea that "everything is everywhere, but the environment selects", implying that microorganisms disperse widely and that local environmental conditions determine which taxa establish (Martiny et al., 2006; Cockell, 2021). However, advances in sequencing and spatially extensive microbial surveys have increasingly challenged this assumption, showing that microbial communities can also be structured by dispersal limitation, habitat availability or connectivity and landscape history. Because soil microbial communities regulate nutrient cycling, soil processes and influence plant performance, understanding how they respond to landscape structure is important for explaining biodiversity patterns in changing environments (Delgado-Baquerizo et al., 2016; Tedersoo et al., 2020).

Soil fungi are key components of soil microbial communities and contribute to several ecosystem functions, including decomposition, nutrient cycling, plant performance and ecosystem productivity (Bahram et al., 2020; Averill et al., 2022). These functions are mediated by fungal guilds with contrasting ecological roles, including saprotrophs, pathogens, and symbiotrophs (Peay et al., 2016). Among them, arbuscular mycorrhizal (AM) fungi are especially relevant because they form symbiotic associations with most terrestrial plants and contribute to nutrient acquisition, stress tolerance and primary productivity (Smith and Read, 2010). Their dependence on host plants and suitable soil conditions, combined with dispersal through spores, hyphal fragments and colonised roots, makes AM fungi a useful group for examining how belowground communities respond to both local environmental filters and broader landscape context.

1.2 Land-use change and landscape legacies

Land-use change is one of the main drivers of biodiversity dynamics worldwide, altering habitat amount, habitat connectivity, local environmental conditions and the spatial arrangement of ecological communities (Fahrig, 2003; Tscharntke et al., 2005). However, biodiversity at a given location is only partly determined by the current state of the habitat. Contemporary communities also reflect historical effects of landscape change, because organisms rarely respond instantaneously to changes in land-cover composition (Jackson and Sax, 2010; Lira et al., 2019). These delayed responses can lead to gradual local extinctions, colonisation lags and mismatches between present-day landscape structure and observed community patterns (Kuussaari et al., 2009).

Delayed biodiversity responses have been convincingly demonstrated in plant and animal communities, where habitat loss, fragmentation and changes in management can leave long-lasting effects on local species richness, composition and community completeness (Helm et al., 2006; Gustavsson et al., 2007; Kuussaari et al., 2009). Historical land use can be more strongly associated with present-day species diversity than current land use, as shown for grassland plants and soil microbial communities, with such legacy effects often attributed to slow changes in soil properties, species persistence after habitat change and past landscape configuration.

Delayed responses are also expected in soil microbial communities. Soils can retain physical, chemical and biological legacies of past land use (Fichtner et al., 2014). Microbial community structure depends on dispersal, habitat continuity, host availability and local environmental filtering (Fichtner et al., 2014; Mennicken et al., 2020). The combination of the former processes suggests that present-day soil microbial communities reflect not only current soil conditions, but also historical land-use legacies and the spatial arrangement of habitats through time (Brinkman et al., 2017).

Delayed biodiversity responses are commonly described through the concepts of extinction debt and colonisation credit. Extinction debt occurs when species persist temporarily after habitat loss or degradation, whereas colonisation credit occurs when newly available suitable habitats remain unoccupied because colonisation is slow (Tilman et al., 1994; Hanski and Ovaskainen, 2002). These concepts highlight why historical landscape information is needed to interpret whether present-day communities primarily reflect contemporary environmental filtering, persistence from past landscapes or incomplete colonisation of newly available habitats.

1.3 Scale dependence in landscape ecology

Ecological processes are scale-dependent (Levin, 1992). Habitat availability measured at different spatial extents can reflect different ecological influences, ranging from local habitat conditions to nearby source communities and broader opportunities for dispersal (Holland et al., 2004). Studies on macroorganisms show that relevant scales can vary widely among taxa and ecological contexts. For example, cerambycid beetle species responded to forest cover at scales ranging from 20 to 2000 m, indicating that even related species may perceive and respond to landscapes at different spatial extents (Holland et al., 2004). Similarly, forest plant communities in northern France were better explained by landscape composition at broader spatial extents than by smaller scales, suggesting that fine-scale analyses may miss broader spatial effects related to past landscape structure or long-distance dispersal (Avon et al., 2015).

The spatial extent at which landscape structure best explains a biodiversity response is known as the scale of effect (Jackson and Fahrig, 2012). Local environmental conditions may be driven by fine-scale variation among sites, whereas processes related to dispersal, habitat continuity and regional species pools may operate across broader spatial extents (Cadotte and Fukami, 2005). Therefore, evaluating landscape structure at multiple spatial scales is necessary to distinguish local habitat associations from broader landscape effects.

Scale dependence is also relevant for soil microbial communities. Although microorganisms can disperse through several pathways, their distributions may still be spatially structured when successful establishment depends on suitable environmental conditions, host organisms or propagule availability (Bäcker et al., 2026). In soils, microbial communities may therefore respond not only to local environmental filters, but also to the spatial arrangement of habitats, source communities and dispersal pathways in the surrounding landscape (Mony et al., 2020). A multi-scale approach can therefore provide a clearer understanding of whether belowground communities are mainly associated with local conditions, nearby source habitats or broader landscape context.

1.4 Soil microbial communities in changing landscapes

Soil microbial communities are central to terrestrial ecosystem functioning. They regulate nutrient cycling, decomposition, soil aggregation and plant performance (Delgado-Baquerizo et al., 2016; Tedersoo et al., 2020). Their responses to landscape structure remain less understood than those of plants and animals. Microbial communities are often studied in relation to local soil conditions, such as pH, nutrient availability and vegetation, but they are also embedded within broader landscapes. Habitat availability, connectivity and land-use history may influence microbial diversity by shaping dispersal pathways, source communities and the environmental filters that determine which taxa establish locally (Mony et al., 2020).

This is particularly relevant because microorganisms are not always unrestricted dispersers. Many microbial groups show spatial structure and may be limited by propagule dispersal, host availability or habitat continuity (Peay et al., 2010; Davison et al., 2012; Kivlin et al., 2021). Moreover, soils can retain physical, chemical and biological legacies of past land use, creating conditions under which microbial communities may respond to both contemporary habitat conditions and longer-term landscape histories (Gustavsson et al., 2007; Ranheim Sveen et al., 2026).

1.5 Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal (AM) fungi form symbiotic associations with the roots of most terrestrial plant species and contribute to nutrient exchange, soil structure, plant performance and vegetation dynamics (Smith and Read, 2010; Brundrett and Tedersoo, 2018). By mediating carbon, nitrogen and phosphorus cycling between above- and belowground ecosystem components, AM fungi link soil microbial communities with plant communities and ecosystem functioning (Van Der Heijden et al., 2008). Variation in AM fungal diversity and composition may therefore influence plant nutrition, stress tolerance, soil aggregation and the ability of vegetation to respond to environmental change.

Patterns of AM fungal diversity are governed by both local environmental filters and broader spatial processes. Local soil conditions, including pH, soil type, moisture and nutrient availability, can influence AM fungal richness and community composition, while host plant identity and plant community type determine the availability of compatible symbiotic partners (Kivlin et al., 2011; Davison et al., 2015, 2020). At broader scales, geographic distance, dispersal limitation and habitat filtering can also contribute to variation in AM fungal community structure (Kivlin et al., 2011; Boeraeve et al., 2019). Therefore, AM fungal communities should not be understood only as responses to local soil conditions, but also as communities shaped by dispersal, host availability and landscape context.

These ecological characteristics make AM fungi potentially sensitive to both spatial and temporal landscape processes. They disperse through spores, hyphal fragments and colonised roots, and their propagules may move through wind, water, animals and human-mediated soil movement (Correia et al., 2019; Chaudhary et al., 2020; Paz et al., 2021). However, successful establishment depends on suitable host plants and soil conditions, so dispersal does not necessarily translate into community assembly. At the same time, propagules can persist in soils, allowing communities to respond slowly to habitat change or retain associations with former habitat conditions (Carrillo-Saucedo et al., 2018; Aguilar-Trigueros et al., 2025). This combination of local filtering, dispersal limitation and propagule persistence provides a mechanistic basis for expecting AM fungal communities to reflect both present-day landscape context and historical land-use legacies.

1.6 Land-use change, disturbance and AM fungal communities

Land-use change can influence AM fungal communities through several pathways. Intensive agriculture, urbanisation, fertilisation, pollution and mechanical disturbance can reduce AM fungal diversity or alter community composition, although reported responses are often context-dependent (van der Heyde et al., 2017). Some studies have found lower AM fungal diversity in intensively managed habitats than in natural or semi-natural systems, while others report weak or inconsistent richness responses but clearer changes in community composition (Moora et al., 2014; Xiang et al., 2014; Pereira et al., 2022).

This context dependence suggests that AM fungal responses to land-use change may depend on more factors than local disturbance intensity alone (van der Heyde et al., 2017). Differences among studies may originate from variation in land-use history, surrounding habitat availability, spatial scale, host plant communities, soil conditions and the particular biodiversity metric studied. For example, changes in AM fungal richness may not always parallel changes in community composition, because land-use change can replace sensitive taxa with disturbance-tolerant taxa without immediately causing a decline in local diversity (Pereira et al., 2022).

Historical landscape structure may be especially relevant for AM fungi because their communities can respond slowly to habitat loss (Mennicken et al., 2020). Long-term habitat transformation may gradually reduce the abundance of disturbance-sensitive taxa or alter the pool of viable propagules available for colonisation (Saar et al., 2012; Liu et al., 2023). Incorporating historical landscape structure into analyses can therefore help evaluate whether present-day AM fungal diversity reflects only current habitat conditions or also legacies of former habitat availability.

1.7 Multiple facets of biodiversity

Biodiversity responses to landscape change can occur through several facets, not only through changes in local diversity. Communities may maintain similar richness while differing in species identity, ecological strategies or community completeness. Therefore, landscape effects can be underestimated when biodiversity is described using a single metric.

Species richness (alpha diversity) captures locally co-occurring taxa, whereas compositional measures describe differences in species identity among communities. Functional structure can reflect shifts towards taxa with particular ecological strategies, such as disturbance tolerance. Dark diversity, defined as the set of suitable but locally absent species, can provide information about dispersal limitation, colonisation lags, and community completeness. Considering these facets together provides a broader view of how landscape structure influences community assembly.

Taken together, these ideas suggest that AM fungal communities should be studied not only as responses to local soil conditions, but also as components of changing landscapes. Their present-day diversity may reflect local environmental filters, nearby habitat availability, historical land-use legacies and scale-dependent spatial processes. Examining these mechanisms across contrasting land-use systems can therefore provide a clearer understanding of how belowground biodiversity responds to landscape change.

II. AIMS

The overall aim of this thesis was to examine how landscape structure across space and time influences soil microbial communities, with a particular focus on arbuscular mycorrhizal (AM) fungi. Specifically, this thesis addressed the following questions:

1. Does historical landscape structure explain present-day AM fungal diversity better than current landscape structure across contrasting land-use systems? (**I, II, III**)
2. How does the spatial scale at which landscape structure is measured influence soil microbial diversity and community composition? (**I, II, III**)
3. Do different facets of biodiversity, including observed diversity, compositional turnover, functional structure, and dark diversity, differ in their responses to landscape structure and environmental conditions? (**I**, **II, III**)
4. Are landscape–diversity relationships consistent across microbial groups? (**III, IV**)

To address these questions, I analysed soil microbial communities across contrasting ecosystem types and land-use contexts in Estonia, including agricultural fields, urban green spaces and temperate forests. I combined DNA-based community data with historical maps, GIS-derived landscape variables, soil measurements and multi-scale analyses to evaluate how AM fungal diversity, composition, functional structure and dark diversity relate to historical and present-day landscape structure across spatial scales. Comparisons with other fungal guilds and urban soil bacteria provided a broader context for assessing whether landscape relationships occur beyond AM fungal communities.

III. METHODS

The methods are summarised across the four studies included in this thesis. Shared procedures are described in general terms, whereas methodological differences among studies are indicated using Roman numerals corresponding to the publications.

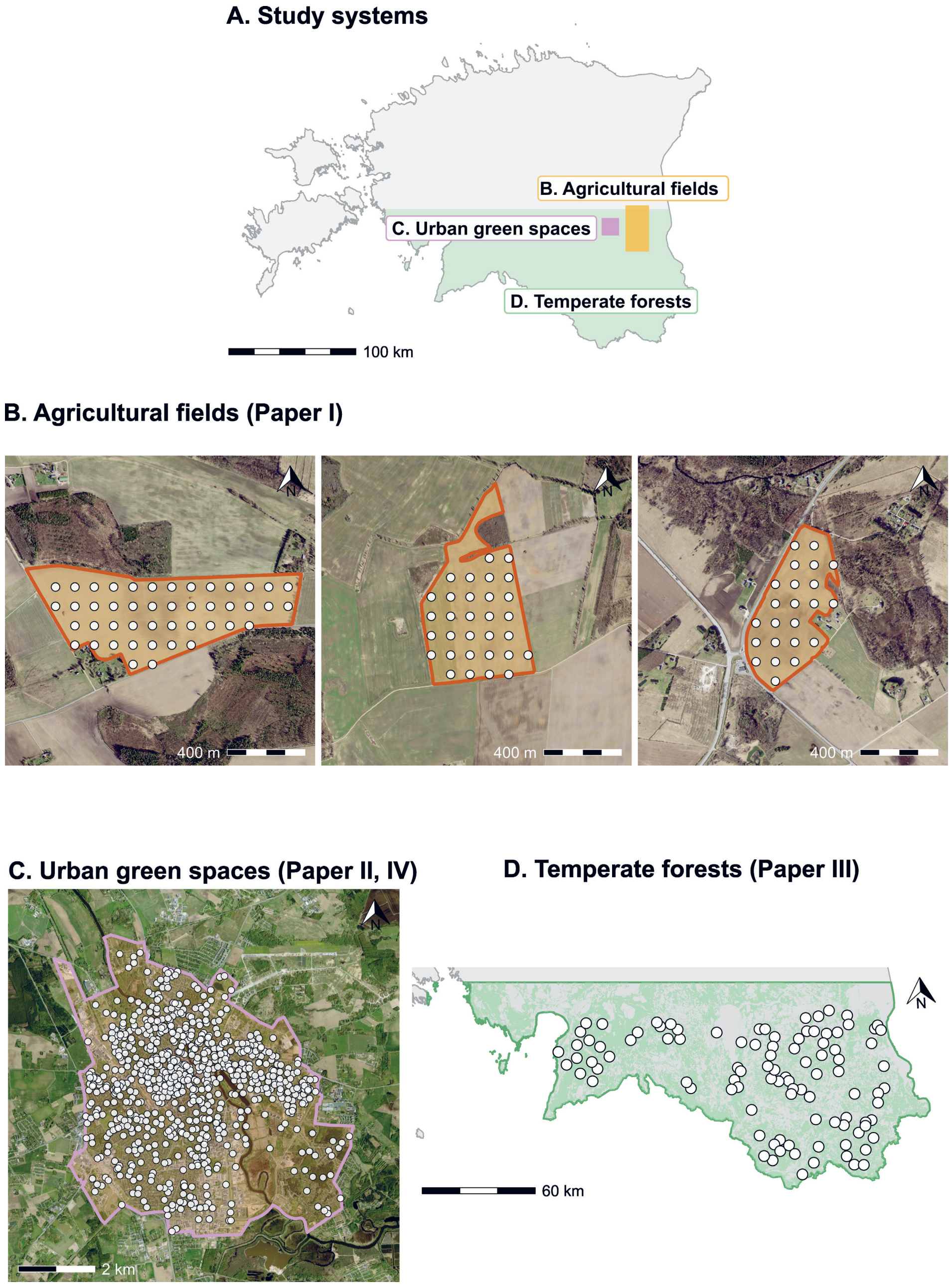
Papers III and IV included additional components beyond the scope of this thesis. Paper III also evaluated vascular plants, epiphytes and carabid beetles, whereas this thesis focuses on fungal diversity, particularly AM fungi and other fungal functional groups. Paper IV also analysed childhood atopy in relation to soil Gammaproteobacteria diversity, whereas this thesis focuses on the ecological component of that study, including soil Gammaproteobacteria diversity, plant diversity, soil properties and urban land-use context.

3.1 Sampling sites and study design

All studies included in this thesis were conducted in Estonia, mainly in southern Estonia and the city of Tartu (**Figure 1**). Mean annual temperature was approximately 6–6.3 °C and annual precipitation 673–713 mm across the study systems. The thesis included three contrasting ecosystem types and land-use contexts: agricultural fields (**I**), urban green spaces (**II, IV**) and temperate forests (**III**). These systems were selected to represent different levels of anthropogenic influence.

In **Paper I**, sampling was conducted in three organically managed agricultural fields in southern Estonia (**Figure 1B**). The fields were located within approximately 50 km of each other and experienced broadly similar climatic conditions. During the sampling year, all fields were cultivated with wheat (*Triticum aestivum*) intercropped with white clover (*Trifolium repens*). To characterise fine-scale spatial variation in AM fungal diversity within fields, sampling followed a north–south oriented 100 × 100 m grid, with samples collected at each grid intersection. In total, 99 soil samples were collected across the three fields. Sampling was conducted after crop harvest and before tillage or fertilisation to minimise the influence of immediate field operations on soil microbial communities.

In **Papers II** and **IV**, sampling was conducted across urban green spaces in Tartu, the second largest city in Estonia (**Figure 1C**). The urban sampling was conducted during the peak vegetation period between June and September 2021, with sampling locations distributed throughout the city. The dataset used for AM fungal analyses in **Paper II** included 778 urban green spaces: 678 public green spaces, such as parks, woodland patches, lawns, sports fields, playgrounds, roadside tree lines and graveyards, and 100 private gardens. **Paper IV** used a related subset of 743 urban green spaces for soil *Gammaproteobacteria* analyses, including public green areas, private green spaces and children's daycare yards. These urban green-space categories represented differences in human accessibility, management intensity and potential contact between people and soil microbial communities.



A. Study systems

B. Agricultural fields (Paper I)

C. Urban green spaces (Paper II, IV)

D. Temperate forests (Paper III)

Figure 1. Overview of the study areas and sampling design across Estonia. *A) Map of Estonia showing the location of the three study systems analysed in this thesis: agricultural fields (B), urban green spaces in Tartu (C) and temperate forests (D). Sampling points are shown as white dots in each panel. The agricultural field panel shows grid-based soil sampling within three fields, the urban panel shows citywide sampling across urban green spaces in Tartu, and the forest panel shows the distribution of temperate forest sites across southern Estonia.*

At each urban sampling site, soil was collected from 10 randomly selected locations within an area of up to 500 m^2. Vegetation and litter layers were removed before sampling, and topsoil was collected using sterile single-use equipment. The 10 subsamples were homogenised into a composite sample and divided into portions for molecular and soil chemical analyses.

In **Paper III**, sampling was conducted across 100 mature forest sites in southern Estonia (**Figure 1D**). The sites represented a broad gradient of temperate forest types, ranging from nemoral forests on nutrient-rich soils to boreal forests on nutrient-poor acidic soils. All sites were located within legally protected forest areas, and the average distance between neighbouring sites was approximately 5.6 km. Soil sampling was conducted during the summer of 2016. At each forest site, soil was collected from nine evenly distributed locations within a 10 × 10 m plot, using sterile sampling equipment. Soil from the upper mineral layer beneath the litter was pooled into a composite sample and used for fungal DNA analyses and soil physicochemical analyses.

3.2 Molecular analyses

Soil microbial communities were analysed using DNA metabarcoding. Across all studies, DNA was extracted from dried soil using the PowerMax Soil DNA Isolation Kit (Qiagen). The target marker region and sequencing platform differed depending on the microbial group analysed.

Arbuscular mycorrhizal fungal communities were characterised using AM fungal-specific primers WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008), targeting the small-subunit ribosomal RNA gene (**I–III**). In **Papers I** and **III**, amplicons were sequenced on an Illumina MiSeq platform using 2 × 300 bp paired-end sequencing, whereas in **Paper II** sequencing was performed on an Illumina NovaSeq platform using 2 × 250 bp paired-end sequencing.

Broader fungal communities in **Paper III** were characterised using the internal transcribed spacer region amplified with primers fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990). Soil bacterial communities in **Paper IV** were characterised using the 16S rRNA gene, targeting the V4–V5 region with primers 515F (Parada et al., 2016) and 926R (Walters et al., 2015). These bacterial analyses focused on Gammaproteobacteria.

3.3 Bioinformatics

Raw sequencing data were processed using marker-specific bioinformatic pipelines. Across datasets, reads were demultiplexed, checked for correct primer sequences, quality filtered using an average quality threshold of 30, screened for chimeric sequences and assigned taxonomically using appropriate reference databases. Low-yield samples and low-abundance taxa were removed before downstream ecological analyses.

For AM fungal datasets (**I–III**), SSU reads were assigned to virtual taxa using the MaarjAM database (Öpik et al., 2010). In **Papers I** and **II**, AM fungal reads were processed using the gDAT pipeline (Vasar et al., 2021). Paired-end reads from **Paper I** were merged with FLASH (Magoč and Salzberg, 2011), whereas reads from **Paper II** were concatenated after quality filtering. Chimeric sequences were removed with VSEARCH (Rognes et al., 2016) using the MaarjAM database as reference. In **Paper III**, paired-end SSU reads were merged with FLASH (Magoč and Salzberg, 2011), screened for chimeras using USEARCH (Edgar et al., 2011) with the MaarjAM database, and assigned to virtual taxa. Across AM fungal datasets, taxonomic assignment was generally based on BLAST (Camacho et al., 2009) searches against MaarjAM, applying 97% sequence identity and 95% alignment length thresholds.

For broader fungal communities in **Paper III**, ITS reads were quality filtered, merged with FLASH (Magoč and Salzberg, 2011) and screened for chimeric sequences using USEARCH (Edgar et al., 2011) with the UNITE database as reference (Nilsson et al., 2019). ITS sequences were assigned to Species Hypotheses using UNITE, and low-abundance taxa were removed before analysis. Fungal taxa were further classified into functional guilds using FUNGuild (Nguyen et al., 2016), allowing separate analyses of ectomycorrhizal fungi, saprotrophs and plant pathogens. AM fungal virtual taxa identified with MaarjAM were treated as a separate AM fungal group.

For bacterial communities in **Paper IV**, 16S rRNA gene reads were processed using the gDAT (Vasar et al., 2021) pipeline, merged with FLASH (Magoč and Salzberg, 2011) and screened for chimeras using VSEARCH (Rognes et al., 2016). Reads were clustered at 97% sequence similarity, and cluster centroids were assigned taxonomically using the SILVA (Quast et al., 2012) database. *Gammaproteobacteria* were then selected from the bacterial dataset for downstream analyses, and low-abundance clusters were removed before ecological analyses.

3.4 Historical and present-day landscape analyses

Historical and present-day landscape structure was quantified using topographic maps, land-cover datasets and geographic information systems. Landscape variables were calculated across multiple spatial and temporal scales to describe local and broader landscape conditions around each sampling site. Spatial data were mainly obtained from the Republic of Estonia Land and Spatial Development Board (www.geoportaal.maaamet.ee), and study-specific variables were extracted or digitised according to the objectives of each paper.

In **Paper I**, natural habitat availability around agricultural sampling points was quantified from topographic maps representing three time periods: 1894, 1969 and 2022. Forests and meadows were classified as natural habitats, and their proportional availability around each sampling point was calculated within radii of 50, 100 and 200 m. Elevation was also extracted from a 1 m resolution digital elevation model (www.geoportaal.maaamet.ee) to account for local terrain variation.

In **Paper II**, historical and present-day habitat connectivity was calculated for four land-use types in Tartu and its surroundings: forest, grassland, cropland and built-up areas. Land use was reconstructed for four time points: 1897, 1923, 1966 and 2022. A 100 × 100 m grid was created across the city and a surrounding 2 km buffer, and each grid point was assigned to a land-use type for each time period. Connectivity between each sampling site and each land-use type was calculated using Hanski's connectivity index (Hanski, 1994) across eight spatial scales from 50 to 1000 m.

In **Paper III**, forest habitat availability around mature forest sites was estimated from topographic maps representing the 1900s, 1930s, 1970s and 2010s. Historical maps were digitised as 100 × 100 m raster layers, and forest availability was calculated as the proportion of forest pixels within 500, 1000, 2000 and 5000 m radii around each study site.

In **Paper IV**, present-day urban land-cover composition around *Gammaproteobacteria* sampling sites was extracted from the Estonian Basic Map (www.geoportaal.maaamet.ee). Six land-cover types were quantified within radii of 50, 100, 200, 300, 400 and 500 m: woodlands, lawns, grasslands or other open vegetation, residential areas, industrial areas, and roads or other paved surfaces. Because these land-cover proportions formed compositional data, additive log-ratio transformations were applied using roads and paved surfaces as the reference category.

3.5 Statistical analyses

Soil microbial communities were characterised using complementary metrics, including alpha diversity, community composition, functional structure and dark diversity. Across studies, alpha diversity was estimated using asymptotic diversity metrics to account for differences in sequencing depth, mainly with the iNEXT package (Hsieh et al., 2022). In **Paper I**, AM fungal diversity was measured as asymptotic virtual taxon richness. In **Papers II–IV**, diversity was expressed as the Shannon index-based effective number of species extrapolated to the asymptote, including AM fungi in **Paper II**, fungal functional groups in **Paper III**, and *Gammaproteobacteria* and plants in **Paper IV.**

Community composition was analysed using beta-diversity metrics. In **Paper I**, Jaccard dissimilarity was partitioned into turnover and nestedness components (Baselga, 2010). In **Paper II**, AM fungal compositional turnover was calculated from presence–absence virtual taxon data and summarised for each site as the mean pairwise dissimilarity to all other sites. Functional structure in **Paper II** was quantified using an AM fungal ruderality index (García de León et al., 2018a), calculated as the log ratio of cultured to uncultured AM fungal virtual taxa after variance-stabilising transformation with DESeq2 (Love et al., 2014). In **Paper III**, dark diversity was estimated using the DarkDiv package (Carmona and Pärtel, 2021) to identify suitable but locally absent taxa within each functional group.

Statistical analyses evaluated relationships between biodiversity metrics, landscape variables and local environmental conditions. Regression-based models were used across studies, with model type depending on the response variable and study design. Models included landscape variables and soil properties as local environmental covariates, while spatial structure was accounted for where relevant. Because landscape variables measured across different time periods, spatial scales or land-use types were often correlated, spatio-temporal variants of landscape predictors were analysed in separate models rather than included simultaneously. Competing models were then compared using Akaike's Information Criterion to identify the temporal period and spatial scale at which landscape variables best explained each biodiversity response.

Model assumptions were checked for the best-supported models where applicable, and residual spatial autocorrelation was evaluated using Moran's I (Paradis et al., 2004; Carmona and Pärtel, 2021). Predictor effects were visualised using the visreg package (Breheny and Burchett, 2020).

In **Paper I**, generalized linear models were used to relate AM fungal richness, turnover and nestedness to natural habitat availability across three spatial scales and three time periods. Richness was modelled using a Poisson distribution, whereas turnover and nestedness were analysed using Gaussian models after logit-transforming natural habitat availability (Fox et al., 2023). Soil chemistry, summarised by the first two axes of a principal component analysis, and elevation were included as covariates.

In **Paper II**, linear models were used to relate AM fungal alpha diversity, compositional turnover and ruderality to connectivity with different land-use types across time and space. Separate models were fitted for each combination of land-use type, time period and spatial scale. Models also included soil chemical variables, public access type and spatial polynomial terms to account for spatial structure (Borcard et al., 1992).

In **Paper III**, generalized additive models were used to analyse relationships between observed and dark diversity and forest availability across temporal periods and spatial scales. Separate models were fitted for each combination of forest availability period and spatial scale. Models included local environmental conditions, climatic variables, wood volume, soil properties and geographic coordinates.

In **Paper IV**, linear models were used to evaluate relationships between *Gammaproteobacteria* diversity and urban environmental variables. Models included plant diversity, soil pH, soil nutrient concentrations, land-cover composition around each sampling site and public access type. Land-cover composition was quantified at multiple spatial scales and included in separate models to evaluate scale-dependent relationships with *Gammaproteobacteria* diversity.

IV. RESULTS

4.1 Historical and present landscape structure

Present-day AM fungal alpha diversity reflected historical landscape structure more strongly than contemporary landscape structure in agricultural fields and urban green spaces (**I, II**) (**Figure 2A**). In contrast, this pattern was not detected for observed AM fungal diversity in temperate forests, where landscape relationships were clearer for dark diversity than for observed diversity (**III**).

In agricultural fields, present-day AM fungal alpha diversity was more strongly associated with historical natural habitat availability reconstructed from 1894 than with present-day landscape structure (**I**). Historical landscape models consistently outperformed models based on contemporary habitat availability, indicating that past habitat distribution continues to influence belowground communities more than a century later. AM fungal turnover in agricultural systems also showed associations with historical landscape structure, whereas nestedness was more strongly related to present-day landscape variables.

Similarly, in urban green spaces, present-day AM fungal alpha diversity was positively associated with historical grassland connectivity, especially when using the 1923 map (**II**) (**Figure 2B**). In contrast, AM fungal turnover was more strongly associated with present-day cropland connectivity. Functional community structure, measured as AM fungal ruderality, was not explained by either historical or present-day landscape structure, but instead showed stronger relationships with local environmental conditions and management intensity.

In temperate forests, observed AM fungal diversity was not significantly associated with habitat availability across space and time (**III**) (**Figure 2C**). In contrast, AM fungal dark diversity showed strong relationships with present-day forest availability, indicating that landscape structure may influence the pool of potentially suitable but locally absent AM fungal taxa even when no clear relationships are detected for observed diversity.

Historical landscape structure most consistently influenced AM fungal alpha diversity, whereas compositional, functional and dark diversity metrics often responded differently or were more strongly associated with present-day landscape structure and local environmental conditions.

4.2. Spatial scale dependence

The spatial scales at which landscape structure was most strongly associated with AM fungal biodiversity differed among biodiversity facets and study systems (**I–III**). In general, the best-supported relationships were detected at relatively local to intermediate spatial scales, ranging from approximately 100 m to 500 m (**Figure 2**).

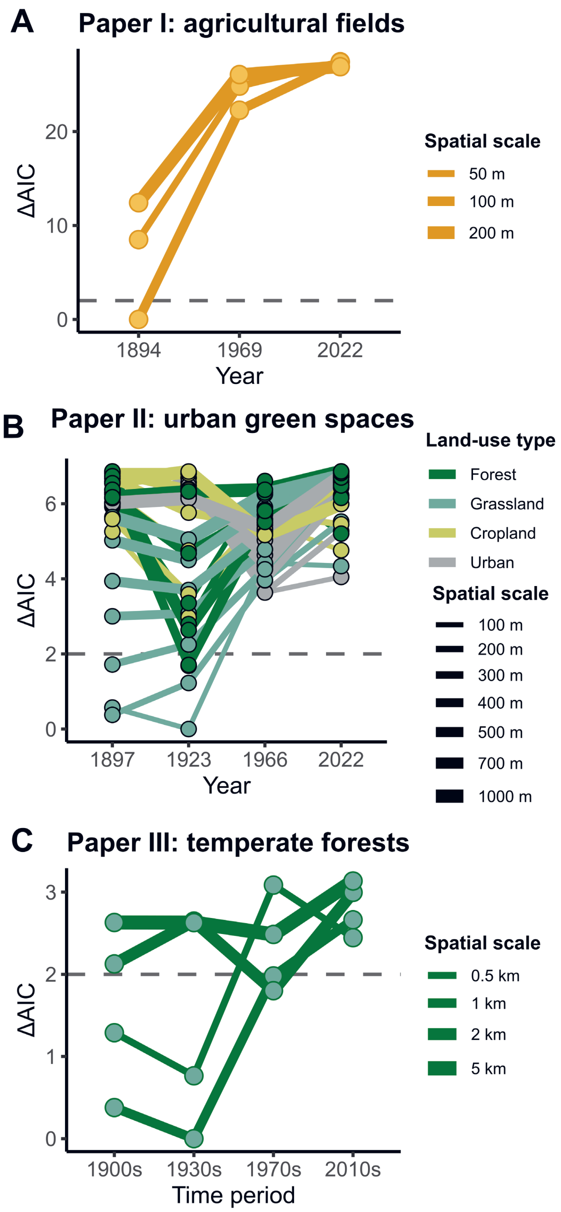


Figure 2. Model support for AM fungal landscape relationships across temporal periods and spatial scales (modified from Paper I, II and III). *ΔAIC values are shown for candidate landscape models in the three AM fungal studies; lower values indicate stronger support, and the dashed line marks ΔAIC = 2. (A) In agricultural fields, AM fungal richness was best supported by historical natural habitat availability in 1894 at 100 m. (B) In urban green spaces, AM fungal alpha diversity was best supported by historical grassland connectivity in 1923 at 100 m. (C) In temperate forests, observed AM fungal diversity showed no clear supported relationship with forest availability across the tested temporal periods and spatial scales. Colours indicate land-use or habitat type; thicker lines indicate broader spatial scales.*

In agricultural fields, historical natural habitat availability showed the strongest relationship with AM fungal alpha diversity at approximately 100 m, whereas turnover was best associated with historical landscape structure at around 200 m (**I**). Nestedness was more strongly associated with present-day landscape variables, with the best-supported relationship also detected at approximately 100 m.

Similarly, in urban green spaces, AM fungal alpha diversity was most strongly associated with historical grassland connectivity at approximately 100 m, while turnover showed its strongest relationship with present-day cropland connectivity at around 200 m (**II**). Functional community structure, measured as AM fungal ruderality, was not clearly explained by either historical or present-day landscape structure; nevertheless, the best landscape model for ruderality was detected at approximately 400 m.

In temperate forests, AM fungal dark diversity was associated with present-day forest availability at 500 m, the smallest spatial scale tested in that study (**III**). Observed AM fungal diversity did not show significant relationships with forest availability at any of the tested spatial scales.

4.3 Multiple facets of biodiversity

Different metrics of AM fungal biodiversity showed contrasting relationships with landscape structure and environmental conditions across study systems (**Figure 3**) (**I–III**). In general, historical landscape structure was most consistently associated with AM fungal alpha diversity, whereas compositional and functional diversity more frequently reflected present-day landscape structure or local environmental conditions.

AM fungal alpha diversity was positively associated with historical habitat availability in both agricultural and urban systems. In agricultural fields, AM fungal alpha diversity increased with historical natural habitat availability reconstructed from 1894, whereas in urban green spaces, diversity increased with historical grassland connectivity reconstructed from 1923 (**I, II**). In contrast, observed AM fungal diversity in temperate forests did not show significant relationships with habitat availability across space and time (**III**).

Patterns of AM fungal community composition frequently differed from those observed for alpha diversity. In agricultural systems, AM fungal turnover was associated with historical landscape structure, whereas nestedness was more strongly related to present-day landscape variables (**I**). In urban green spaces, turnover was more strongly associated with present-day cropland connectivity than with historical grassland connectivity (**II**). Sites surrounded by greater cropland connectivity showed lower compositional turnover, indicating increased similarity among AM fungal communities.

AM fungal functional community structure responded differently from both alpha diversity and turnover. AM fungal ruderality was not clearly associated with either historical or present-day landscape structure, although the best-supported landscape model occurred at broader spatial scales and showed only marginal significance. Instead, ruderality showed stronger relationships with local environmental conditions, particularly soil phosphorus concentration and management intensity, with significantly higher ruderality in private gardens than in public green spaces (**II**).

Finally, AM fungal dark diversity showed distinct responses compared with observed diversity. In temperate forests, dark diversity was significantly associated with present-day forest availability, whereas observed AM fungal diversity did not show significant relationships with habitat availability across space and time (**III**).

Overall, these findings demonstrate that different facets of AM fungal biodiversity capture distinct ecological responses to landscape structure, reflecting differences in community assembly processes, environmental filtering, and temporal dynamics.

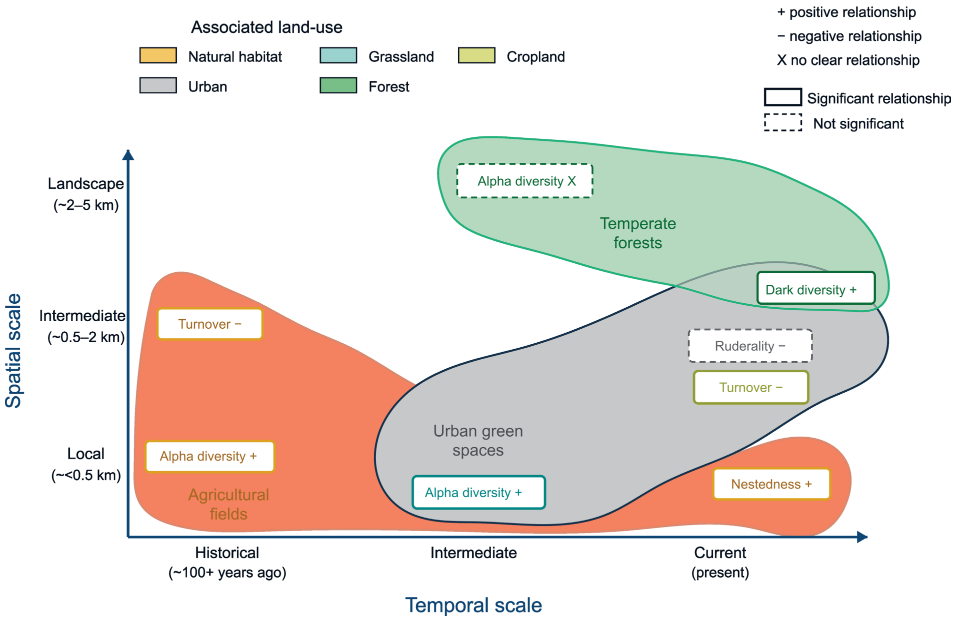


Figure 3. **Conceptual summary of the main spatiotemporal landscape relationships detected for arbuscular mycorrhizal fungal diversity across agricultural fields, urban green spaces and temperate forests**. *The x-axis represents historical to current landscape structure, and the y-axis represents local to broader spatial scales. Coloured ellipses group the study systems, and box colours indicate the associated land-use or habitat type. Symbols show the direction of response: positive (+), negative (−), or no clear relationship (X). Solid box borders indicate significant relationships, while dashed borders indicate weak or non-significant relationships.*

4.4 Comparison across microbial groups

Landscape–diversity linkages were observed beyond AM fungi, but the direction and spatial scale of these relationships differed among microbial groups (**III, IV**). In temperate forests, fungal guilds showed contrasting associations with forest availability. Ectomycorrhizal fungal diversity was positively associated with present-day forest availability at broad spatial scales, with the strongest relationship at approximately 5000 m (**III**). Plant pathogen diversity was also positively associated with present-day forest availability, but at a finer spatial scale of approximately 500 m. By contrast, saprotrophic fungal diversity was negatively associated with historical forest availability reconstructed from 1970 at approximately 1000 m.

In urban soils, *Gammaproteobacteria* diversity was associated with present-day environmental and land-cover conditions (**IV**). *Gammaproteobacteria* diversity increased with plant diversity and woodland proximity, decreased with soil potassium concentration, and was higher in children's daycare yards than in public green spaces. These results indicate that present-day urban habitat composition and local environmental conditions structure soil microbial diversity.

Taken together, these results show that landscape effects on microbial biodiversity are widespread but strongly group-specific. While AM fungi frequently showed strong associations with historical landscape structure, other microbial groups responded differently to habitat availability, present-day land use, and local environmental conditions.

V. DISCUSSION

In this thesis, I examined the role of historical and present-day landscape structure in shaping soil microbial communities, with a particular focus on arbuscular mycorrhizal (AM) fungi. By exploring soil microbial communities across agricultural, urban and forest ecosystems with contrasting land-use histories, I show in this thesis that belowground diversity can reflect both past landscapes and present-day environmental conditions. Historical landscape structure provided the clearest explanation for present-day AM fungal alpha diversity in agricultural and urban systems, where past habitat availability explained diversity patterns better than current landscape configuration (**I, II**). Other AM fungal biodiversity facets, including compositional turnover, functional structure and dark diversity, were more closely aligned with present-day landscape structure or local environmental filters (**I–III**). However, comparisons with other fungal guilds and soil bacteria showed that these patterns were not general to all microbial groups, as ectomycorrhizal fungi, saprotrophs, pathogens and *Gammaproteobacteria* responded to different landscape contexts (**III, IV**). Overall, these findings show that the role of landscape structure in soil microbial communities depends on the temporal period considered, the spatial scale, the biodiversity metric studied, and the microbial group.

5.1 Historical landscapes leave century-long signatures on AM fungal diversity

Papers I and **II** showed that present-day AM fungal alpha diversity can retain century-long signatures of former habitat availability in anthropogenic landscapes. In agricultural fields, AM fungal richness was best explained by natural habitat availability reconstructed from 1894, while in urban green spaces, AM fungal alpha diversity was most clearly associated with grassland connectivity reconstructed from 1923 (**I, II**). These patterns are consistent with an extinction debt, where present-day diversity still reflects habitats that have already been lost or reduced, because local species losses occur slowly after landscape change. Previous studies in former agricultural soils have found that land-use history explained microbial community composition better than current vegetation or soil properties (Jangid et al., 2011). In oak forests, anthropogenic disturbance effects remained detectable for more than 100 years after land-use change (Fichtner et al., 2014). In ancient forest landscapes fragmented approximately 150 years earlier, past forest structure was especially important for symbiotic fungi, including AM fungi (Mennicken et al., 2020). Together, these studies suggest that AM fungal communities may respond slowly to habitat loss and landscape simplification.

A likely mechanism is that historically diverse habitats acted as source areas for AM fungal species. Grasslands are particularly relevant because they often harbour high AM fungal diversity (Davison et al., 2015; Van Nuland et al., 2025) and can contribute to the regional species pool available for local communities (Pärtel et al., 2017). When forests, meadows or grasslands were more common around local sites, AM fungal communities may have received a stronger inflow of propagules through spores, hyphal fragments and colonised roots. This continuous propagule input could have maintained higher local diversity through rescue or mass effects, where dispersal from surrounding source habitats compensates for local losses and increases the probability that species persist in local communities (Brown and Kodric-Brown, 1977; Shmida and Wilson, 1985). After landscape transformation, this inflow of propagules may have weakened because fewer diverse source habitats remained nearby. If local AM fungal species are lost only gradually, this pattern can be interpreted as an extinction debt: communities may still contain species supported by past landscape conditions, even though the present landscape no longer provides the same level of habitat availability or propagule input.

The results from agricultural fields supported this interpretation. In **Paper I**, sites with greater historical natural habitat availability had higher AM fungal richness and lower compositional turnover. Historical natural habitats may have served as source habitats, forming richer AM fungal communities and reducing species replacement among sites (Shmida and Wilson, 1985). Conversely, sites with lower historical natural habitat availability showed stronger turnover, indicating that long-term agricultural disturbance did not simply produce nested species loss, but rather promoted the replacement of AM fungal species. Similar patterns have been reported in other agricultural systems, where intensive land-use change altered AM fungal community composition even when richness responses were weak or inconsistent (Sepp et al., 2018; Pereira et al., 2022; Vahter et al., 2022). Therefore, the agricultural results suggest that historical habitat availability may influence both the number of AM fungal species present locally and the identity of species that persist after long-term land-use change.

In urban green spaces, historical grassland connectivity points to a legacy of former open habitats in present-day AM fungal diversity. In **Paper II**, AM fungal alpha diversity was most clearly associated with grassland connectivity reconstructed from 1923, supporting the idea that grasslands can act as reservoirs of AM fungal diversity (Van Nuland et al., 2025). This agrees with studies from other cities showing that AM fungi can be common and diverse in urban soils, although urbanisation does not always affect richness in the same way and changes in community composition are often clearer (Whitehead et al., 2022; Verbeek et al., 2025). However, this legacy does not mean that AM fungal communities have remained unchanged since the historical period. More likely, former grassland connectivity increased the set of AM fungal species available to urban sites, while present-day soil nutrients, host plants and management conditions influenced which species were maintained locally. In this sense, urban AM fungal communities are best understood as novel communities with historical inputs, rather than as direct subsets or remnants of past natural communities (Epp Schmidt et al., 2017; Scholier et al., 2023).

In temperate forests, century-long landscape signatures were not evident in observed AM fungal diversity. Unlike in agricultural fields and urban green spaces, observed AM fungal diversity in **Paper III** did not show a clear relationship with historical or present-day forest availability, indicating that forest cover was not a strong predictor of local AM fungal diversity in this system. As previously mentioned, AM fungal diversity is often high in open herbaceous habitats, especially grasslands, where compatible host roots are abundant (Öpik et al., 2006; Moora et al., 2014). The expansion of young forests on former agricultural land may not necessarily improve AM fungal recolonisation, and may instead reduce the availability of open-habitat or forest-edge source communities. Moreover, the positive association between present-day forest availability and AM fungal dark diversity suggests that many suitable AM fungal taxa were absent from local forest communities. This pattern may reflect reduced diaspore inflow from open habitats or forest edges, meaning that local forest communities contained only part of the AM fungal species pool that could potentially occur there.

5.2 Spatial scale dependence

The relationship between landscape structure and AM fungal diversity depended strongly on the spatial scale at which the surrounding landscape was measured. Across **Papers I–III**, the clearest AM fungal responses were detected at fine to intermediate spatial scales, from approximately 100 m to 500 m. This scale dependence indicates that AM fungal communities respond not only to habitat type or habitat amount, but also to whether landscape context is measured as nearby source habitat or as a broader neighbourhood. This distinction is important because local environmental filters, propagule inflow from nearby habitats and broader landscape connectivity are expected to operate at different spatial extents (Levin, 1992; Jackson and Fahrig, 2012).

In agricultural fields, historical natural habitat availability at 100 m best explained AM fungal richness, whereas in urban green spaces historical grassland connectivity at 100 m was the strongest predictor of AM fungal alpha diversity (**I, II**). This repeated fine-scale signal suggests that nearby historical habitats may have been especially important as source areas for AM fungal propagules. Although fungi can disperse over long distances (Correia et al., 2019; Chaudhary et al., 2020; Paz et al., 2021), successful dispersal may decline strongly with distance and may be limited by establishment failure in disturbed habitats (Norros et al., 2012). Therefore, the 100 m scale detected for AM fungal alpha diversity in **Papers I** and **II** indicates that nearby source habitats are an important contributor to local soil communities.

Compositional responses occurred at similar but slightly broader scales than alpha diversity. In agricultural fields and urban green spaces, AM fungal turnover was most strongly associated with landscape structure at approximately 200 m (**I, II**). This suggests that local richness may depend strongly on very nearby source habitats, whereas differences in species identity among sites may integrate a broader surrounding landscape. This distinction is consistent with studies showing that land-use change and disturbance can alter AM fungal community composition even when richness responses are weak or inconsistent (Jansa et al., 2003; García de León et al., 2018b). In urban green spaces, turnover decreased with present-day cropland connectivity at 200 m, suggesting that nearby agricultural land use may contribute to community homogenisation, probably through the decline of sensitive taxa and the relative dominance of disturbance-tolerant AM fungi (Aguilar-Trigueros et al., 2025).

The forest results should be interpreted more cautiously because the smallest scale tested in **Paper III** was 500 m due to the 100 m resolution of the rasterised historical habitat maps. Therefore, the association between AM fungal dark diversity and present-day forest availability at 500 m should not be taken as evidence that finer-scale habitat structure is unimportant. It only indicates that suitable but absent AM fungal taxa reflected present-day forest availability at the finest spatial scale that could be reliably tested in that study (**III**).

This relatively fine-scale response contrasts with studies on macro-organism groups, where historical landscape effects often emerge at broader spatial scales. For example, extinction debt in Estonian alvar grassland plants was most clearly detected at a 5 km scale, suggesting that long-lived plant communities can reflect historical habitat availability across a wider landscape context (Helm et al., 2006). Other studies have also shown that relevant landscape scales can vary from hundreds of metres to several kilometres among plants and insects, depending on dispersal ability, habitat specialization and life history (Holland et al., 2004a; Avon et al., 2015). Compared with these examples, the 100–200 m scales detected for AM fungal alpha diversity and turnover in agricultural and urban systems suggest a stronger role of nearby source habitats and fine-grained habitat mosaics.

These results show that there is no single scale of effect for AM fungal communities. The strongest scale depended on the biodiversity facet and the ecological process considered: alpha diversity was most closely linked to nearby historical source habitats, compositional turnover reflected a somewhat broader neighbourhood, and forest AM fungal dark diversity responded at the smallest forest-availability scale tested. Multi-scale analyses are therefore necessary in belowground landscape ecology, because choosing only one spatial extent could miss important relationships between landscape structure and AM fungal biodiversity.

5.3 Multiple facets of biodiversity

Landscape change can affect biodiversity beyond changes in species richness or abundance, by reorganising community composition, filtering ecological strategies and leaving suitable species absent from local communities. AM fungal richness may respond weakly or inconsistently to land-use intensity, whereas community composition can show clearer shifts between natural, agricultural and disturbed habitats (Faggioli et al., 2019; Vahter et al., 2022). Therefore, considering multiple biodiversity facets provides a broader view of AM fungal community assembly than local diversity alone (Baselga, 2010; Pärtel et al., 2011).

The community composition results showed that landscape structure influenced not only how many AM fungal taxa occurred locally, but also which taxa occurred. In agricultural fields, historical natural habitat availability was associated with lower AM fungal turnover, suggesting that greater past availability of source habitats reduced species replacement among local communities (**I**). Because turnover reflects species replacement among sites, it can result from environmental sorting or from historical changes in environmental conditions (Qian et al., 2005; Baselga, 2010). The results suggest that historical landscape structure influenced not only local AM fungal richness, but also the identity of taxa persisting in field soils. This interpretation is consistent with evidence that land use can leave long-term soil legacies, with microbial communities resembling past ecosystems decades after conversion and land-use history sometimes explaining microbial composition better than current vegetation or soil properties (Steenwerth et al., 2002; Jangid et al., 2011). In urban green spaces, turnover decreased with present-day cropland connectivity, indicating a different compositional process: nearby agricultural land use may contribute to AM fungal community homogenisation by reducing differences in species identity among sites (**II**). Such patterns have been observed at larger spatial scales (Banerjee et al., 2024), with anthropogenic activities decreasing species turnover.

Functional structure pointed to local filtering rather than historical landscape effects. In urban green spaces, AM fungal ruderality was not clearly explained by historical or present-day landscape connectivity but was more closely associated with soil phosphorus and management-related differences between public green spaces and private gardens (**II**). Functional shifts in AM fungal communities may respond more directly to local nutrient conditions and disturbance than to landscape history. Nutrient effects on AM fungi are context-dependent: N and P additions can increase AM biomass in nutrient-limited sites but reduce it in more fertile soils, and responses can differ among AM fungal genera (Treseder and Allen, 2002). Therefore, the positive association between soil phosphorus and ruderality in **Paper II** may indicate a shift towards taxa better able to tolerate or recover from nutrient enrichment, rather than a simple decline in AM fungal diversity. This interpretation is consistent with evidence that anthropogenic land use increases the proportion of easily cultured AM fungal taxa, probably because of their efficient colonisation strategies and greater ability to recover from disturbance (García de León et al., 2018a). Similarly, experimental disturbance of meadow and arable-field soils showed that chemical and mechanical disturbances can favour different AM fungal families, while increasing the abundance of culturable AM fungi (Liu et al., 2023).

Although observed AM fungal diversity did not show a clear relationship with forest availability, AM fungal dark diversity was associated with present-day forest availability (**III**). The landscape signal was expressed not in the taxa detected locally, but in the taxa estimated to be suitable yet absent. In this system, dark diversity therefore suggested incomplete local AM fungal communities, possibly reflecting reduced propagule inflow from open habitats or forest edges, local losses, or filtering by forest conditions. Because AM fungal propagule arrival and establishment depend on suitable source habitats, host plants and soil conditions (Delavaux et al., 2024), these absences likely reflect constraints on community assembly rather than simple absence of habitat suitability.

5.4 Landscape effects are widespread but group-specific

Soil microbial groups differ strongly in their ecological roles, resource use and dependence on hosts or substrates, so the same landscape structure is unlikely to have similar effects across all taxa. Saprotrophic fungi are key decomposers of dead organic matter (McLaughlin et al., 2001), mycorrhizal fungi mediate plant nutrient and water uptake (Smith et al., 2017), and plant pathogens depend on susceptible host tissues (McLaughlin et al., 2001). Therefore, ectomycorrhizal fungi, AM fungi, saprotrophs and pathogens are expected to respond differently to landscape structure because they depend on different hosts, substrates and habitat conditions.

Ectomycorrhizal fungi showed the clearest forest-associated mycorrhizal response. Their diversity was positively associated with present-day forest availability at broad spatial scales, with the strongest relationship at approximately 5 km (**III**). Although EcM fungi can disperse through spores, previous studies have detected dispersal limitation at scales of tens to hundreds of metres (Peay et al., 2010; Peay and Bruns, 2014), suggesting that the availability of nearby source forests can constrain local community diversity. At broader scales, the response detected in **Paper III** may reflect the availability of forest to EcM host communities. In line with this, previous research has shown that EcM fungal richness is higher in old-growth or undisturbed temperate forests than in young or early successional forests, and that recovery of EcM diversity after disturbance may take decades (Odriozola et al., 2020; Jõks et al., 2023).

Saprotrophic and pathogenic fungi showed different patterns from EcM fungi. Saprotrophic fungal diversity was negatively associated with historical forest availability around 1970 at approximately 1 km (**III**). This pattern may reflect their broader substrate use and their capacity to exploit organic material in younger or more recently transformed forests. Saprotrophic communities can change strongly during forest succession; for example, secondary succession has been reported to increase saprotrophic abundance and later recover saprotrophic diversity, while also altering EcM–saprotroph relationships (Wang et al., 2023). Saprotrophic activity can also be modified by interactions with mycorrhizal fungi, either through competition for nutrients, or through priming effects driven by labile carbon inputs (Gadgil and Gadgil, 1971; Fernandez and Kennedy, 2016). Saprotrophic responses to forest availability are therefore likely to depend on substrate supply, successional stage and interactions with other fungal guilds, rather than on forest continuity alone. Plant pathogen diversity, in contrast, was positively associated with present-day forest availability at approximately

0.5 km (**III**), consistent with a more local response to nearby host availability or favourable forest microhabitats.

Urban soil *Gammaproteobacteria* extended the taxon-specific pattern beyond fungi. In **Paper IV**, *Gammaproteobacteria* diversity was associated mainly with present-day urban conditions: it increased with plant diversity and nearby woodland cover, decreased with soil potassium concentration, and was higher in children's daycare yards than in public green spaces (**IV**). The stronger association of *Gammaproteobacteria* with contemporary vegetation, soil fertility and green-space type is consistent with the sensitivity of bacterial communities to local soil properties (Fierer and Jackson, 2006), vegetation structure (Baruch et al., 2021) and land-use intensity (Grierson et al., 2023). This contrast supports the broader conclusion that landscape relationships in soil microbial communities are context- and taxon-dependent.

5.5 Implications for land management and restoration

Belowground biodiversity management should consider both past and present landscape structure. Historical land-cover information can help identify landscapes where AM fungal species pools may still retain signatures from former source habitats, while present-day habitat quality and management determine which taxa can persist, recolonise or become dominant. This is especially relevant for agricultural and urban systems, where historical natural habitats and grasslands may still indicate areas of high AM fungal conservation value, but current disturbance, fertilisation and vegetation management influence community composition and functional structure (Stewart et al., 2024).

In agricultural landscapes, management should prioritise the preservation and restoration of semi-natural elements close to crop fields. Grasslands, forest edges, field margins, hedgerows, wooded patches and uncultivated strips can act as nearby sources or stepping stones for AM fungal propagules (González Fradejas et al., 2022). Because the strongest AM fungal alpha-diversity responses occurred at fine spatial scales, even relatively small habitat elements may matter if they are located close to local soil communities. This means that belowground biodiversity can benefit not only from large, protected habitats, but also from fine-scale habitat mosaics embedded within disturbed landscapes (Tipton et al., 2016; Pirhofer Walzl et al., 2022).

In urban landscapes, conserving remnant grasslands, woodland patches and less intensively managed green spaces should be part of urban planning to prevent biodiversity loss (Threlfall et al., 2017). These habitats should not be treated as empty or replaceable green surfaces, because they may support above and belowground species pools that support local native biodiversity (Aronson et al., 2014). Replacing them with frequently mown lawns, highly fertilised ornamental vegetation or heavily disturbed soils may reduce the capacity of urban green spaces to maintain diverse AM fungal communities. Urban restoration should therefore promote plant diversity (Verbeek et al., 2025), lower soil disturbance and reduce excessive fertilisation (Whitehead et al., 2022), especially in places where historical natural habitat connectivity suggests a potential legacy of AM fungal diversity.

Restoration should also avoid assuming that improving local vegetation or soil conditions will immediately restore AM fungal communities. If nearby source habitats are absent, recolonisation may be slow or incomplete. In such cases, restoration may need to combine local actions, such as reducing fertilisation, soil disturbance and intensive mowing, with landscape-level actions that increase connectivity to source habitats (Kuussaari et al., 2009). Where communities are strongly depleted, assisted soil or plant inoculation could be considered, but only with local or regionally appropriate material and with careful evaluation of ecological risks.

Management targets should include more than high AM fungal richness. Community composition and functional structure may respond relatively directly to present-day management, such as nutrient enrichment, disturbance and local habitat quality (Vahter et al., 2022). However, long-term stability of belowground functions also requires maintaining high AM fungal alpha diversity, so that ecological functions are supported by multiple taxa rather than by a narrow set of disturbance-tolerant species. For monitoring, this means that richness, composition, functional structure and dark diversity can provide complementary indicators: richness identifies locally diverse communities, composition reveals homogenisation or species replacement, functional metrics indicate disturbance filtering, and dark diversity points to suitable taxa that are missing from local communities.

VI. CONCLUSIONS

In this thesis, I investigated how past and present landscapes are reflected in arbuscular mycorrhizal communities across agricultural, urban, and forest ecosystems in Estonia. The findings show that belowground diversity cannot be understood from present-day conditions alone, but also reflects landscape history, spatial scale, and differences among microbial groups. The main conclusions of the thesis are the following:

1. Historical landscape structure was most consistently reflected in AM fungal diversity.
   Present-day AM fungal alpha diversity retained signals of historical habitat availability in agricultural fields and urban green spaces. Historical natural habitat availability reconstructed from 1894 was associated with AM fungal diversity in agricultural fields, while historical grassland connectivity reconstructed from 1923 was associated with AM fungal diversity in urban green spaces. However, this pattern was not universal across all systems or biodiversity facets, as observed AM fungal diversity in temperate forests was not significantly related to forest availability.

2. AM fungal diversity was linked to nearby landscapes, mostly within a few hundred meters.
   The strongest associations between landscape structure and AM fungal alpha diversity were detected at approximately 100 m for AM fungal alpha diversity in agricultural fields and urban green spaces, around 200 m for compositional turnover, and at 500 m for AM fungal dark diversity in forests, which was the smallest scale tested in that study. These results indicate that nearby habitat context can be especially important for AM fungal communities, although the relevant scale depends on the biodiversity facet and study system. Different biodiversity facets captured distinct ecological responses.

3. Different biodiversity facets captured different AM fungal responses to landscape structure and local conditions.
   AM fungal alpha diversity, compositional turnover, nestedness, ruderality and dark diversity did not respond identically to landscape structure. Historical landscape structure was most consistently associated with AM fungal alpha diversity. AM fungal compositional turnover and nestedness differed in their temporal associations with landscape structure. AM fungal ruderality was more closely related to local soil conditions and management intensity than to landscape connectivity. AM fungal dark diversity revealed landscape effects in temperate forests that were not detected using observed diversity alone.

4. Landscape–diversity relationships were widespread but group-specific.
   Comparisons with other fungal guilds and urban soil bacteria showed that microbial groups differed in their relationships with landscape structure. Ectomycorrhizal fungi, saprotrophic fungi, plant pathogenic fungi and *Gammaproteobacteria* responded to different temporal and spatial components of the landscape. These differences indicate that microbial responses to land-use change cannot be generalised from a single taxonomic or functional group.

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SUMMARY

Land-use change alters habitat availability, connectivity and local environmental conditions, with consequences for both aboveground and belowground biodiversity. Soil microbial communities are central to ecosystem functioning, but the role of landscape structure in shaping their diversity remains less understood than for plants and animals. Their responses to landscape change are still often interpreted mainly through present-day local conditions, even though microbial communities may also depend on habitat availability, connectivity and land-use history. This thesis addressed whether present-day soil microbial diversity, with a particular focus on arbuscular mycorrhizal fungi, also reflects historical landscape structure and spatial scale-dependent landscape processes.

Arbuscular mycorrhizal fungi are root-associated symbionts that contribute to plant nutrient acquisition, soil functioning and vegetation dynamics. Their communities may respond to landscape change in complex ways because they depend on suitable host plants and soil conditions, disperse through spores, hyphal fragments and colonised roots, and can persist in soil over long periods. These characteristics suggest that AM fungal communities may retain signals of past habitat availability while also responding to present-day land use and local environmental filters.

The aim of this thesis was to examine how historical and present-day landscape structure influence soil microbial communities across spatial scales. Specifically, I asked whether historical landscape structure explains present-day AM fungal diversity better than current landscape structure; at which spatial scales landscape relationships are strongest; whether taxonomic, compositional, functional and dark diversity respond differently; and whether similar landscape relationships occur in other microbial groups. To address these questions, I used agricultural fields, urban green spaces and temperate forests in Estonia as study systems, combining DNA-based community data, historical maps, GIS analyses and soil measurements.

The results showed that AM fungal diversity can retain long-term signals of historical landscape structure. In agricultural fields, AM fungal richness was most strongly associated with natural habitat availability reconstructed from 1894, indicating a legacy effect lasting more than a century. This pattern is best interpreted as the persistence of AM fungal populations or propagule pools, rather than the survival of the same individual fungi since the historical period. In urban green spaces, AM fungal alpha diversity was most strongly associated with grassland connectivity reconstructed from 1923, showing that historical open habitats can still be linked to present-day belowground diversity in an urban landscape. In contrast, observed AM fungal diversity in temperate forests did not show a clear relationship with historical or present-day forest availability, although AM fungal dark diversity was associated with present-day forest availability.

Landscape relationships were scale-dependent. In agricultural fields and urban green spaces, the strongest associations for AM fungal alpha diversity were detected at fine spatial scales of approximately 100 m, while compositional turnover was most strongly associated with landscape structure at approximately 200 m. In temperate forests, AM fungal dark diversity responded to present-day forest availability at 500 m, the smallest scale tested in that study. These results indicate that nearby habitat availability can be especially important for AM fungal communities, although the relevant scale depends on the ecosystem and biodiversity facet considered.

Different biodiversity metrics responded to different factors. AM fungal alpha diversity was most consistently associated with historical habitat availability, whereas compositional turnover was more often linked to present-day land use. In agricultural fields, AM fungal turnover was associated with historical natural habitat availability, suggesting that past source habitats influenced not only local richness but also species replacement among sites. In urban green spaces, AM fungal turnover decreased with present-day cropland connectivity, suggesting community homogenisation in landscapes influenced by agricultural land use. Functional structure, measured as AM fungal ruderality, was not clearly explained by historical or present-day landscape connectivity, but was instead related mainly to local soil phosphorus and management-related differences between public and private green spaces. In temperate forests, dark diversity provided additional information by revealing suitable but locally absent AM fungal taxa that were not reflected in observed diversity alone.

Comparisons with other microbial groups showed that landscape effects were not restricted to AM fungi, but differed among taxa, temporal periods and spatial scales. In temperate forests, ectomycorrhizal fungal diversity was positively associated with present-day forest availability at broad spatial scales, with the strongest relationship at approximately 5 km. Plant pathogen diversity was also positively associated with present-day forest availability, but at a finer scale of approximately 0.5 km, whereas saprotrophic fungal diversity was negatively associated with historical forest availability reconstructed from the 1970s at approximately 1 km. In urban soils, *Gammaproteobacteria* diversity was associated mainly with present-day conditions at local neighbourhood scales, especially woodland cover within 100 m, together with plant diversity, soil potassium concentration and green-space access type. These results indicate that soil microbial responses to landscape structure are widespread but group-specific.

This thesis shows that belowground biodiversity can reflect both past and present landscapes. Historical landscape structure was especially important for AM fungal alpha diversity in agricultural and urban systems, whereas present-day land use and local environmental conditions were more important for other biodiversity facets and microbial groups. These findings highlight that belowground biodiversity management should consider both historical and present-day landscape structure, including nearby habitat sources, local soil conditions and the spatial scales at which different microbial groups respond.

SUMMARY IN ESTONIAN

Mulla mikroobikooslused muutuvates maastikes: arbuskulaarmükoriisaseente mustrid ajas ja ruumis

Maakasutuse muutused on üks peamisi elurikkuse muutumise põhjustajaid kogu maailmas. Metsade, märgalade, poollooduslike rohumaade ja teiste looduslähedaste elupaikade hävimine, killustumine ja seisundi halvenemine muudavad mitte ainult organismidele sobivate elupaikade hulka, vaid ka nende paiknemist maastikus. Sellised muutused mõjutavad organismide levimisvõimalusi, elupaikade omavahelist ühendatust ning kohalikke keskkonnatingimusi, milles kooslused kujunevad ja toimivad. Kui inimmõjuliste maastikumuutuste mõju taimedele ja loomadele on põhjalikult uuritud, teatakse märksa vähem sellest, kuidas need muutused mõjutavad mulla mikroobikooslusi. Mulla mikroobikooslusi käsitletakse peamiselt kohalike keskkonnatingimuste kaudu, näiteks mulla pH, toitainete sisalduse, taimkatte ja häiringute põhjal. Samas kujunevad ka mikroobikooslused maastikulises kontekstis ning nende liigiline koosseis ja mitmekesisus võivad sõltuda ümbruskonna elupaikade olemasolust ja paiknemisest maastikus. Oluline on arvestada ka mineviku maastike ja keskkonnatingimustega, sest tänapäevased mikroobikooslused võivad endiselt peegeldada varasemaid elupaiku ja levikumustreid.

Käesolevas doktoritöös uuriti, kuidas maastikupilt eri ruumiskaaladel ning ajaloolised maakasutused mõjutavad mulla mikroobikooslusi, keskendudes eeskätt arbuskulaarmükoriisaseentele. Need seened elavad sümbioosis enamiku maismaataimede juurtega, aidates taimedel omastada toitaineid, parandades mulla struktuuri ning suurendades taimede stressitaluvust. Samuti mõjutavad nad taimkoosluste kujunemist ja liigilist koosseisu. Arbuskulaarmükoriisaseened vajavad sobivaid peremeestaimi ja mullaolusid, kuid levivad eoste, seeneniidistiku fragmentide ja koloniseeritud juurte kaudu. Seetõttu mõjutavad nende kooslusi nii kohalikud keskkonnatingimused kui ka laiemad maastikulised protsessid. Lisaks võivad arbuskulaarmükoriisaseened püsida mullas pika aja jooksul nii eoste kui ka elujõuliste populatsioonidena. Nii võivad tänapäevased kooslused endiselt peegeldada varasemaid maakasutusviise ja elupaigatingimusi.

Doktoritöö peamine eesmärk oli selgitada, kuidas ajalooline ja tänapäevane maastikustruktuur mõjutavad mulla mikroobikooslusi erinevatel ruumiskaaladel. Täpsemalt uuriti, kas ajalooline maastikustruktuur on tänapäevase arbuskulaarmükoriisaseente mitmekesisusega tugevamalt seotud kui praegune maastikustruktuur (I–III), millistel ruumiskaaladel avalduvad maastikumõjud kõige selgemini (I–III), kas elurikkuse erinevad tahud reageerivad maastikule ja keskkonnatingimustele erinevalt (I–III) ning kas sarnaseid maastikumõjusid esineb ka teistes mullamikroobide rühmades (III, IV). Need küsimused on olulised, sest maastikumõjud ei pruugi avalduda ainult ühel ruumiskaalal ning mikroobikoosluste mitmekesisuse eri tahud võivad sõltuda erinevatest ökoloogilistest protsessidest. Töö põhines neljal Eestis läbi viidud uuringul, mis hõlmasid põllumajandusmaastikke (I), linnahaljasalasid (II, IV) ja parasvöötme metsi (III). Uuringutes kasutati DNA-põhiseid kooslusandmeid koos ajalooliste kaartide, GIS-analüüside, mulla keemiliste näitajate ning mitmemõõtmeliste statistiliste meetoditega.

Esimeses artiklis uuriti arbuskulaarmükoriisaseente mitmekesisust põllumajandusmuldades. Lõuna-Eestis paikneval kolmel mahepõllul koguti mullaproove 100 × 100 meetrise ruudustiku järgi kokku 99 proovivõtupunktist. Ajalooliste kaartide põhjal määrati looduslike elupaikade – peamiselt metsade ja niitude – levik aastatel 1894, 1969 ja 2022. Looduslike elupaikade osakaal arvutati 50, 100 ja 200 meetri raadiuses iga proovivõtupunkti ümber.

Seejärel analüüsiti arbuskulaarmükoriisaseente liigirikkuse ning eri proovivõtupunktides esinenud mikroobikoosluste erinevuste seoseid maastikustruktuuri, mulla omaduste ja reljeefiga.

Selgus, et põllumajandusmuldades oli arbuskulaarmükoriisaseente tänapäevane liigirikkus kõige tugevamalt seotud 1894. aasta looduslike elupaikade osakaaluga, eriti umbes 100 meetri ulatuses. Tänapäeva põllumuldade mikroobide mitmekesisus võib seega peegeldada rohkem kui sajanditaguseid maastikuolusid. See ei tähenda siiski, et samad seened oleksid mullas püsinud kogu selle aja vältel. Pigem võib ajalooliste elupaikade mõju säilida mullas püsivate eoste, pikaealiste populatsioonide või aeglaste kooslusmuutuste kaudu. Mida suurem oli ajalooliste looduslike elupaikade osakaal ümbruskonnas, seda sarnasemad olid eri proovivõtupunktide mikroobikooslused. Tänapäevaste looduslike elupaikade osakaalu suurenedes suurenes ka see, mil määral liigivaesemad kooslused sisaldasid samu liike nagu liigirikkamad kooslused. Seega mõjutavad pikaajalised maakasutuse muutused nii kohalike koosluste liigirikkust kui ka seda, millised liigid eri paikades säilivad.

Teine artikkel keskendus arbuskulaarmükoriisaseentele Tartu linna rohealadel. Linnastumine loob mosaiikse maastiku, kus rohealad erinevad vanuse, hoolduse, mulla omaduste ja ümbritseva maakasutuse poolest. Uuringus analüüsiti 778 roheala mullaproove nii avalikelt haljasaladelt kui ka koduaedadest. Ajalooliste kaartide põhjal hinnati, kui tugevalt olid uurimiskohad seotud ümbritsevate metsade, rohumaade, põllumajandusmaade ja hoonestatud aladega aastatel 1897, 1923, 1966 ja 2022. Seejuures arvestati nii eri tüüpi elupaikade kaugust kui ka nende hulka ümbruskonnas. Seoseid analüüsiti eri kaugustel, 50 meetrist kuni ühe kilomeetrini.

Tartus oli arbuskulaarmükoriisaseente liigirikkus suurem kohtades, mille ümbruses leidus minevikus rohkem rohumaid – kõige tugevam oli see seos 1923. aasta kaartide põhjal umbes 100 meetri ulatuses. See näitab, et kunagised avatud elupaigad mõjutavad tänapäeva linnamuldade mikroobikooslusi veel praegugi. Uuritud mikroobikoosluste omavahelised erinevused oli seevastu tugevamalt seotud tänapäevaste põllumajandusmaade läheduse ja ulatusega umbes 200 meetri raadiuses. Mida rohkem leidus ümbruskonnas põllumajandusmaad, seda sarnasemad olid arbuskulaarmükoriisaseente kooslused eri rohealadel. Funktsionaalne koosseis näitas aga teistsugust mustrit: häiringuid taluvate seente osakaal sõltus peamiselt mulla fosforisisaldusest ning avalike ja erahaljasalade erinevast hooldusest. Tänapäevase linnamaastiku mõju oli seejuures nõrk ning suurema hoonestatud ala osakaalu korral oli häiringuid taluvaid seeni mõnevõrra vähem.

Kolmandas artiklis uuriti parasvöötme metsi, et hinnata, kuidas ümbritsevate metsade hulk mõjutab arbuskulaarmükoriisaseente elurikkust. Analüüs hõlmas 100 vana metsaga uurimisala Lõuna-Eestis ning mitut organismirühma. Käesoleva doktoritöö seisukohalt olid kõige olulisemad tulemused seotud arbuskulaarmükoriisaseente ja teiste seenerühmade võrdlusega. Metsade osakaalu hinnati sajandi jooksul koostatud kaartide põhjal eri kaugustel, poole kilomeetri kuni viie kilomeetri ulatuses uurimisaladest. Lisaks vaadeldud liigirikkusele analüüsiti ka tumedat elurikkust ehk liike, mis võiksid antud kasvukohas esineda, kuid mida seal tegelikult ei leitud.

Erinevalt põldudest ja linnade rohealadest ei olnud metsades arbuskulaarmükoriisaseente liigirikkus selgelt seotud ei ajaloolise ega tänapäevase metsade osakaaluga maastikus. Küll aga oli tume elurikkus suurem seal, kus ümbruskonnas leidus tänapäeval rohkem metsi väikseimal uuritud ruumiskaalal ehk umbes 500 meetri ulatuses. See näitab, et maastik võib mõjutada nende liikide hulka, mis oleksid kasvukohale sobivad, kuid mida seal tegelikult ei leitud. Teised seenerühmad reageerisid maastikule erinevalt: ektomükoriisaseente mitmekesisus suurenes koos tänapäevase metsade osakaaluga suurematel ruumiskaaladel, taimehaigusi põhjustavate seente mitmekesisus sõltus aga tänapäevaste metsade olemasolust väiksemal ruumiskaalal ning lagundajaseente mitmekesisus vähenes seal, kus ümbruskonnas oli 1970. aastatel rohkem metsi.

Neljandas artiklis uuriti linnamuldade gammaproteobaktereid, et võrrelda nende mustreid arbuskulaarmükoriisaseente omadega. Gammaproteobakterid on olulised mitte ainult mulla mikroobide elurikkuse, vaid ka nn elurikkuse hüpoteesi seisukohalt. Selle järgi võib kokkupuude mitmekesiste keskkonnamikroobidega toetada inimese immuunsüsteemi arengut ja vähendada allergiariski. Tartu 743 rohealal analüüsiti gammaproteobakterite mitmekesisuse seoseid ümbruskonna maakasutuse, taimede liigirikkuse, mulla omaduste ja rohealade kasutusviisidega. Erinevalt arbuskulaarmükoriisaseente uuringutest keskenduti siin ainult tänapäevastele tingimustele. Selgus, et gammaproteobakterite mitmekesisus suurenes koos taimede liigirikkuse ja läheduses paiknevate metsaste aladega, eriti umbes 100 meetri ulatuses, ning vähenes suurema kaaliumisisaldusega muldades. Samuti oli gammaproteobakterite mitmekesisus suurem lasteaedade õuealadel kui avalikel haljasaladel.

Kõigi nelja artikli tulemused näitasid, et mulla mikroobikooslused peegeldavad nii ajaloolisi kui ka tänapäevaseid maastikke. Ajaloolised maastikumustrid osutusid eriti oluliseks arbuskulaarmükoriisaseente liigirikkuse kujundajana põldudel ja linnade rohealadel. Samas ei ilmnenud ajaloolised mõjud kõikides süsteemides ühtemoodi: metsades ei olnud arbuskulaarmükoriisaseente liigirikkus selgelt seotud metsade osakaaluga maastikus, kuid metsade praegune hulk maastikus mõjutas siiski nende liikide hulka, mis võiksid neis metsades esineda, kuid mida sealt ei leitud.

Doktoritöö tulemused näitasid samuti, et mulla mikroobikoosluste seosed maastikuga sõltuvad tugevalt ruumiskaalast. Põldudel ja linnakeskkonnas ilmnesid kõige tugevamad seosed umbes 100 meetri ulatuses, samas kui eri paikade mikroobikoosluste omavahelised erinevused olid seotud veidi suurema ruumiskaalaga, umbes 200 meetri ulatuses. Metsades sõltus erinevate seenerühmade mitmekesisus maastikust kuni viie kilomeetri ulatuses. See tähendab, et mulla mikroobide elurikkuse jaoks ei ole olemas üht „õiget" ruumiskaalat — sobiv skaala sõltub organismirühmast, uuritavast elurikkuse tahust ja sellest, kas oluline on liikide levimine, kohalike tingimuste mõju või ajalooline maakasutus.

Samuti selgus eri uuringutes, et elurikkuse erinevad tahud annavad üksteist täiendavat teavet. Liigirikkus, mikroobikoosluste omavahelised erinevused, funktsionaalne koosseis ja tume elurikkus ei olnud maastikuga seotud ühtemoodi. Kui liigirikkus peegeldas kõige järjekindlamalt ajaloolisi elupaiku, siis funktsionaalne koosseis sõltus rohkem kohalikest keskkonnatingimustest ja hooldusest. Seetõttu annaks ainult liigirikkuse uurimine puuduliku pildi sellest, kuidas maastikumuutused mulla mikroobikooslusi kujundavad.

Maastiku mõju ei ilmnenud ainult arbuskulaarmükoriisaseente puhul, vaid ka teistes seene- ja bakterirühmades. Samas sõltusid need seosed organismirühmast: erinevad mikroobid olid seotud erinevate maastike, ajaperioodide ja ruumiskaaladega. See näitab, et mullamikroobe ei saa käsitleda ühe ühtse rühmana, sest nende ökoloogilised nõuded ja levimisviisid erinevad suuresti.

Doktoritöö tulemused näitavad, et mulla mikroobide elurikkust ei määra üksnes kohalikud mullaolud. Mikroobikooslusi kujundavad samaaegselt ajalooline maakasutus, tänapäevane maastik, kohalikud keskkonnatingimused ja ruumiskaala. Seetõttu tuleks mulla elurikkuse kaitsel ja taastamisel arvestada nii ajaloolise maakasutuse siiani kestva mõjuga kui ka tänapäevaste elupaikade kvaliteediga. Poollooduslike rohumaade, metsaservade, väikeste metsalaikude ja mosaiiksete maastike säilitamine võib aidata toetada mulla mikroobide mitmekesisust, kuid erinevad mikroobirühmad võivad maastikumuutustele järgneda erineva kiiruse ja ulatusega.

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PUBLICATIONS

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