ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2025:41
FACULTY OF NATURAL RESOURCES AND AGRICULTURAL SCIENCES

Linking tree species diversity, productivity, and carbon sequestration in mixed-species forest plantations

From patterns to mechanisms

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SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2025

Acta Universitatis Agriculturae Sueciae
2025:41

Cover: Artistic illustration depicting the leaves of four species featured in this thesis: *Quercus robur, Acer rubra, Pinus pinaster* and *Anacardium excelsum* (Artist: Klara Jensen; 2025)

ISSN 1652-6880
ISBN (print version) 978-91-8046-476-5
ISBN (electronic version) 978-91-8046-526-7
https://doi.org/10.54612/a.2kmifmq5mk
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Print: SLU Grafisk service, Uppsala 2025

Linking tree species diversity, productivity, and carbon sequestration in mixed-species forest plantations

Abstract

Mixed-species forestry is a promising strategy for addressing global challenges such as climate change mitigation, biodiversity conservation, and sustainable timber production. In this thesis, I investigate the large-scale effects of species mixing in young tree stands on soil carbon (C) storage and accumulation, soil organic matter (SOM) chemistry and stability, aboveground productivity, and the mechanisms driving these outcomes. Drawing on data from TreeDivNet, a global network of tree diversity experiments, I assessed the roles of functional traits and environmental context. Willow species identity and diversity influenced SOM chemistry and thermal stability, while species identity affected soil C accumulation at one of two sites. In nine European experiments, topsoil C stocks were generally higher in mixtures than in monocultures, particularly in colder, less fertile, and more climatically stable sites. Fungal richness was positively associated with soil C stocks, though it did not vary significantly across diversity levels. At the global scale, aboveground productivity increased with species richness, plateauing at four to five species and becoming more stable at higher richness. Functional diversity promoted productivity, while structural diversity had a negative effect except at high richness. Selection effects predominated over complementarity effects, with acquisitive species (high leaf nitrogen, low wood density) performing best in mixtures. Across eleven experiments in Europe and Brazil, woody and litterfall biomass were higher in mixtures. Increases in woody biomass were associated with shifts in specific leaf area and leaf area index. Overall, this thesis emphasizes the importance of functional traits and environmental context in designing mixed-species plantations to optimize for both climate mitigation and productivity.

Keywords: tree species diversity, functional traits, functional diversity, environmental context-dependency, soil carbon accumulation, soil organic matter chemistry, climate change mitigation, biodiversity

Samband mellan trädslagsdiversitet, produktivitet och kolinlagring i blandskog

Abstract

Blandskogsskötsel är en lovande strategi för att hantera globala utmaningar såsom klimatförändringar, bevarande av biologisk mångfald och hållbar virkesproduktion. I denna avhandling undersöker jag storskaliga effekter av trädslagsblandning i unga trädplanteringar på inlagring av markkol, markens organiska materials kemi och stabilitet, produktivitet samt de mekanismer som driver dessa. Med data från TreeDivNet, ett globalt nätverk av träddiversitetsexperiment, analyserade jag betydelsen av funktionella egenskaper och miljökontext. I odlingar av *Salix* påverkade både artsidentitet och diversitet SOM-kemi och termisk stabilitet, medan artsidentitet påverkade markkolackumulering på en av två försöksplatser. I nio europeiska experiment var kolförråden i ytjorden generellt högre i blandbestånd än i monokulturer, särskilt på kallare och mindre bördiga platser med stabilare klimat. Artrikedom bland marksvampar varierade inte signifikant mellan olika diversitetsnivåer men var positivt kopplad till markkollagret. På global skala ökade produktiviteten med ökad artrikedom och planade ut vid fyra till fem arter. Funktionell diversitet främjade produktiviteten, medan strukturell diversitet hade en negativ effekt utom vid hög artdiversitet. Selektionseffekter dominerade över komplementaritetseffekter, där arter med resursanskaffande strategier (högt kväveinnehåll i bladen, låg vedtäthet) presterade bäst i blandningar. I elva experiment i Europa och Brasilien var både vedbiomassa och förnafallsbiomassa högre i blandningar. Ökningar i vedbiomassa var kopplade till förändringar i specifik bladarea och bladareaindex. Sammanfattningsvis betonar denna avhandling vikten av funktionella egenskaper och miljökontext för att designa blandade skogsplantager som optimerar både klimatnytta och produktivitet.

Nyckelord: trädartsdiversitet, funktionella egenskaper, funktionell diversitet, miljösammanhangsberoende, markkolbindning, kemi i markens organiska material, klimatförändringsmildring, biodiversitet

Dedication

To coffee and sunshine.

"If you don't know where you're going, any road will get you there."

- Lewis Carroll

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Jensen, J., Fransson, P., Baum, C., Leinweber, P., Eckhardt, K.-U., Weih, M. (2024). Variety and Site Drive *Salix* Mixture Effects on Soil Organic Matter Chemistry and Soil Carbon Accumulation. Forests, 15 (8), https://doi.org/10.3390/f15081339

II. Werner, R., Jensen, J., Fransson, P., Baum, C., Sandén, H., Rewald, B., Godbold, D. L., Mayer, M., Guillemot, J., Robin, A., Brancalion, P. H. S., Koricheva, J., Ponette, Q., Muys, B., Verheyen, K., Scherer-Lorenzen, M., Bauhus, J., Beyer, F., Hajek, P., Jactel, H., Weih, M. Effects of tree species richness on topsoil carbon and fungal diversity in European planted mixed forests are modulated by environmental conditions (submitted manuscript)

III. Jensen, J., Blondeel, H., Guillemot, J., Schnabel, F., Serrano-León, H., Auge, H., Baeten, L., Barsoum, N., Bauhus, J., Baum, C., Bermudez, R., Beyer, F., Brancalion, P., Cavender-Bares, J., Eisenhauer, N., Felton, A., Ferlian, O., Fiedler, S., Gebauer, T., Godbold, D., Hajek, P., Hall, J. S., Hölscher, D., Jactel, H., Kreft, H., Lapadat, C., MacLaren, C., Martin-StPaul, N., Meredieu, C., Mereu, S., Messier, C., Montgomery, R. A., Muys, B., Nock, C. A., Parker, J. D., Parker, W. C., Paterno, G. B., Perring, M. P., Ponette, Q., Potvin, C., Reich, P., Rentch, J., Rewald, B., Robin, A., Scherer-Lorenzen, M., Sandén, H., Sinacore, K., Standish, R., Stefanski, A., Verheyen, K., Williams, L. J., Weih, M. Diversity in resource use strategies promotes productivity in young planted tree species mixtures (submitted manuscript)

IV. Jensen, J, Blondeel, H., MacLaren, C., Ahmed, I. U., Augusto, L., Baeten, L., Bakker, M. R., Bauhus, J., Baum, C., Beyer, F., Bönisch, E., Brancalion, P., Dietrich, P., Eisenhauer, N., Fanin, N., Felton, A., Ferlian, O., Fransson, P., Fritsch, E., Glynn, C., Godbold, D. L., Guillemot, J., Haider, S., Hajek, P., Jactel, H., Mereu, S., Meredieu, C., Muys, B., Nordh, N.-E., Ponette, Q., Rewald, B., Robin, A., Saito, D., Sánchez-Bermejo, P. C., Sandén, H., Scherer-Lorenzen, M., Serrano-León, H., Verheyen, K., Werner, R., Yi, H., Weih, M. Tree species diversity drives aboveground carbon sequestration through light-related trait shifts (submitted manuscript)

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The contribution of Joel Jensen to the papers included in this thesis was as follows:

I. Main author. Participated in the conceptualization, design, methodology, data collection, data analysis, interpretation and writing of the manuscript.

II. Shared main author. Participated in the conceptualization, design, methodology, data collection, investigation, data analysis, interpretation and writing of the manuscript.

III. Main author. Participated in the conceptualization, design, methodology, data collection, investigation, data analysis, interpretation and writing of the manuscript.

IV. Main author. Participated in the conceptualization, design, methodology, data collection, investigation, data analysis, interpretation and writing of the manuscript.

During this doctorate, Joel Jensen contributed to the following papers not included in this thesis:

I. Lindroos, O., Söderlind, M., **Jensen, J.**, Hjältén, J. (2021). Cost analysis of a novel method for ecological compensation—a study of the translocation of dead wood. *Sustainability* 13(11), 6075. https://doi.org/10.3390/su13116075

II. Banin, L.F., Raine, E.H., Rowland, L.M., Chazdon, R.L., Smith, S.W., Rahman, N.E.B., Butler, A., Philipson, C., Applegate, G.G., Axelsson, E.P., Budiharta, S., Chua, S.C., Cutler, M.E.J., Elliott, S., Gemita, E., Godoong, E., Graham, L.L.B., Hayward, R.M., Hector, A., Ilstedt, U., **Jensen, J.**, Kasinathan, S., Kettle, C.J., Lussetti, D., Manohan, B., Maycock, C., Ngo, K.M., O'Brien, M.J., Osuri, A.M., Reynolds, G., Sauwai, Y., Scheu, S., Silalahi, M., Slade, E.M., Swinfield, T., Wardle, D.A., Wheeler, C., Yeong, K.L., Burslem, D.F.R.P. (2022). The road to recovery: a synthesis of outcomes from ecosystem restoration in tropical and sub-tropical Asian forests. *Philosophical Transactions of the Royal Society B* 377, 20210090. https://doi.org/10.1098/rstb.2021.0090

III. Sundqvist, M.K., Hasselquist, N.J., **Jensen, J.**, Runesson, J., Goodman, R.C., Axelsson, E.P., Alloysius, D., Lindh, A., Ilstedt, U., Aguilar, F.X. (2024). Accounting for deep soil carbon in tropical forest conservation payments. *Scientific Reports* 14, 16772. https://doi.org/10.1038/s41598-024-16772-0

IV. Roturier, S., **Jensen, J.**, Nutti, L.-E., Barbillon, P., Ollier, S., Bergström, D. (2024). Assessing the restoration and the dispersal of reindeer lichen after forest fire in northern Sweden: results after eleven growing seasons. *Ecological Engineering* 209, 107415. https://doi.org/10.1016/j.ecoleng.2024.107415

V. Blondeel, H., Guillemot, J., Martin-StPaul, N., Druel, A., Bilodeau-Gauthier, S., Bauhus, J., Grossiord, C., Hector, A., Jactel, H., **Jensen, J.**, Messier, C., Muys, B., Serrano-León, H., Auge, H., Barsoum, N., Birhane, E., Bruelheide, H., Cavender-Bares, J., Chu, C., Cumming, J.R., Damtew, A., Eisenhauer, N., Ferlian, O., Fiedler, S., Ganade, G., Godbold, D.L., Gravel, D., Hall, J.S., Hölscher, D., Hulvey, K.B., Koricheva, J., Kreft, H., Lapadat, C., Liang, J., Liu, X., Meredieu, C., Mereu, S., Montgomery, R., Morillas, L., Nock, C., Paquette, A., Parker, J.D., Parker, W.C., Paterno, G.B., Perring, M.P., Ponette, Q., Potvin, C., Reich, P.B., Rentch, J., Rewald, B., Sandén, H., Sinacore, K., Standish, R.J., Stefanski, A., Tobin, P.C., van Breugel, M., Vergara Fagundes, M., Weih, M., Williams, L.J., Zhou, M., Scherer-Lorenzen, M., Verheyen, K., Baeten, L. (2024). Tree diversity reduces variability in sapling survival under drought. *Journal of Ecology* 112(6), 1525–1540. https://doi.org/10.1111/1365-2745.14294

VI. Decarsin, R., Guillemot, J., le Maire, G., Blondeel, H., Meredieu, C., Achard, E., Bonal, D., Cochard, H., Corso, D., Delzon, S., Doucet, Z., Druel, A., Grossiord, C., Torres-Ruiz, J.M., Bauhus, J., Godbold, D.L., Hajek, P., Jactel, H., **Jensen, J.**, Mereu, S., Ponette, Q., Rewald, B., Ruffault, J., Sandén, H., Scherer-Lorenzen, M., Serrano-León, H., Simioni, G., Verheyen, K., Werner, R., Martin-StPaul, N. (2024). Tree drought–mortality risk depends more on intrinsic species resistance than on stand species diversity. *Global Change Biology* 30, e17503. https://doi.org/10.1111/gcb.17503

VII. Koricheva, J., Barton, K.E., Felix, J.A., Cooper, A., **Jensen, J.**, Jucker, T., Ruohomäki, K. (2025). Using long-term tree diversity experiments to explore the mechanisms of temporal shifts in forest ecosystem functioning. *Oikos* 2025, e10872. https://doi.org/10.1111/oik.10872

VIII. Bourdin, A., Augusto, L., Joly, F.-X., Baeten, L., Bres, C., Chahine, T., Guillemot, J., Hajek, P., Jactel, H., **Jensen, J.**, Mereu, S., Muys, B., Ponette, Q., Sandén, H., Parker, W.C., Paquette, A., Messier, C., Robin, A., Scherer-Lorenzen, M., Serrano-León, H., Weih, M., Castagneyrol, B., Bakker, M.R., Fanin, N. (2025). Context dependency of tree diversity effects on standardized substrates decomposition: role of tree functional composition, mycorrhizal type and climatic conditions. (submitted manuscript)

IX. Zheng, L., Ibáñez, I., Williams, L., Zhu, K., Serrano-León, H., **Jensen, J.**, Eisenhauer, N., Verheyen, K., Scherer-Lorenzen, M., Schnabel, F., Kreft, H., Guerrero-Ramírez, N.R., Hölscher, D., Paterno, G.B., Irawan, B., Ponette, Q., Messier, C., Paquette, A., Stefanski, A., Mereu, S., Bauhus, J., Hajek, P., Nock, C.A., Cavender-Bares, J., Parker, W.C., Quosh, J., Ferlian, O., Auge, H., Potvin, C., Yan, E., Yang, B., Zhang, L., Zhao, Z., Sinacore, K., Hall, J.S., Guillemot, J., Robin, A., Brancalion, P.H.S., Sundawati, L., Reich, P.B. (2025). Neighborhood diversity increases tree growth more in wetter climates but not in wetter years. (submitted manuscript)

X. Werner, R., Rewald, B., Godbold, D.L., Mayer, M., Bakker, M.R., Fanin, N., **Jensen, J.**, Serrano-León, H., Sandén, H. Beyond mean reaction norms: trait variability of trees under interspecific competition above and below ground. (manuscript)

XI. Rittelmann-Woods, E., **Jensen, J.**, [additional authors]. Global synthesis on the effects of woody plant diversity on soil organic carbon storage. (manuscript)

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Abbreviations

SOM	Soil organic matter
OTU	Operational taxonomic unit
ITV	Intraspecific trait variability
SLA	Specific leaf area
BA	Basal area
LAI	Leaf area index
LNC & LNCM	Leaf nitrogen content per unit mass
LNCA	Leaf nitrogen content per unit area
LPCM	Leaf phosphorous content per unit mass
MAT	Mean annual temperature
MAP	Mean annual precipitation
NDE	Net diversity effect
FDis	Functional dispersion
CWM	Community-weighted mean

1. Introduction

1.1 The current state of forestry and the role of mixed-species forestry

Modern forestry has been shaped by the need to meet global demand for wood products, with approximately 30 % of the world's forest area now dedicated to timber production (FAO 2020). To achieve efficiency and predictability in wood production, which has direct economic benefits, most forests are currently managed as even-aged, single-species plantations, systems that are structurally and genetically homogeneous. These monocultures are widely adopted across both temperate and tropical regions, typically focusing on a limited number of commercially valuable tree species, such as Scots pine and Norway spruce in Northern Europe, or eucalyptus, acacia, and teak in tropical and subtropical zones (Messier *et al.*, 2021). The appeal of monocultures lies in their operational simplicity: they allow for uniform silvicultural treatments, standardized harvesting regimes, and streamlined supply chains designed for specialized industrial uses (Nock et al. 2016; Verheyen et al. 2016).

However, the emphasis on production efficiency often comes at the expense of ecological resilience and multifunctionality. Monocultures tend to underperform in delivering a broader suite of ecosystem services, including biodiversity conservation, disturbance resistance, and long-term carbon (C) sequestration (Gamfeldt et al. 2013; Felton et al. 2016, 2020). As societal and scientific expectations shift toward ecological sustainability, there is increasing pressure on production forestry to align with goals such as climate resilience, recreational value, and habitat conservation, objectives that frequently conflict with the cost- and yield-driven priorities of conventional forest management (Bennett et al. 2009; Raudsepp-Hearne et al. 2010).

Against this backdrop, mixed-species forestry has gained traction as a promising alternative. It aims to maintain or even exceed the timber yields of monocultures while enhancing the delivery of multiple ecosystem services (Morin et al. 2011; Paquette & Messier 2011; Zhang et al. 2012). In particular, species mixtures can help counteract the biodiversity losses associated with structural simplification in plantation systems (Lindenmayer & Franklin 2002; Felton et al. 2020). Although the performance of mixed stands can vary depending on context (Ratcliffe et al. 2017), they have been associated with higher overall ecosystem service provision and are increasingly seen as a means to reconcile timber production with ecological sustainability (van der Plas et al. 2016; Baeten et al. 2019).

Although tree species diversity is not guaranteed to influence ecosystem functioning, a growing body of evidence suggests that species mixtures can outperform monocultures under comparable site conditions. Meta-analyses have shown that mixed stands are, on average, 15–24 % more productive than their monoculture counterparts (Zhang et al. 2012; Jactel et al. 2018). Beyond productivity, species mixtures are frequently associated with enhanced forest resilience, including reduced vulnerability to storms and windthrow (Agestam et al. 2006; Valinger & Fridman 2011), pests and pathogens (Pautasso et al. 2005; Jactel & Brockerhoff 2007), drought (Pretzsch et al. 2013; Pardos et al. 2021), and in some cases, fire (Felton et al. 2016). Each of these stressors is expected to intensify with climate change.

However, the benefits of diversity are context-dependent, and the current literature does not offer universal support for positive outcomes. In some instances, species mixing has produced neutral or negative effects (Baeten et al. 2019), such as increased susceptibility to ungulate browsing (Milligan & Koricheva 2013) or heightened fire risk (Hurteau et al. 2014). Contrasting findings between systems show the need for a nuanced perspective, and a deeper dive into context-dependent and mechanistic explanations of tree diversity effects on forest functioning.

A global network of tree diversity experiments (TreeDivNet; https://treedivnet.ugent.be/; Verheyen *et al.*, 2016; Paquette *et al.*, 2018a) provides a large-scale platform to support research that addresses questions related to tree stand diversity effects and underlying mechanisms (Figure 1).

While the individual TreeDivNet experiments vary in some aspects, such as the spatial arrangement of species (e.g. rows versus patches) and management practices like fertilization and irrigation, they share a number of key features. Notably, TreeDivNet experiments hold even-aged stands with each tree species being represented across all levels of species richness, allowing researchers to disentangle the effects of species identity from those of species diversity. Moreover, the geographic distribution of the experiments facilitates analyses that both account for and address environmental context-dependency in relation to edaphic and climatic conditions.

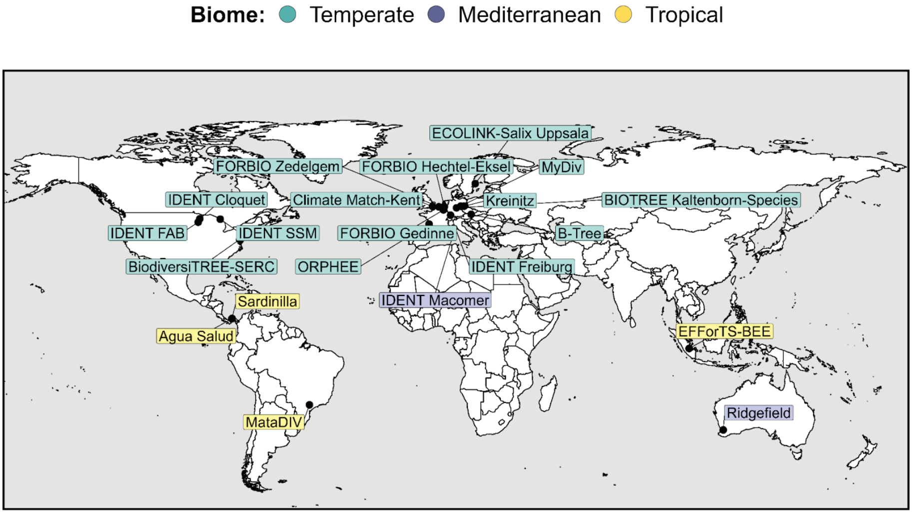

Figure 1. From Paper III. Locations of the 21 tree diversity experiments from the TreeDivNet network included in Paper III, colored by biome.

1.2 Forestry in light of climate change

Climate change is increasingly reshaping ecosystems through a cascade of environmental stressors, including rising global temperatures, altered precipitation regimes, and an increase in the frequency and severity of extreme weather events (IPCC 2021). These shifts are intensifying natural disturbance regimes and modifying environmental conditions, placing pressure on ecosystems' structure, function, and resilience. At the heart of climate change lies the accumulation of greenhouse gases (particularly carbon dioxide; CO_2) in the atmosphere, which trap heat and drive global warming (Royal Society, 2018). Terrestrial ecosystems play a critical role in this effort by sequestering C in both biomass and soils (Locatelli et al. 2015). Forests alone are estimated to store approximately 870 petagrams (Pg) of C globally, with about 45 % of forest C residing in soils (Pan et al. 2024:20). Some estimates suggest that total global soil C may reach up to 3,300 Pg C (Jansson & Hofmockel 2020). Accordingly, both afforestation and the enhancement of C storage in existing forests, above- and belowground, are among the most effective strategies for mitigating climate change (Canadell & Raupach 2008; Fawzy et al. 2020; IPCC 2021).

At the same time as forests are an efficient means to mitigate the consequences of climate change, forestry is inherently exposed to multiple risks associated with the changing climate, including storm damage, drought, pests, and market volatility, all of which are projected to intensify under climate change (Ammer 2017; IPCC 2021); emphasizing the urgency of developing forestry practices that enhance the adaptability and resilience of production forests. In parallel, there is increasing demand for forests to sequester more C while maintaining high productivity. In this context, mixed-species forestry has emerged as a promising strategy for both climate adaptation and mitigation (Bolte et al. 2009; Kolström et al. 2011; Paquette et al. 2018b; Rumpel et al. 2020). Reasons for this include the potential benefits in C sequestration (Augusto & Boča 2022; Zheng et al. 2024), biodiversity (Cavard et al. 2011b; Liu et al. 2018), resilience to climate dependent stressors such as drought (Pretzsch et al. 2013; Blondeel et al. 2024; Decarsin et al. 2024), pests and pathogens (Jactel & Brockerhoff 2007; Castagneyrol et al. 2017). One of the primary aims of this thesis is to explore and quantify the potential benefits of mixed-species forestry, where the broad scope of TreeDivNet allowed me to address the relevant questions at a larger scale than most prior research based on individual forest stands.

1.3 Key ecological mechanisms in mixed-species systems

Understanding why species mixtures sometimes do and sometimes do not enhance forest functioning, for example in terms of productivity or resilience against disturbances, requires a closer look at species interactions. In mixed stands, trees engage in both inter- and intraspecific interactions, unlike monocultures where there is only intraspecific competition between trees. These interactions can alter resource use and influence stand-level performance. Mixed-species forests often exhibit higher productivity than the average of their monocultures (overyielding), and in some cases even outperform the best monoculture (transgressive overyielding) (Schmid et al. 2008; Jactel et al. 2018; Zheng et al. 2024).

Three primary mechanisms can help explain the effects of species interactions: niche differentiation (also known as competition reduction), facilitation, and selection effects (Loreau 2000; Power & Mitchell 2004; Thompson et al. 2014). Niche differentiation and facilitation, which are not always easily distinguishable, and are both characterized by trait variation (Loreau 2000), are therefore grouped together as complementarity effects (Ammer 2019). Complementarity and selection effects, however, can be partitioned following Loreau & Hector (2001).

Niche differentiation occurs when species use different or the same resources at different times or in different spatial locations, thereby reducing competition and increasing total resource uptake (Thompson et al. 2014; Pretzsch et al. 2017). It is not only the number of species but rather functional, structural, or phylogenetic diversity that can drive niche complementarity (Díaz et al. 2007; Cadotte et al. 2008; Lei et al. 2009). Management strategies that combine species with contrasting traits (for example, rooting depth or shade tolerance) can tap into underutilized resource pools and improve stand productivity (Pretzsch & Zenner 2017). Other dimensions of niche differentiation include canopy architecture (Zhang & Chen 2015; Williams et al. 2017), phenological differences (Sapijanskas et al. 2014), decomposition dynamics (Hättenschwiler et al. 2005), and water-use efficiency (Forrester 2015).

Facilitation occurs when one species improves the growing conditions for another, thereby increasing its performance or survival (Bravo-Oviedo et al. 2018). A classic example is the inclusion of nitrogen (N)-fixing species in mixtures, which can benefit neighboring trees by increasing soil N availability. Marron & Epron (2019) found an 18 % productivity gain in such mixtures, though others report no consistent effects (Zhang et al. 2012; Jactel et al. 2018). This discrepancy of results could possibly be explained due to site-specific nutrient limitations. Facilitation can also occur through mechanisms such as hydraulic lift, where deep-rooted species transport water to upper soil layers (benefiting shallow-rooted neighbors) (Pretzsch et al. 2013). Furthermore, facilitation may enable species to persist outside their optimal environmental conditions by growing with other species that alleviate physiological stress (O'Brien et al. 2019).

Selection effects occur when one or a few species with high functional contributions to an ecosystem dominate a community, thereby driving overall ecosystem performance (Loreau & Hector 2001). A positive selection effect arises when the dominant species performs better in mixtures than in monoculture (Ammer 2019). In contrast, selection effects are negative when low-performing species dominate, potentially diminishing ecosystem functioning. Closely related is the sampling effect, which describes the increased probability of including a species capable of dominating the stand as species richness increases. Over time, strong selection pressure may lead to the competitive exclusion of less-fit species, ultimately reducing biodiversity (Niklaus et al. 2017). Like niche differentiation and facilitation, both selection and sampling effects are closely linked to functional traits (Tobner et al. 2016).

These mechanisms can all be occurring simultaneously, and the design of TreeDivNet, with species present within all diversity levels within a site, allows us to distinguish between them and disentangle them, even when synchronously positive and negative. Once delineated, these diversity effects can be further examined in relation to functional trait expression.

1.4 Species interactions and functional traits

Species interactions are often mediated by functional traits, which are morphological, physiological, phenological, chemical or phylogenetic characteristics that influence how organisms respond to environmental conditions and interact with one another (Violle et al. 2007; Díaz et al. 2022). These traits reflect underlying ecological strategies and are central to understanding species performance and coexistence in community and trait-based ecology. In this thesis, functional traits are used with the above definition to investigate diversity effects and species interactions (Papers III and IV). Examples of functional traits relevant to delineating tree species interactions include specific leaf area (SLA; leaf area per leaf biomass); reflecting growth rate and resource use efficiency, leaf N content (LNC); essential for photosynthetic capacity, and wood density; important to functions such as tree growth, mechanical strength, and resistance to environmental stress (Funk et al. 2008; Maynard et al. 2022).

An important distinction made in trait-based ecology refers to the difference between interspecific and intraspecific variation. While interspecific differences have long been a central focus, especially in relation to species' ecological strategies, the contribution of intraspecific trait variability (ITV) is increasingly recognized (Westerband et al. 2021; Serrano-León et al. 2022), and is examined in this thesis (Paper IV). Interspecific trait differences often reflect contrasting life-history characteristics of the involved species.

For example, species in the genus *Macaranga* (native to tropical Southeast Asia) tend to grow quickly, have low wood density, and high SLA, traits that suit them to rapid canopy formation following disturbance (Wright et al. 2010; Gustafsson et al. 2016). In contrast, *Dipterocarpus* species show slower growth, higher wood density, and lower SLA, traits associated with longer-term dominance in mature forests (Gustafsson et al. 2016).

Such consistent interspecific differences have led many ecological studies to rely on species-mean trait values when describing plant communities (Funk et al. 2017). However, this approach may overlook the ecological significance of ITV, which can shape competitive dynamics (Bolnick et al. 2011), enable adaptation to changing environments (Reich 2014), and confer resistance to stressors such as herbivory (Boege & Dirzo 2004) and freezing (Koehler et al. 2012). Trait values are inherently plastic, responding to environmental and biotic contexts (Schmitz et al. 2015). For example, ITV has been associated with variation in canopy openness (Carlucci et al. 2015), soil nutrient availability (Freschet et al. 2015), and broader geographic gradients, including latitude and temperature (Albert et al. 2010; Jucker et al. 2014). As a result, trait-based analyses must account for environmental variation when applied across different sites or time periods. Moreover, ITV can differ substantially across traits and species (Herrick & Blesh 2021) and contributes to total trait variation (Siefert et al. 2015). As such, considering

ITV can enhance predictions of ecosystem functioning, particularly under global change scenarios (Alberto et al. 2013).

The variability and distribution of functional traits within a community comprise its functional diversity, a community property that plays a central role in mediating ecosystem processes (Tilman 2001). Functional diversity often explains diversity effects on ecosystem functioning better than more taxonomic measures (Cadotte et al. 2011). As species are added to a community, functional diversity typically increases in tandem with taxonomic diversity, up to a threshold. Beyond this point, functional redundancy is typically more prevalent, where additional species no longer contribute novel traits (Pretzsch et al. 2017). This principle is especially relevant in the context of mixed-species forests, where the presence of diverse functional strategies can lead to more efficient resource partitioning, particularly within the canopy (Williams et al. 2017). Increased architectural plasticity and light-use efficiency in such stands have been linked to enhanced biomass accumulation (Pretzsch 2014). For instance, enhanced light availability in mixed stands can alleviate competitive constraints, enabling trees to alter their growth strategies. Thus, functional traits not only elucidate the interactions and processes within mixed forests, but also provide a framework for identifying ecological strategies and anticipating the outcomes of forest composition on ecosystem performance.

1.5 Functional trade-offs and plant growth strategies

Even when carefully assessed across different spatial and temporal scales, the explanatory power of plant functional traits depends strongly on the biotic and abiotic context in which they are expressed. There is no universally optimal value for any given trait. Instead, species are positioned along trade-off gradients that reflect their underlying functional strategies (such as growth rate, water use, or reproductive output). For example, SLA has been shown to reflect a trade-off between resource acquisition and leaf longevity (Díaz et al. 2016). These plant-level trade-offs often scale up to influence landscape-level trade-offs, for example between provisioning services (e.g. biomass, fiber, or bioenergy production) and regulatory services (e.g. water purification or soil conservation), a well-known challenge in agroecosystem ecology (Millennium ecosystem assessment 2005).

Trade-offs between functional traits can be evidenced through individual traits (such as wood density or LNC) or through suits of traits (trait syndromes) that form broader resource-use or economic spectra. These spectra may be organ-specific (such as the leaf economic spectrum; (Wright et al. 2004) or integrated across the whole plant, as in the fast–slow growth continuum, which contrasts rapid growth and reproduction with conservative, long-lived strategies (Reich 2014; Salguero-Gómez et al. 2016). When selecting traits to understand or predict ecosystem processes, it is useful to prioritize those that have well-established links to plant function and strategy. The LNC is one such trait. N is essential for photosynthesis, and higher N levels typically support faster resource acquisition (Garnier & Navas 2012). However, N is also limiting plant growth in many ecosystems and has competing uses even within an individual plant (e.g. in stems or reproductive tissues; (Weih et al. 2021). In addition, high leaf nutrient concentrations can increase herbivory risk (Casotti & Bradley 1991; Wright et al. 2004). This emphasizes a classic trade-off: enhanced photosynthetic capacity comes at the cost of increased vulnerability and opportunity cost of not being allocated elsewhere. High leaf N concentration is therefore often indicative of an acquisitive growth strategy, while lower concentrations may be associated with a conservative strategy. Identifying functional strategies in this way could inform species selection in forest systems. For example, acquisitive species may be better suited to fertile environments with low disturbance, while conservative species may perform better under resource-limited conditions.

(Díaz et al. 2016) used functional trait profiles to classify plant growth strategies across a wide range of species. Their analysis identified a small set of traits as especially informative, characterizing trade-off gradients in relation to six key functional traits (SLA, leaf area, leaf N content, wood density, maximum height and seed mass). The trait configuration pointed out by (Díaz et al. 2016) clustered into two distinct "hotspots", corresponding to the centroids of woody and non-woody species. In relation to each other, the non-woody cluster (characterized by lower adult height and smaller seed mass) reflects an acquisitive strategy while the woody cluster (with higher values for the same traits) reflects a more conservative strategy. However, these acquisitive-conservative gradients exist also within the clusters, and can help identify species in relation to their growth strategies. Subsequent work by (Guillemot et al. 2022; MacLaren et al. 2023) further continued on this path, where functional traits such as SLA, leaf N content and plant height were considered useful in aligning species along an acquisitive-conservative strategic gradient. In this thesis (Paper III), LNC and wood density were used to characterize the functional identity of tree species.

1.6 Tree mixture effects on soils: carbon accumulation, carbon chemistry and fungal communities

Plant diversity is increasingly recognized as a driver not only of aboveground biomass but also of belowground processes, including the formation and stabilization of soil organic matter (SOM), a key reservoir for terrestrial C (Lehmann et al. 2020). The soil C pool is influenced by both the quantity and quality of organic inputs, such as leaf and root litter, and root exudates, which vary greatly between plant species and vegetation types (Warembourg et al. 2003; Berg & McClaugherty 2020).

The SOM formation reflects the balance between organic inputs (e.g., leaf and root litter turnover, and exudates) and SOM turnover (Gleixner 2013; Lehmann & Kleber 2015). The persistence of SOM is influenced by the chemical composition and thermal stability of its constituent molecules, some, such as lignin and suberin, are energetically costly to degrade and therefore contribute to more stable SOM pools (Leinweber et al. 2008; Bradford 2013; Gleixner 2013). Thermal stability is often used as a proxy for resistance to microbial decomposition (Leinweber et al. 2008; von Lützow et al. 2008).

Among the soil microbial communities, fungi are central to belowground C dynamics, especially in forests, contributing both to decomposition and to the formation of stable SOM. Saprotrophic fungi is the main functional guild breaking down plant-derived litter, while ectomycorrhizal fungi may slow down decomposition by competing for N. However, ectomycorrhizal fungi may also contribute to SOM degradation since some species have retained their ancestral capacity to oxidise organic matter (Lindahl & Tunlid 2015). Fungal necromass, particularly melanized hyphae, is chemically resistant and contributes to long-term SOM accumulation (Godbold et al. 2006; Ekblad et al. 2013; Zak et al. 2019; Zang et al. 2024).

Tree diversity can influence fungal diversity and composition through direct pathways (e.g. increased ectomycorrhizal host range) and indirect pathways (e.g. altered litter inputs, root exudates, and soil microclimate)

(Weißbecker et al. 2018; Liu et al. 2020; Gillespie et al. 2021). Higher fungal diversity has been linked to greater soil C storage and enhanced forest productivity and resilience (Yang et al. 2017; Luo et al. 2024:202; Sachsenmaier et al. 2024). However, fungal responses vary by functional guild and environmental context, with tree species identity often playing a stronger role than tree species richness alone (Waldrop et al. 2006; Tedersoo et al. 2016; Griffin et al. 2019). Other drivers such as soil type, climate, and land-use history also shape fungal communities (Tedersoo et al. 2014; Djemiel et al. 2024).

Advancing our understanding of plant-soil-fungi interactions is essential for evaluating the long-term role of biodiversity in soil C sequestration and ecosystem functioning, and is an objective that Papers I-II of this thesis aims to address.

1.7 Context-dependency of plant-plant interaction

As emphasized throughout this thesis and addressed in Papers I and II, the effects of species diversification on forest functioning are highly dependent on environmental context. While the general relationship between biodiversity and ecosystem functioning is well established, current research is increasingly focused on understanding the mechanisms behind this relationship and how the relevant mechanisms are modulated by environmental, biological, and temporal factors. A deeper understanding of this context-dependency is essential for improving the reproducibility of experimental findings and for the successful upscaling and implementation of mixed-species management strategies.

One prominent framework for explaining context-dependent outcomes is the stress gradient hypothesis (Bertness & Callaway 1994), which proposes that facilitative interactions between plants become more important under stressful conditions. This implies that the productivity benefits of species mixtures may be strongest in environments where growth is limited by abiotic stress (e.g. drought, cold, wind, or heat), or by biotic pressures such as high planting density. Several studies have reported increased diversity effects under higher planting densities, potentially due to the emergence of stronger facilitative relationships (Boyden et al. 2005; Amoroso & Turnblom 2006; Condés et al. 2013; Forrester et al. 2013). However, opposite trends have also been observed (Garber & Maguire 2004; Río & Sterba 2009), highlighting ongoing debate around the universality of the stress gradient hypothesis. For example, (Holmgren & Scheffer 2010) revised the original framework to suggest that complementarity is maximized not under the most extreme stress, but under moderate stress conditions.

In relation to the role that environmental gradients play in modulating biodiversity–ecosystem functioning relationships, (Joswig et al. 2022) showed that plant trait variation is strongly shaped by their environment, with latitude negatively affecting size-related traits and climate–soil variables jointly explaining up to 77 % of variation in size and economic traits globally across 20,000 species. This helps explain why outcomes of species mixing vary between locations, as trait-based species interactions are central to diversity effects. For example, (Jing et al. 2022) found that diversity effects on wood production were positive primarily in arid regions, while positive effects on stability were more common in humid regions. (Ratcliffe et al. 2017) identified water limitation as the most important driver of context-dependent diversity effects (a finding supported by (Chen et al. 2024), though contradicted by (Belluau et al. 2021). (Craven et al. 2020) further demonstrated that mean annual temperature and precipitation both influence the magnitude of diversity effects on net primary productivity. Further demonstrating the importance of climate in influencing outcomes of species mixing, (Blondeel et al. 2024) reported that under drought stress, species which had low survival when grown in monoculture, fared better when grown in mixture and that tree survival under extreme drought increased with increasing functional diversity. Compared to climate variables, the role of soil properties has received less attention, though there is growing evidence that factors such as soil acidity, fertility, N availability, and topography can significantly shape biodiversity–functioning relationships (Ferretti et al. 2014; Forrester & Pretzsch 2015; Mina et al. 2018; Ammer 2019).

Tree and stand age is another critical factor influencing the strength and direction of diversity effects. Multiple studies have found that the benefits of tree diversity tend to increase with stand development (Cavard et al. 2011a; Forrester 2014; Tobner et al. 2016; Vogel et al. 2019; Zeller & Pretzsch 2019), and that long-term diversity effects may even exceed those of common management interventions such as N fertilization (Tilman et al. 2012). However, there is not full agreement on this point. For instance, (Silva Pedro et al. 2015) observed stronger diversity benefits in early-successional stages. (Tatsumi 2020) found a positive relationship between stand age and net diversity effect on productivity, which was driven by increasing complementarity and decreasing selection effects over time. These patterns were linked to vertical canopy partitioning (which reduces competition) and suppression of low-performing species. In later stages of stand development (after 15 years), higher survival in mixed stands further enhanced overall productivity. These findings suggest that temporal scale must be considered in planning for diversity effects, and that patience may be required for the benefits of species mixing to fully emerge.

In summary, the effects of species diversification on forest performance are not fixed outcomes, but rather emergent properties that depend on multiple interacting factors, including environmental conditions, forest age, species traits, and planting density. The understanding and accounting for this context-dependency is important for designing effective mixed-species plantations and is further addressed in this thesis (Paper II).

2. Aims and research questions

The overall aim of this thesis is to explain the patterns and investigate the mechanisms underlying the impact of tree species diversification on carbon sequestration and aboveground productivity in mixed-species forests. Specific questions to assess include:

- How are topsoil C accumulation, soil organic matter (SOM) chemistry and fungal community structure influenced by tree species identity and diversity? (Papers I-II)

- How does tree species diversity affect aboveground productivity and carbon sequestration? (Papers III-IV)

- How do community- and species-level functional traits respond to species mixing, and how are these responses linked to diversity effects on aboveground biomass production? (Paper IV)

- How do environmental conditions modulate the relationships between species mixing and topsoil C sequestration? (Papers I-II)

3. Methods

3.1 Overview of experimental network (TreeDivNet)

All papers included in this thesis are based on data from a range of experimental sites within the TreeDivNet (https://treedivnet.ugent.be/; Verheyen et al. 2016; Paquette et al. 2018a; see Table 1). Specifically, Paper I utilized data from two experiments, Paper II from ten experiments, Paper III from 21, and Paper IV from eleven experiments. While I directly contributed to data collection in several sites, especially at the ECOLINK-Uppsala experiment, much of the data used in this thesis was provided by the PI´s of the respective experiments and their teams, and subsequently harmonized by me for comparative analysis.

Although some experiments were not fully consistently designed, with inconsistencies such as varying plot sizes in B-Tree or different planting densities in BIOTREE Kaltenborn-Species, most experiments maintained internal consistency. Most important was that all trees within a given site were even-aged, and that species were represented in all diversity levels, both monocultures and mixtures, which allowed for the disentanglement between species and diversity effects, as well as the partitioning of diversity effects. The only experiment that did not fit these characteristics was Ridgefield, as such, this site was only used for analyses where this was not necessary. Between experiments, however, there was considerable variability, e.g. plot sizes ranged from 10 to 2304 m^2, planting densities from 1,111 to 62,500 stems per hectare, and experiment ages spanned 4 to 23 years. The experiments also covered a wide climatic gradient, including tropical, Mediterranean, temperate, and boreal regions. A selection of tree species suited to local conditions were used in all experiments.

Table 1. Site characteristics for all tree diversity experiments included in this thesis. Mean annual temperature (MAT) and mean annual precipitation (MAP) were derived from http://www.worldclim.org/current.

Experiment name	**Country**	**Biome**	**Planting year**	**Planting density [trees ha^{-1}]**	**MAT [°C]**	**MAP [mm]**	**Richness gradient**
Agua Salud	Panama	Tropical	2008	1,111	25.5	2712	1, 2, 5
B-Tree	Austria	Temperate	2013	10,000	9.7	624	1, 2, 4
BiodiversiTREE-SERC	USA	Temperate	2013	1,736	13.2	1068	1, 4
BIOTREE Kaltenborn-Species	Germany	Temperate	2004	2,500-5,000	7.4	693	1, 2, 3, 4
Climate Match-Kent	UK	Temperate	2011	2,500	10.1	677	1, 4
ECOLINK-Rostock	Germany	Temperate	2014	15,625	8.4	600	1, 2
ECOLINK-Uppsala	Sweden	Temperate	2014	15,625	5.8	551	1, 2, 3, 4
EFForTS-BEE	Indonesia	Tropical	2013	2,500	26.8	2491	1, 2, 3, 6
FORBIO Gedinne	Belgium	Temperate	2010	4,444	8.3	1060	1, 2, 3, 4
FORBIO Hechtel-Eksel	Belgium	Temperate	2012	4,444	10.1	713	1, 2, 3, 4
FORBIO Zedelgem	Belgium	Temperate	2010	4,444	9.5	816	1, 2, 3, 4
IDENT Cloquet	USA	Temperate	2010	62,500	3.7	762	1, 2, 6
IDENT FAB	USA	Temperate	2013	49,438	6.3	751	1, 2, 5
IDENT Freiburg	Germany	Temperate	2013	49,438	10.5	841	1, 2, 4, 6
IDENT Macomer	Italy	Mediterranean	2014	62,500	13.9	879	1, 2, 4, 6
IDENT SSM	Canada	Temperate	2013	62,500	3.7	916	1, 2, 4, 6
Kreinitz	Germany	Temperate	2005	12,500	9.2	575	1, 2, 3, 5, 6
MataDIV	Brazil	Tropical	2019	1,887	19.3	1314	1, 3, 6
MyDiv	Germany	Temperate	2015	10,000	8.9	493	1, 2, 4

Experiment name	Country	Biome	Planting year	Planting density [trees ha^{-1}]	MAT [°C]	MAP [mm]	Richness gradient
ORPHEE	France	Temperate	2008	2,500	12.6	1000	1, 2, 3, 4
Ridgefield	Australia	Mediterranean	2010	2,000	16.2	478	1, 2, 4
Satakunta	Finland	Boreal	1999	4,444	3.8-4.0	597-613	1, 2, 5
Sardinilla	Panama	Tropical	2001	1,111	25.9	2854	1, 3, 6

3.2 Data collection

3.2.1 Soil data (Papers I & II)

For Paper I, soil samples were collected from two experimental sites: ECOLINK-Rostock, Germany, and ECOLINK-Uppsala, Sweden. At each site, nine samples per plot were taken from 18 plots during April in both 2014 and 2021. For Paper II, soil sampling was conducted in spring 2022 across 220 plots in 10 experimental sites, with ten subsamples collected per plot. A subset of 152 samples was selected for fungal community analysis, Fungal species were characterized using operational taxonomic units (OTUs) as proxies for species identification.

In both studies, sampling avoided plot borders and was limited to the upper 10 cm of soil (after removal of surface litter), a layer known for its high fine-root biomass, elevated fungal activity, and pronounced sensitivity to tree richness effects (Prescott & Grayston 2013; Wambsganss et al. 2021; Spohn et al. 2023). For each plot, subsamples were pooled and homogenized; the composite samples then dried at 40 °C for 24 to 48 h, sieved through a 2 mm mesh. All soil samples underwent chemical analysis following drying at 105 °C for 24 h. Soil pH was measured in 0.1 mol $CaCl_2$ at a 1:2.5 (w/v) soil-to-solution ratio. C and N concentrations were determined using a CN analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany).

3.2.2 Aboveground productivity and biomass (Papers III & IV)

Diameter and height measurements were collected from individual trees in each experiment. Tree diameter data were used to calculate the basal area per tree, which was then extrapolated to a per-hectare basis and divided by the number of years since planting to estimate species- and stand-level productivity, as reported in Paper III. The same diameter data also supported the estimation of species- and stand-level woody biomass in Paper IV, using allometric equations tailored to individual tree species at each site. These equations were selected to best represent the range of tree sizes, species, locations, and measurement heights. In addition to woody biomass, aboveground biomass estimates in Paper IV included litterfall biomass, assessed as the dry weight of leaf litter collected per hectare annually using litter traps. Understory biomass was also included and represented the dry weight per hectare of grasses, herbs, ferns, and shrubs. The percentage cover of major morphological groups in each plot was quantified and converted to dry weight per hectare using the PhytoCalc model, following (Heinrichs et al. 2010).

3.2.3 Functional trait data (Papers III & IV)

In Paper III, species-specific functional traits values of specific leaf area (SLA), leaf N concentration (LNC) and wood density (WD) were selected to represent an acquisitive-conservative resource use gradient and were used to estimate the functional identity and diversity of stands, using data measured in site where possible and otherwise supplemented with values from the TRY Plant Trait Database (Kattge et al. 2011). In Paper IV, species-specific functional trait values were primarily derived from measurements taken in monocultures at each study site and supplemented with literature and database values when site-specific data were unavailable. The database values were also derived from the TRY database (Kattge et al. 2011) as well as the global wood density database (Chave et al. 2009:20; Zanne 2009). The traits considered were SLA, WD, leaf area index (LAI), leaf N concentration per leaf mass (LNCM), and tree height increment

In Paper IV, functional traits measured on-site included SLA, LAI, WD, LNCM, leaf N concentration per leaf area (LNCA), leaf P concentration per leaf mass (LPCM), leaf C:N ratio, leaf N:P ratio, and annual tree height increment. The SLA was calculated from scanned leaf area (ImageJ; (Collins 2007) divided by dry weight after drying at 70 °C. The LAI was assessed using site-specific but comparable methods at peak canopy. The LNCM and LPCM were obtained from dried, ground leaf samples analyzed for C, N, and P. The P content was measured via microwave digestion and ICP-OES, while C and N were measured with an elemental analyzer, and P by Olsen extraction at FORBIO (Dhiedt et al. 2022). The LNCA was calculated as LNCM/SLA. Nutrients were assessed at species-per-plot and plot levels. Wood density was measured from increment cores using XCT (De Mil et al. 2016; Serrano-León et al. 2024), except at MyDiv, where water displacement was used. Tree height increment was derived as max height/age. At ECOLINK Uppsala, height was estimated via diameter-based allometries (Hoeber et al. 2018). While methods partly varied across sites, they were consistent within sites, minimizing impacts on within-site analyses. While efforts were made to collect trait data using the same protocols between sites, methodologies sometimes varied between study sites. However, they were applied consistently within each site and since our analyses focused on within-site variability in Paper IV, these differences should not significantly impact the main conclusions.

3.2.4 Climate data (Paper II)

To analyze the climatic aspect of context-dependent effect on soil C storage Environmental variables used in Paper II, mean annual temperature (MAT) since establishment and mean annual precipitation (MAP) were collected from nearby climate stations for five sites while national data triangulation was used for the three FORBIO sites and ECOLINK-Rostock. To capture climatic variability, I calculated the interannual coefficient of variation (CV) for both temperature and precipitation based annual averages.

3.3 Metrics for quantifying diversity effects and plant-plant interactions

To be able to investigate drivers of tree diversity effects, in Papers II and IV, a net tree diversity effect (NDE) was calculated as the ratio of observed to expected values in mixtures (Hector et al. 2002; Scherer-Lorenzen et al. 2007). Expected values were based on weighted averages of monoculture means, with weights reflecting either number of individuals (Paper III) or relative basal area (Paper IV). For traits derived from plot-level measurements in Paper IV (e.g., biomass, LAI), NDEs were unweighted.

To more in depth identify the mechanisms underlying the net diversity effects on productivity, I applied the additive partitioning method by (Loreau & Hector 2001) to the stand productivity in Paper III. This method decomposes the NDE into two components: selection effects and complementarity effects. The selection effect was quantified as the covariance between species' monoculture productivity and the difference between their observed and expected contributions in mixtures. A positive selection effect suggests dominance by inherently productive species, whereas a negative effect may indicate that high-yielding species underperform in mixtures. The complementarity effect was calculated as the mean deviation of observed productivity from expected productivity across all species in a given mixture. A positive complementarity effect indicates that species perform better together than expected based on monoculture values.

To assess functional diversity in Paper III, functional dispersion was calculated (FDis; (Laliberté & Legendre 2010), representing the mean distance of each species to the centroid in trait space, weighted by relative species abundance (i.e., number of stems per species). FDis was computed for individual traits (e.g., FDis$_{LNC}$, FDis$_{WD}$) as well as a combined trait profile (FDis$_{all}$). Functional identity was captured through community-weighted means (CWMs) for key traits like leaf N content (LNC) and wood density (WD), using the number of stems per species as weights. In Paper IV, functional diversity was similarly represented by FDis, but calculated with equal species weights within each plot, reflecting the experimental design; and FDis was used instead of species richness. The CWMs in Paper IV were calculated using basal area proportions per species, providing a biomass-weighted measure of functional composition that accounted for species dominance.

To investigate mediators of effects of species richness on stand productivity in Paper III, structural diversity was calculated using the CV and the Gini coefficient of tree heights per plot.

To enhance comparability across sites and species with differing baselines (e.g., in productivity), standardization was applied either within or across experiments, depending on the variable (see individual papers for details). Continuous variables that varied within experiments (e.g., productivity, species-per-plot trait values) were standardized within experiments, while those constant within experiments (e.g., species-specific traits, climate variables) were standardized across experiments. Standardization was primarily performed using z-scores (subtracting the mean and dividing by the standard deviation), preserving each variable's relative distribution and central tendency. An exception was functional diversity metrics in Paper III, which were standardized using min-max scaling (rescaled between 0 and 1) to facilitate comparisons on a uniform scale. Diversity effect measures (i.e. NDE, selection effects and complementarity effects) were not transformed, as they were already expressed relative to monocultures within each site.

3.4 Data harmonization

Although this thesis involved substantial fieldwork, a large amount of the data was shared from other experiments. Due to differences in experimental design, scope, and the nature of long-term field measurements, the datasets obtained from different sites often varied considerably in structure and content. As a result, harmonization of these datasets was required prior to analysis. All data management and harmonization steps were conducted in R and fully scripted to ensure reproducibility and transparency, with each step in the processing workflow documented in code.

This data was then filtered according to the specifications of each question asked by each paper. For example, to best capture the interactions of as mature trees as possible, data only from the most recent inventories were used. Additionally, some experiments applied additional treatments such as fertilization or irrigation to explore interactions with tree diversity. To enhance comparability across experiments and ensure a focus on the primary variable of interest, this thesis focused on plots in which tree species diversity was the sole manipulated factor. These and other considerations typically led to a large difference between the data available and the data used. As an example, for Paper III, the diameter data consisted of roughly 700 000 individual measurements, but after fitting it to my specifications, 83600 measurements remained; around 12 %.

3.5 Statistical analysis

All statistical analyses were conducted in R (R Core Team, 2022). Across all studies, mixed-effects models were used to assess treatment effects while accounting for the hierarchical structure of the data. Specifically, site and block nested within site were used as random effects to account for nested and hierarchical study designs for Papers I-IV. For Paper III, also species composition nested in site was added as a random effect to promote generalization beyond the specific species combinations represented in the data. In Papers I–III, variance structures were incorporated to model heteroscedasticity across sites or species richness levels. Estimated marginal means were used to account for unbalanced datasets in Papers I-II and IV. All p-values involving multiple comparisons were adjusted using Tukey corrections. All models were visually evaluated for normality, homoscedasticity, and multicollinearity.

In Paper I, specific comparisons across sites, varieties within sites, varieties across sites, as well as the disparities between expected and observed mixture values within sites and observed mixture values across sites were assessed directly subsequent to multiple comparisons tests.

Linear and nonlinear mixed-effects regression models were used throughout Papers I-IV to test relationships between continuous variables, and analyses of variance (ANOVA) to test differences between groups.

Principal component analysis (PCA) was used in Papers I-II, where in Paper I, PC1 and PC2 were used to perform a principal component regression analysis in order to assess multivariate differences in SOM chemical composition between treatments. In Paper II, a PCA-derived fertility index based on soil pH and C:N ratios was included as a covariate in models assessing diversity effects on C stocks. A Mantel test was used to assess correlations between fungal and tree community dissimilarity, using Bray-Curtis and Jaccard matrices, respectively, applying a Spearman's rank correlation to account for non-linearity. In Paper IV, species-specific shifts in woody biomass and functional traits between monoculture and mixture conditions were tested using one-sample t-tests.

Structural equation models (SEM; (Lefcheck 2016) were applied in Papers III-IV, in Paper III to test functional and structural diversity as mediators of effects of species richness on stand productivity and in Paper IV to test diversity effects on functional traits on diversity effects on, both directly and as mediators of functional diversity. SEM model fit was evaluated using Fisher's C statistic, and directional separation tests were applied where relevant.

4. Results and discussion

The progression of papers reflects an increase in spatial, ecological, and analytical scope. Paper I examines mixture effects on soil organic matter (SOM) chemistry and soil C accumulation using two *Salix* variety trials in Sweden and Germany. Paper II extends to a network of ten experiments across Europe and Brazil, assessing topsoil C and fungal communities in mixed-species tree plantations. Paper III further broadens the scope to 21 experiments in 12 countries across five continents, linking tree diversity to aboveground productivity through resource-use strategies. Finally, paper IV integrates trait-based approaches across 11 experiments in Europe and Brazil, evaluating how shifts in functional traits mediate tree diversity effects on C sequestration. This trajectory, from belowground to aboveground processes, and from local to continental scales, mirrors a thematic shift from identifying patterns to mechanistically explaining patterns. Paper I focuses on how species identity and local site conditions shape SOM composition and stability. Papers II and III introduce species richness, trait variation, and context-dependency as key explanatory factors, while paper IV shows the role of intraspecific trait variability and trait-mediated pathways in driving productivity and C dynamics in mixed-species forests.

4.1 Topsoil C accumulation, SOM chemistry and fungal community structure (Papers I-II)

Papers I and II explore the belowground processes of C accumulation, SOM chemistry in terms of quality and thermal stability, as well as fungal community structure in relation to tree species mixing. Previous research has found both positive effects of tree species mixing on soil C levels (Chen et al. 2018, 2020:20; Mayer et al. 2020:22020), while others reported C stocks in mixed stands generally falling between those of the respective pure stands (Wiesmeier et al. 2013; Cremer et al. 2016). In many cases, soil C appears to be more strongly influenced by species identity than by diversity per se (Dawud et al. 2017; Osei et al. 2021).

Paper I used data from two willow short rotation coppice (SRC) plantations in Sweden (Uppsala) and Germany (Rostock), focusing on the varieties 'Loden' and 'Tora', which are different species and have contrasting characteristics (Hoeber et al. 2018). I found that both species identity and diversity affected soil C accumulation and SOM chemistry, although species identity had a stronger influence on both C accumulation and SOM chemistry. Estimated topsoil C stocks did not differ significantly between mixtures and values expected from monocultures (Figure 2A). However, significantly higher C stocks were found under 'Loden' at the Rostock site (Figure 2B). At Uppsala, diversity effects were observed in SOM chemical composition and thermal stability, but species identity consistently exerted a greater influence across sites. Differences between 'Loden' and 'Tora' were detected in SOM quality and stability, although neither variety showed consistently higher values. These results indicate that species identity may have a greater impact than diversity on both C accumulation and SOM characteristics.

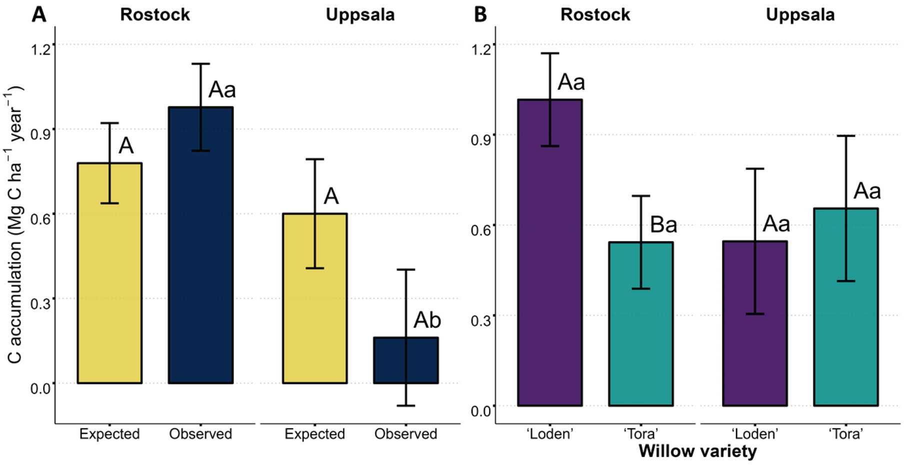

Figure 2. From Paper I. (A) Estimated marginal means of expected and observed topsoil (0-10 cm depth) C accumulation rates at sites Rostock and Uppsala. Site-specific bulk densities 1.3 and 1.4 g cm^3 used in calculations of C stocks in Rostock and Uppsala, respectively. Expected values rep-resent the basal area weighted and averaged mean values of the Salix varieties 'Loden' and 'Tora' grown in monoculture and observed values represent the mean values of 'Loden' and 'Tora' grown in mixture (see equation 3). (B) estimated marginal means of topsoil (0-10 cm depth) C accumulation rates for the Salix varieties 'Loden' and 'Tora' grown in monoculture at sites Rostock and Uppsala. Site-specific bulk densities 1.3 and 1.4 g cm^3 used in calculations of C stocks in Rostock and Uppsala respectively. Different uppercase letters indicate significant pairwise differences between willow varieties within each site (A-B; $p < 0.05$). Different lowercase letters indicate significant pairwise differences for each willow variety between sites (a-b; $p < 0.05$). Standard errors are shown as error bars.

To examine soil C storage together with soil fungal communities across a wider range of locations and tree species combinations, I analysed data from nine experiments in Europe and one in Brazil in Paper II. I divided the species richness gradients into three categories: monocultures (1 species), low diversity (2-3 species) and high diversity (4-6 species) stands. I found that across the experiments, high diversity mixtures stored roughly 9 % more C in the topsoil compared to monocultures (Figure 3A).

Paper II also investigated how soil fungal communities respond to tree species diversity. Contrary to common expectations and earlier findings suggesting increased microbial diversity with greater tree diversity (Weißbecker et al. 2018; Liu et al. 2020), I found no overall increase in fungal species richness in response to tree species diversity (Figure 3B).

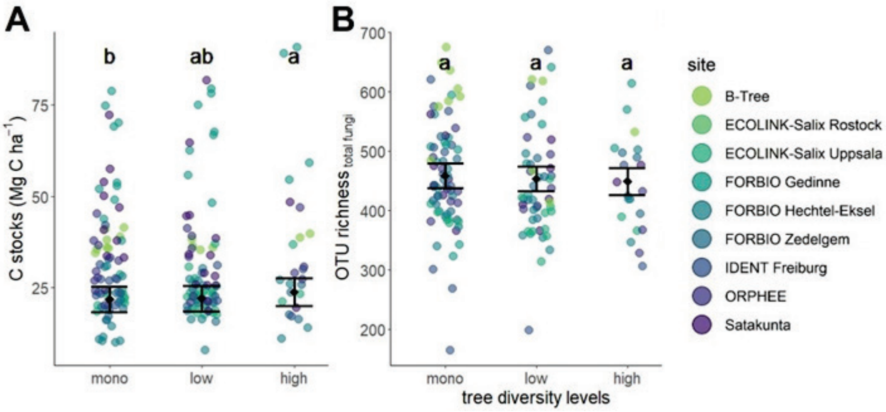

Figure 3. From Paper II. Estimated marginal means of (A) topsoil C stocks and (B) total fungal OTU richness across tree richness levels categorized as monoculture ('mono'), low (2-3 species), and high (4-6 species) diversity. Each point represents an individual sample and is color-coded according to experiment (site). Letters denote significant differences (Tukey's post-hoc test; $p < 0.05$). Black circles with error bars indicate mean ± SE for each diversity level.

Moreover, we found a positive correlation in community dissimilarity between tree and fungal communities (Figure 4), indicating that fungal community composition is influenced by tree species identity. Our results suggest that tree species identity is more important for soil fungal communities than species diversity per se, at least in the relatively young stands of our experiments.

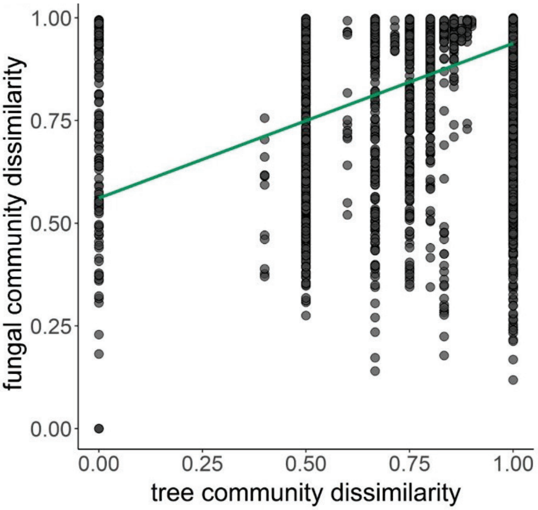

Figure 4. From Paper II. Relationship between tree and fungal community composition. Each point represents a pair of plots, comparing the dissimilarity of their tree and fungal communities. Dissimilarity values range from zero indicating identical species compositions between samples, to 1, denoting completely distinct species assemblages. The line represents a linear regression fit to the data. Mantel test r = 0.268, p = 0.001.

Further analysis in Paper II identified a potential link between fungal richness and the strength of diversity effects on soil C. The positive effect of tree diversity on soil C was more pronounced in plots with higher fungal species richness (Figure 5C). This aligns with previous studies showing positive associations between fungal diversity and soil C (Yang et al. 2017; Zang et al. 2024). Specifically, topsoil C stocks were positively correlated with both total and saprotrophic fungal species richness (Figures 5A and 5B), suggesting a possible mediating role of fungal communities in C storage.

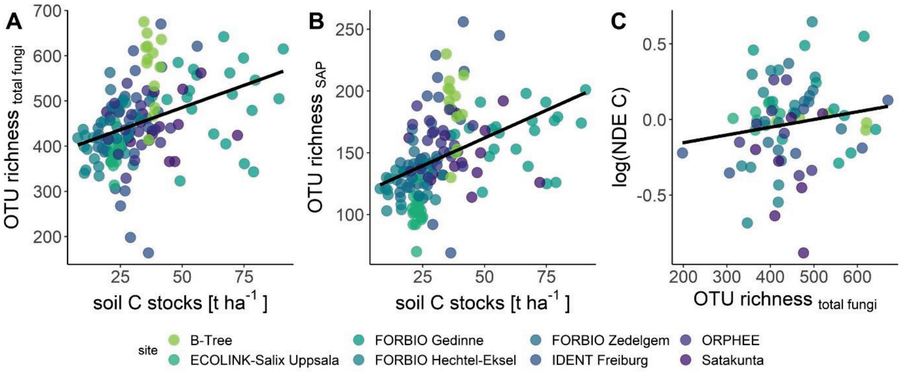

Figure 5. From Paper II. Relationships between topsoil carbon (C) stocks and OTU richness for A) total fungi, and B) saprotrophic (SAP) fungi. C) Correlation between the log-scaled net diversity effect on soil C stocks (NDE C) and the total fungal OTU richness. Each point represents a unique soil sample, color-coded by site. The lines represent a linear fit to the model.

Comparing the results of Papers I and II, both show clear effects of tree species identity on soil conditions; on C stocks, soil chemistry and fungal communities. They differ in the effects of species diversity, in Paper II I found a difference between high diversity stands and monocultures in terms of C stocks, while in Paper I, I found no difference between the willow monocultures and mixtures. Possibly this discrepancy is due to the maximum species richness of two in Paper I, which would have been in the low diversity category in Paper II. It could also be that in Paper I, while different species, the willows might not be functionally different enough in relevant traits to catalyze strong diversity effects on soil C. Although topsoil often contains a disproportionately high concentration of soil C and hosts many species interactions, it represents only a portion of the full soil profile. Deeper layers may also contribute significantly to long-term C storage and biotic interactions. Future studies examining entire soil profiles could provide a more complete understanding of plant–soil–microbe interactions.

4.2 Aboveground productivity and carbon sequestration (Papers III-IV)

The final two chapters of this thesis were dedicated to investigating the growth and stock of aboveground biomass in species monocultures and mixtures, focusing on the use of functional traits to explain diversity–productivity relationships. In Paper III, aboveground productivity increased with species richness in a quadratic pattern across 21 experiments, indicating diminishing returns at higher diversity levels (Figure 6).

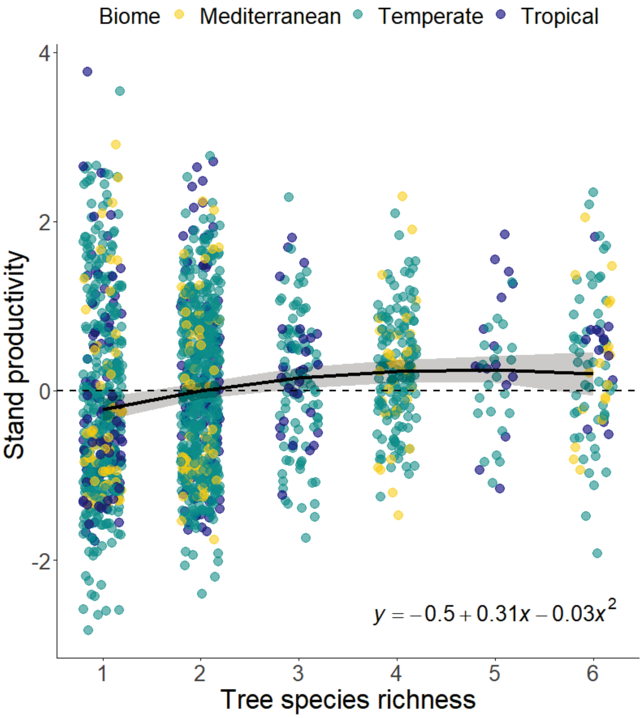

Figure 6. From Paper III. Relationship between stand productivity and species richness across 21 experiments and 3 biomes. Stand productivity corresponds to standardized annual basal area increment. Positive values indicate productivity levels above the average within each experiment. Colors indicate biome. The dashed black line represents the mean stand productivity within each experiment. The solid black line represents the estimated mean productivity, with the shaded area showing a 95 % confidence interval.

Because species often respond differently to different neighbours, particularly under competitive conditions, the effects of species identity often depend on the context of species mixing. Selection effects, where one or a few species dominate a stand and disproportionately influence its overall performance, are a manifestation of species identity. In contrast, complementarity effects arise from positive interactions or resource-use synergies among species.

Using the partitioning framework proposed by (Loreau & Hector 2001), I found that selection effects accounted for 77 % of the total diversity effect on productivity in Paper III. A greater selection than complementarity effect in young stands is consistent with previous research (Tobner et al. 2016; Baeten et al. 2019), which is a dynamic that may change with stand age as complementarity effects emerge more strongly over time (Reich et al. 2012). Notably, I found that the strength of selection effects increased with greater diversity in wood density within a stand (Figure 7D). Wood density is a key functional trait associated with species' ecological strategies (Swenson & Enquist 2007; Chave et al. 2009). A higher diversity of wood densities, and therefore ecological strategies, may allow dominant and fast-growing species to thrive while at the same time limiting competitive exclusion or resource depletion, thereby maintaining overall stand productivity (Chesson 2000; Kunstler et al. 2012).

Our findings suggest that the influence of species identity is not static but shaped by the composition of co-occurring species. In this case, functional diversity, specifically a diversity of wood densities, modulates identity-driven dominance and, by extension, ecosystem functioning. This interaction between identity and diversity emphasizes the importance of designing species mixtures that include functionally distinct species capable of benefiting from, and withstanding, selective processes. Accordingly, stand diversification, through the inclusion of varied wood densities, can be strategically optimized to promote productivity.

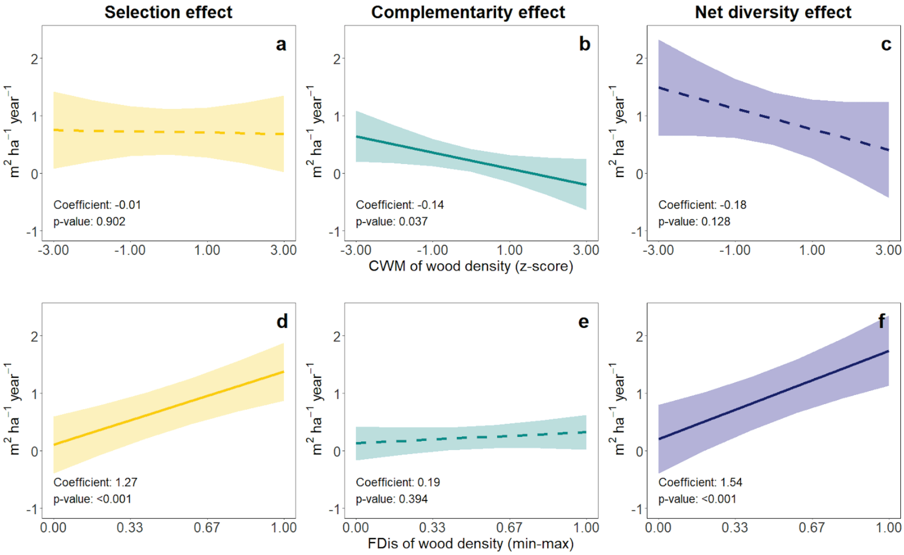

Figure 7. From Paper III. The relationship of selection (a & d; yellow), complementarity (b & e; green) and net diversity (c & f; blue) effects (m^2 ha^{-1} $year^{-1}$) with community weighted means (CWMs; a-c) and functional diversity (FDis; d-f) of wood density (WD) across 20 experiments. CWMs were z-score standardized and FDis values were min-max standardized prior to analysis. Solid lines show the fitted values for variables that had a significant relationship (dashed lines for non-significant) (Supplementary Tables S5-S7). The shaded areas represent a 95 % confidence interval.

In Paper III, I also found that species-level productivity in response to species mixing was linked to functional identity. Specifically, species with a more acquisitive trait profile, characterized by higher leaf N content and lower wood density, tended to perform better in mixtures than species with more conservative traits (Figure 8). These findings are aligned with those of Zheng *et al.* (2024), where acquisitive species were found to be associated with early overyielding in mixtures. Our results in Paper III suggests that acquisitive species are better equipped to take advantage of the more variable growing conditions found in diverse stands. Combined with the strong positive role of selection effects in driving diversity effects on stand growth, our results indicate that including one or more acquisitive species may be a beneficial strategy when designing species mixtures for productivity.

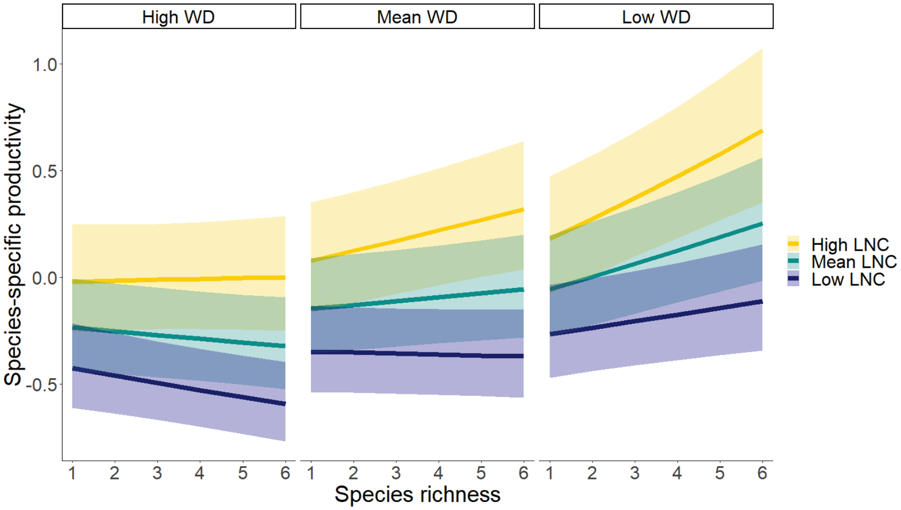

Figure 8. From Paper III. Relationship between species-specific productivity and species richness across a gradient of more acquisitive species (low wood density (WD) and high leaf nitrogen content (LNC)) to more conservative species (high WD and low LNC) across 20 experiments. High and low WD and LNC refer to values that are one standard deviation above and below the mean, respectively. Species-specific productivity corresponds to annual basal area increment, standardized and log-transformed before analysis. Both WD and LNC were z-score standardized across experiments. Fitted values were back- transformed from a logarithmic scale prior to illustration, and the shaded areas show the 95 % confidence interval for the fitted model.

The analyses in Papers III and IV consider both the diversity within individual traits and the broader measure of community functional diversity across multiple traits. In Paper III, I tested the role of functional diversity as an indirect pathway mediating the relationship between species richness and stand productivity using a SEM. As hypothesized in Paper III, increasing species richness was associated with higher functional diversity, which in turn positively influenced stand productivity. In contrast, increasing species richness was also associated with higher structural diversity, which unexpectedly had a negative effect on productivity (Figure 9a), conflicting with results reported by others from individual experiments (Schnabel et al. 2019; Ray et al. 2023).

This negative relationship between structural diversity and stand productivity is somewhat counterintuitive, as structural diversity is often proposed as a positive mediator of the species richness–productivity relationship, typically by promoting canopy stratification and more complete space occupation, thereby increasing light interception (Rissanen et al. 2019; Williams et al. 2021). However, structural diversity is a complex attribute, and its interpretation may depend on both the context and the specific metrics used. Structural diversity metrics capture different aspects of stand architecture and may reflect distinct ecological processes. Absolute measures, such as LiDAR-based canopy density, highlight the role of large, dominant trees, while relative metrics like the Gini coefficient assign equal weight to all individuals, potentially emphasising size inequality caused by competition. In Paper III, we used the Gini coefficient to represent structural diversity and found that it was negatively correlated with productivity, particularly in monocultures and low-diversity mixtures, likely reflecting suppression due to intraspecific competition rather than beneficial stratification (Luu et al. 2013; Urgoiti et al. 2023). For example, (Pretzsch & Hilmers 2024) reported lower biomass in structurally diverse stands due to mortality, and (Ray et al. 2023) found that structural complexity improved light interception only marginally in young stands, potentially requiring high light availability to yield positive effects.

The results from other studies demonstrate the context-specific nature of structural diversity; while it may enhance productivity, it can also reflect competitive imbalance. In our study (Paper IV), both species richness and functional diversity influenced the relationship between stand productivity and structural diversity (Figure 9b), suggesting that promoting functional diversity could help offset the drawbacks of structural inequality in mixed-species stands. Further research is needed to determine when and how structural diversity contributes positively to ecosystem functioning and how to leverage it for efficient species mixtures.

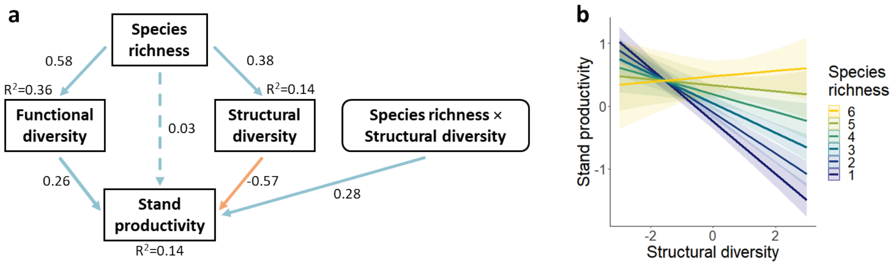

Figure 9. From Paper IV. SEM illustrating direct and indirect links between (a) species richness and standardized stand productivity across 16 experiments (b) and the modelled interaction between species richness and structural diversity on stand productivity. The model displays standardized path coefficients for each pathway, and marginal R^2 values for each endogenous variable. Blue pathways indicate positive correlations, while orange pathways indicate negative correlations. Significant pathways ($p < 0.05$) are shown as solid lines.

Further building on the aboveground biomass in tree species mixtures, in Paper IV, I analyzed different components of aboveground biomass in 11 experiments. Specifically, I assessed aboveground woody biomass, litterfall biomass, and understory biomass, and observed that both woody- and litterfall biomass were higher in mixed-species stands than expected based on the corresponding monocultures (Figure 10). These findings support the idea that species mixtures can lead to greater accumulation of aboveground biomass, and consequently, higher C accumulation, compared to monocultures. In contrast, mixtures sometimes showed reduced biomass due to denser canopy cover limiting light (Figure 12). However, these local negative effects did not translate into reduced understory biomass across all communities (Figure 10), possibly due to concurrently facilitative processes counteracting the increased shading.

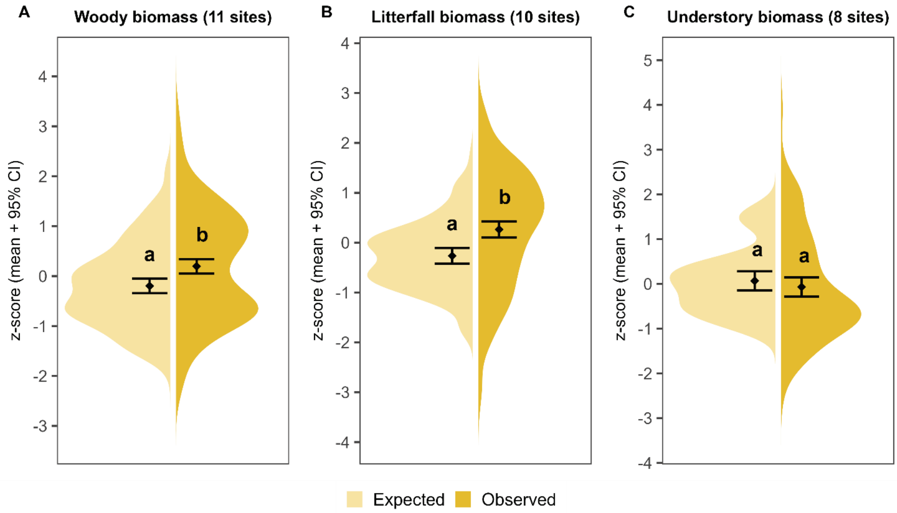

Figure 10. From Paper IV. Relationships between expected (predicted from observations in pure stands; light beige) and observed (measured in mixed stands; dark beige) mixture values for three biomass components: (A) woody biomass, (B) litterfall biomass, and (C) understory biomass. Split violin plots illustrate the distribution of data points of their respective groups. Points represent mean values, and error bars represent corresponding confidence intervals. Different letters denote significant pairwise differences between expected and observed mixture values (a-b; $p < 0.05$).

4.3 Functional trait responses to mixing (Paper IV)

Beyond stand productivity, C sequestration, and soil fungal dynamics, Paper IV examined how species mixing influences functional trait expression at both the community and species levels across 11 sites. I found that community-level trait values for SLA, LAI, and LNCA in mixed stands differed significantly from their expected values based on monocultures (Figure 11). Interestingly, SLA shifts appeared to be driven largely by less dominant species, as SLA values were higher when not weighted by tree basal area. This suggests that subordinate species may have adjusted their traits to persist under the shade of more dominant neighbors, supporting a dynamic in which dominant species drive productivity while subordinate species maintain viability through plastic responses, which aligns with the strong positive selection effects found in Paper III. Such trait adjustments may therefore contribute to the positive net diversity effects on growth.

While results of previous research have been variable, both SLA (Felix et al. 2023:20) and LAI (Williams et al. 2017) have been observed to increase in species mixtures, oftentimes under specific neighborhood contexts (Forey et al. 2016; Serrano-León et al. 2022). At the species level, our results showed trait variability between monoculture and mixture conditions varied considerably. For example, woody biomass exhibited 55 % variability, while LNCM showed 9 %. Despite this variation, SLA was the only trait with a consistently higher mean in mixtures than in monocultures (Figure 13). Trait plasticity is known to differ among both traits and species (Valladares & Niinemets 2008), and shifts in functional trait expression may result from species interactions and on environmental conditions, for example as a consequence of light availability (Williams et al. 2020), as an adaptive strategy to increase resource capture (Sack et al. 2006) or a more passive result of resource limitation (Valladares et al. 2006:200; Burns & Strauss 2012). While responses remain variable, our results demonstrate that functional traits can shift in mixed-species contexts and suggest that light availability may play a central role in mediating species interactions and trait expression.

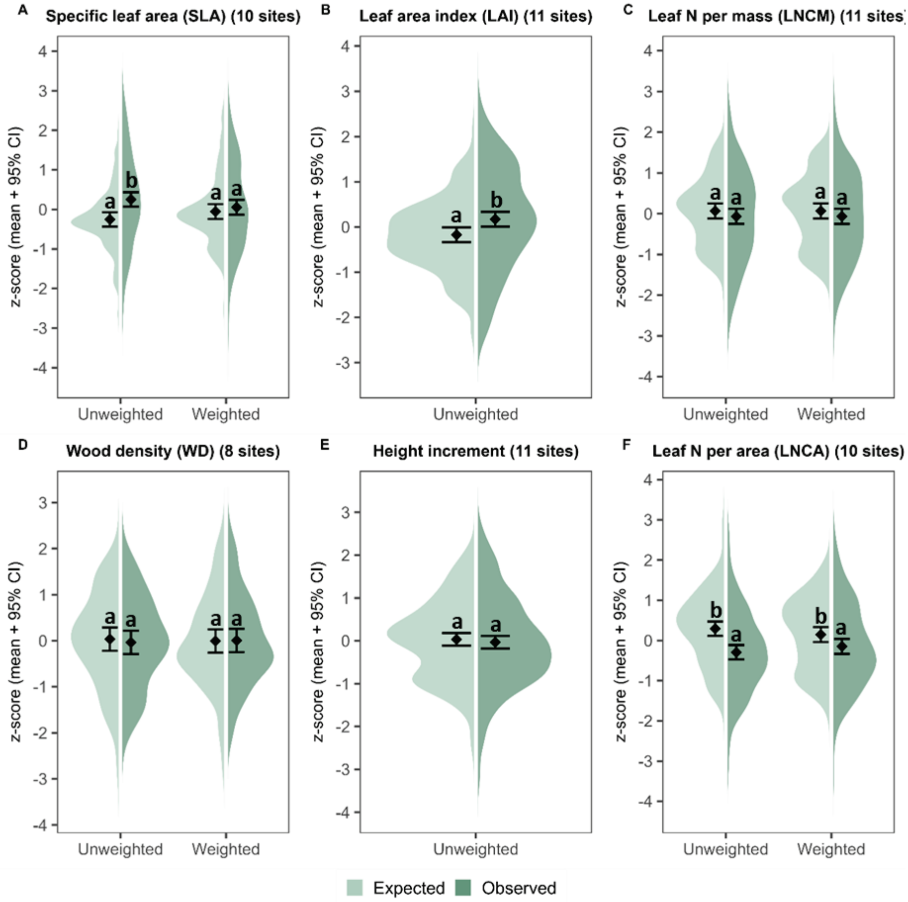

Figure 11. From Paper IV. Relationships between expected (predicted from observations in pure stands; light green) and observed (measured in mixed stands; dark green) mixture values for six functional traits: (A) specific leaf area (SLA), (B) leaf area index (LAI), (C) leaf nitrogen content per mass (LNCM), (D) leaf nitrogen content per area (LNCA), (E) wood density (WD), and (F) height increment. Trait values derived from species-level measurements at the plot level include comparisons weighted and unweighted by species dominance. Split violin plots illustrate the distribution of data points of their respective groups. Points represent estimated marginal means, with error bars indicating corresponding confidence intervals. Different letters denote significant pairwise differences between expected and observed mixture values (a-b; $p < 0.05$).

To assess the extent to which trait shifts mediate biomass outcomes, a second SEM was conducted in Paper IV (Figure 12). This model tested whether shifts in SLA, LAI and LNCM ($\mathrm{NDE}_{\mathrm{SLA}}$, $\mathrm{NDE}_{\mathrm{LAI}}$ and $\mathrm{NDE}_{\mathrm{LNCM}}$) explain the diversity-driven changes in biomass components, including woody biomass ($\mathrm{NDE}_{\text{woody biomass}}$), litterfall biomass ($\mathrm{NDE}_{\text{litterfall biomass}}$) and understory biomass ($\mathrm{NDE}_{\text{understory biomass}}$), or indirectly as mediators of functional diversity.

The SEM explained 41 %, 28 %, and 22 % of the variation in the diversity effect on woody biomass, litterfall, and understory biomass, respectively. It revealed that trait shifts in SLA and LAI, in that order, primarily mediated the positive diversity effects on woody biomass. Given that both traits are closely linked to growth strategies and light acquisition (Wright et al. 2004, 2010; Poorter & Bongers 2006; Díaz et al. 2016), these results suggest that productivity gains in mixtures were largely driven by enhanced canopy development and increased leaf efficiency in capturing light. Specifically, woody biomass was highest in mixtures where community-level trait means shifted toward greater canopy cover (higher LAI) and thinner leaves (higher SLA); adaptations that promote light interception under competitive conditions (Reich 2012). However, a trade-off between high tree canopy density (LAI) and understory vegetation growth was evident: increased LAI was negatively associated with understory biomass, likely due to reduced light availability beneath denser canopies.

Although trait shifts and functional diversity both influenced biomass, only functional diversity directly promoted woody biomass accumulation. It did not significantly explain the observed shifts in trait means, suggesting that mechanisms beyond trait diversity, such as ITV or altered dominance structures, contribute to trait responses in diverse stands.

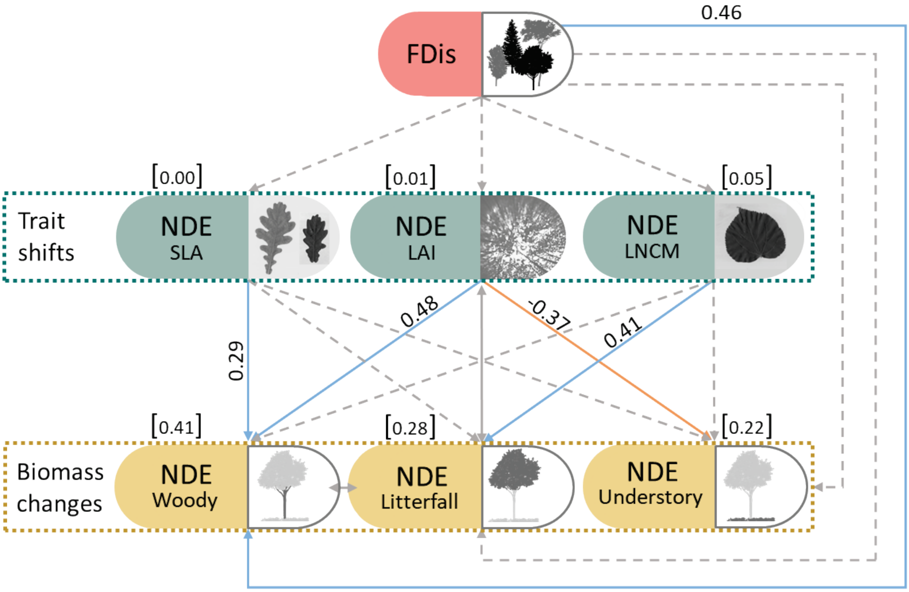

Figure 12. From Paper IV. Structural equation model (SEM) illustrating the direct and indirect relationships between functional diversity (FDis), and net diversity effects (NDE) on specific leaf area (SLA), leaf area index (LAI), leaf nitrogen content per mass (LNCM), as well as woody biomass, litterfall biomass and understory biomass across six experiments. The model presents standardised path coefficients for each significant causal pathway, along with marginal R^2 values for all endogenous variables. Solid blue pathways represent positive effects, solid orange pathways represent negative effects, and solid grey pathways represent non-directional relationships.

Further supporting the idea that trait responses to species mixture depend on their biotic and abiotic context (Forey et al. 2016; Williams et al. 2020), Paper IV found that species varied widely in how their traits and growth changed between monoculture and mixture conditions (Figure 13). Some species showed substantial deviations, while others remained relatively stable. These mixed responses tended to balance each other out at the community level, leading to no consistent directional shift across traits or biomass measures, as also suggested in (Valladares et al. 2006). This suggests that trait responses to diversity emerge from a combination of interspecific interactions, trait plasticity, and species-environment feedbacks, rather than any consistent effect of identity alone.

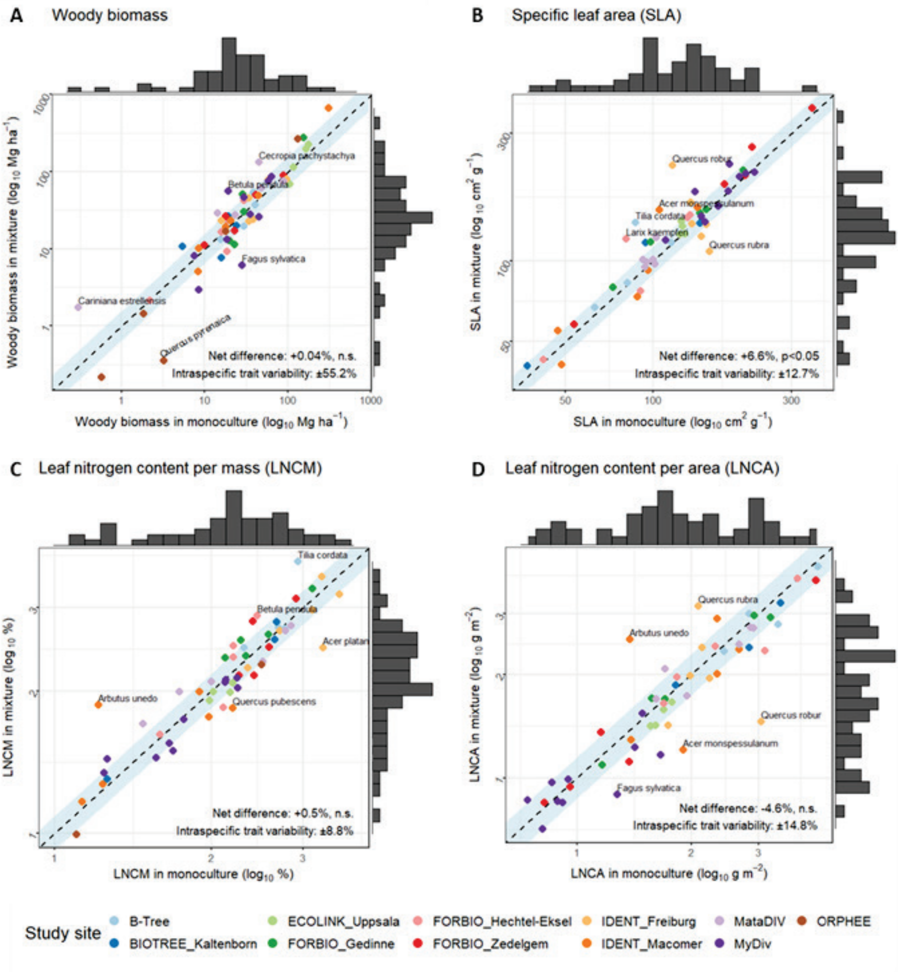

Figure 13. From Paper IV. Figure 5. Relationships between species-level values in monoculture (x-axis) and mixture (y-axis) across sites for four variables: (A) woody biomass, (B) specific leaf area (SLA), (C) leaf nitrogen content per mass (LNCM), and (D) leaf nitrogen content per area (LNCA). All axes are plotted along a logarithmic scale and tick labels are shown on the original scale. The dashed black 1:1 line indicates no difference between monoculture and mixture values. The shaded blue ribbon shows the average intraspecific variation, calculated as a symmetric deviation from the 1:1 line in $\log_{10}$ space. Because the log scale is multiplicative, this ribbon corresponds to a fixed relative change (reported as a percentage in the bottom right of each panel). Net trait shifts (mean signed $\log_{10}$ differences between monoculture and mixture values) and their statistical significance are also reported. Histograms along the top and right margins show the distribution of species values in monoculture and mixture, respectively. The five most reactive species (i.e. those with the largest absolute deviations from the 1:1 line) are labelled in each plot. Points are colored by study site.

Overall, the findings emphasize that trait shifts and community trait composition can mediate diversity effects on biomass accumulation. While some shifts may be linked to ITV, perhaps particularly among less dominant species, community-level responses such as increases in canopy development and light-use efficiency appear to play a more consistent role in driving biomass accumulation. This shows the value of integrating both trait-based and community-level approaches when exploring the mechanisms behind biodiversity–ecosystem functioning relationships.

4.4 Environmental context-dependency (Papers I-II)

While in Paper III no significant difference was found in responses in stand productivity to tree species diversity between biomes (Figure 6), Papers III-IV primarily focused on within-experiment variation to examine diversity–productivity relationships under consistent conditions. Papers I-II, however, also addressed the influence of environmental context on the outcomes of species mixing. These papers highlight how both site-specific conditions and broader climatic and edaphic gradients shape the ecological consequences of tree species mixtures. Other studies have demonstrated, for example, that biodiversity–ecosystem functioning relationships are generally stronger in drier climates with longer growing seasons (Ratcliffe et al. 2017), whereas (Chen et al. 2024) reported that the relationship between functional diversity and soil C accumulation was more pronounced under conditions of higher nutrient and water availability. In Paper I, clear evidence of environmental context-dependency emerged from the analysis of SOM chemical composition. A principal components analysis revealed strong site-level differences in SOM chemistry, but also differences among vegetation treatments within sites (Figure 14). At the Rostock site, SOM under 'Loden' was chemically distinct from that under 'Tora' and the 'Loden:Tora' mixture. However, no such differences were observed at the Uppsala site. This suggests that the influence of both species identity and mixture composition on SOM chemistry is modulated by local conditions, such as climate and soil texture. Notably, site differences in temperature, precipitation, and soil clay content can influence decomposition rates (Castellano et al. 2015; Berg & McClaugherty 2020) and microbial processes

(Baumann et al. 2013; Stockmann et al. 2013), and did so likely also in our study, where it probably contributed to divergent SOM profiles.

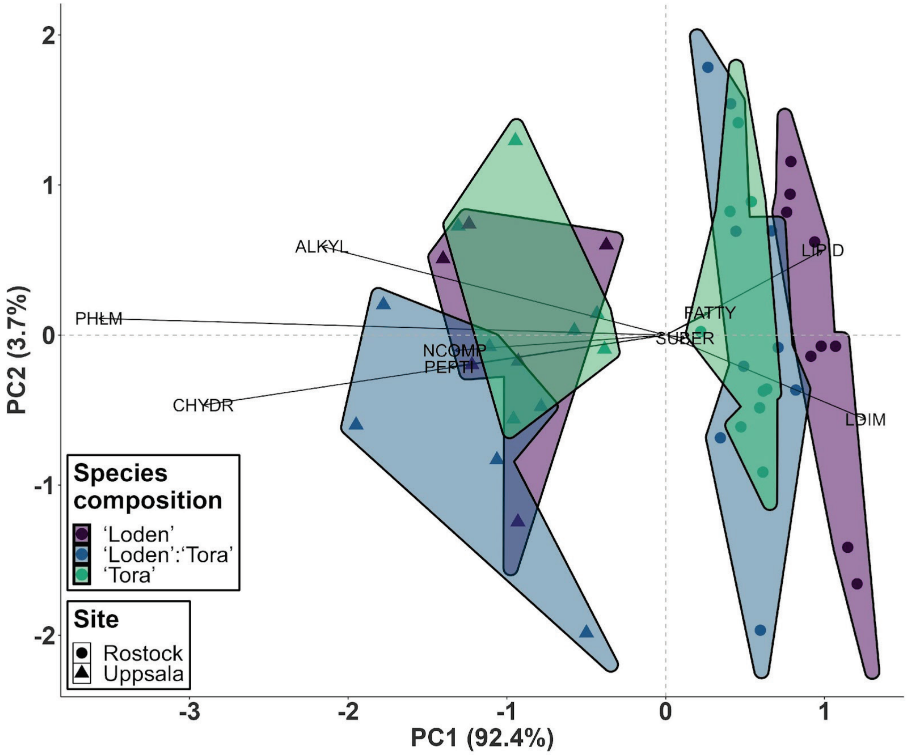

Figure 14. From Paper I. SOM chemical composition: principal components plot of the relative ion intensities (% TII) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see table 2) in topsoil (0-10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala.

In Paper II, context-dependency was directly tested using data from multiple experiments. The analysis showed that the net diversity effect on topsoil C stocks (NDE C) varied systematically across environmental gradients (Figure 15). Specifically, NDE C decreased with increasing mean annual temperature, soil fertility, and interannual variability in both temperature and precipitation. In contrast, cooler, less fertile, and more climatically stable environments tended to support more positive diversity effects on C accumulation. Other studies have also found diversity-derived increases in soil C stocks to increase in colder (He et al. 2013) and less fertile conditions (Pretzsch 2014; Toïgo et al. 2015). Our findings suggest that species mixing may be particularly beneficial for soil C sequestration in low-productivity or less climatically variable ecosystems. Although the mechanisms behind these patterns were not directly tested, the results offer a basis for directing species mixture strategies to regions where the likelihood of positive biodiversity effects is highest.

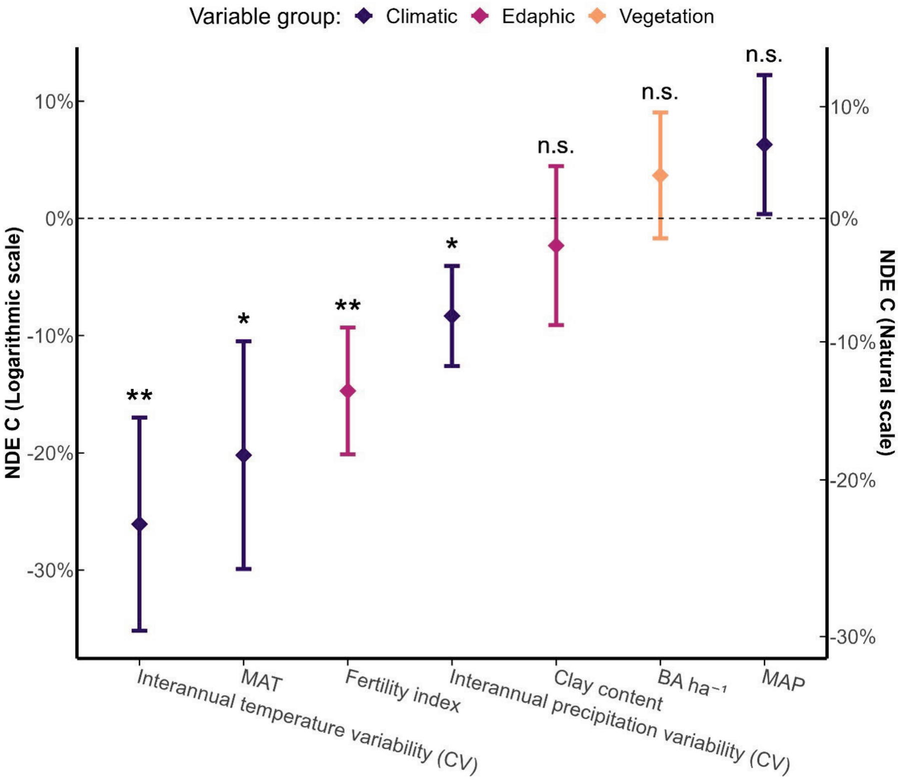

Figure 15. From Paper II. Standardized effects of climatic, edaphic, and vegetation variables on the net diversity effect on topsoil C stocks (NDE C) across nine sites on a logarithmic scale (first y-axis; left) and natural scale (second y-axis; right). Error bars denote standard errors. Climatic variables include mean annual temperature (MAT), mean annual precipitation (MAP), as well as variability in temperature and precipitation (interannual CV). Edaphic variables include the inverted first principal component axis for soil pH and C:N ratio (Fertility index) as well as soil texture (based on clay content). Effects of standing stock is represented by basal area per hectare (BA ha-1). Significant effects on NDE C are indicated as *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$,

n.s. = p >0.05, n.s. = not significant. Values below 0 indicate negative correlation between NDE C and predictors.

To further explore the drivers of soil C accumulation, Paper II used a Random Forest regression model incorporating climatic, edaphic, site, and vegetation variables (Figure 16). Within this model, species composition was more important than species richness in explaining variation in topsoil C stocks, as also found by (Dawud et al. 2017) and (Osei et al. 2021). However, climate- and soil-related variables also ranked highly in explanatory power. These results emphasize the multifactorial nature of soil C dynamics, where plant community properties interact with abiotic conditions. The relatively young age of the study sites may also limit the detectability of long-term diversity effects on soil. Taken together with the time-dependent nature of biodiversity-ecosystem functioning relationships (Ma & Chen 2016; Urgoiti et al. 2022), it is possible that the full effects of species identity and diversity are yet to fully manifest.

It is important to note, however, that soil C dynamics unfold over long timescales, and that plant communities represent only one of many interacting drivers of soil properties. This should be taken into account when comparing their influence to more fundamental factors such as precipitation or soil pH. While the effects of species identity and diversity on soil C stocks may be smaller in magnitude relative to climatic and edaphic conditions, they represent realistic options for management, whereas the latter are largely beyond human control.

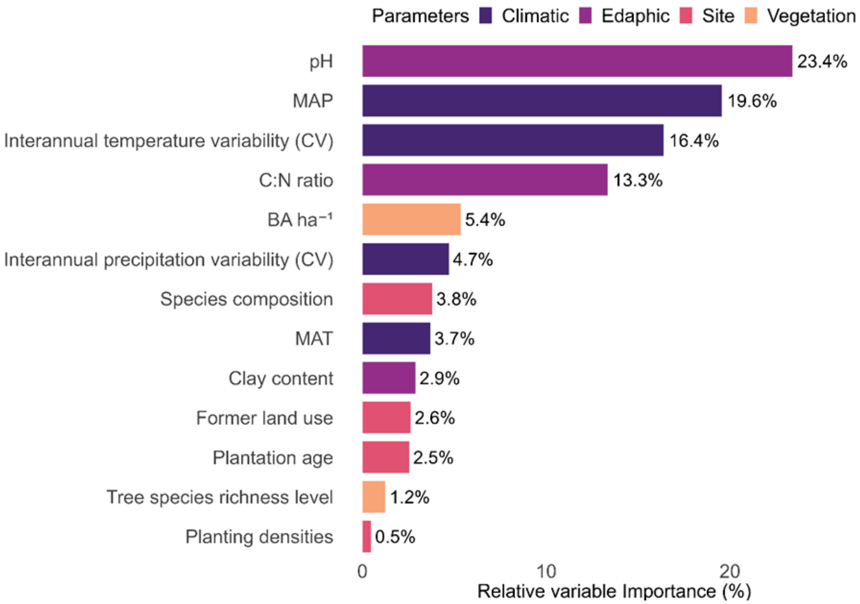

Figure 16. From Paper II. Relative importance (%) of variables in predicting topsoil C stocks as based on results from a Random Forest regression model using permutation importance across 9 sites. Variables are categorized into climatic-, edaphic-, site-, and vegetation-related groups.

Taken together, Papers I and II demonstrate that the ecological effects of tree species diversity are not uniform across landscapes. Instead, they are driven by interactions between species traits, stand structure, and local environmental conditions. Recognizing this context-dependency, as also done in prior research (He et al. 2013; Ratcliffe et al. 2017; Cesarz et al. 2022), is essential for understanding where and when species mixtures are most likely to enhance ecosystem functions such as C storage. These findings show the need for flexible, site-adapted approaches in forest management and biodiversity conservation, especially under changing climatic conditions.

While Papers III-IV in this thesis focused on within-site variability, it is interesting to consider how the aboveground relationships analyzed there may have varied in relation to environmental context. Diversity-productivity relationships have been found to be stronger where wood production is limited by climate (Jucker et al. 2016) and when species mixtures reduce pressure on limiting resources (Forrester 2014). Possibly, then, diversity-productivity relationships would be stronger when functional trait expression shifts to decrease competition for limiting resources.

4.5 Conclusions, implications and future perspectives

This thesis shows that increasing tree species richness can enhance both aboveground productivity and soil C storage. These potential dual benefits support mixed-species forestry as a tool for climate change mitigation without sacrificing, and often improving, productivity. Across sites and experiments, higher diversity tended to increase C sequestration, driven by a combination of functional trait complementarity and selection effects. Notably, there was no evidence of a trade-off between climate change mitigation through C accumulation and wood production. Instead, diverse forests can offer multiple advantages compared to monocultures: often greater productivity and long-term C storage. However, results also showed that diversity effects vary with context. Environmental factors such as temperature, soil fertility, and climate stability shaped the strength and direction of diversity outcomes. Moreover, the influence of species identity and functional traits were often more influential than richness alone.

Looking forward, future research should address the longer-term dynamics of species mixtures, particularly in more mature forests where belowground processes and C accumulation may differ significantly from younger stands. Understanding how diversity effects interact with different silvicultural practices and management goals is also key, especially when integrating species mixtures into operational forestry. Investigating these relationships in natural forest systems, alongside experiments using more globally extensive datasets, would help test the generality of current findings. In particular, further work is needed to refine how trait-based mechanisms and environmental context interact to shape forest functioning across diverse biomes. Integrating these elements will be essential to developing robust, adaptive, and sustainable forest management strategies in a changing world. Overall, the findings of this thesis emphasize the importance of designing species mixtures suited to local conditions using a deliberate combination of species. Taken together, the findings in this thesis support mixed-species forestry as a robust and adaptable management approach that can meet ecological and economic goals under varying environmental conditions.

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Popular science summary

Forests are important to people and societies because they provide timber, regulate climate, water, and air quality, protect soils, support biodiversity, offer spaces for recreation, and play a key role in reducing and adapting to the effects of climate change. How forests are managed is crucial to the benefits they yield, and mixing different tree species instead of placing them in separate locations is a management option with the potential to deliver both ecological and economic gains. While using mixtures of tree species is not new, broad societal and academic interest is relatively recent. Forests, and consequently forest research, depend on slow processes that span long timescales, where new developments can still be several decades old. Since the late 1990s, an increasing number of tree diversity experiments have been established worldwide, and the field continues to expand due to sustained interest.

Despite the growing number of experiments and publications on mixed-species forestry, many questions remain. Why do species interact differently across contexts? How can we understand these interactions well enough to reliably reproduce preferred outcomes from species mixing? Due to the complexity of forest ecosystems, many studies have focused on specific outcomes under specific circumstances. My goal in this thesis was to illuminate a broader part of the picture.

In this pursuit, I used large datasets drawn from the expanding network of tree diversity experiments to investigate general trends in how species mixtures influence ecosystem functioning both above- and belowground. A central tool in my analysis was functional traits: characteristics of plants that can help predict how they perform under different conditions. Given their predictive power, functional traits can be used to examine which types of species perform well individually in mixtures, and which combinations perform well together. However, nature’s complexity introduces uncertainties, and it is not always clear which traits infer which functions, or how different functions influence species interactions.

Focusing on forest stands planted in global and European tree diversity In this pursuit, I used large datasets drawn from the expanding network of tree diversity experiments to investigate general trends in how species mixtures influence ecosystem functioning both above- and belowground. A central tool in my analysis was functional traits: characteristics of plants that can help predict how they perform under different conditions. Given their predictive power, functional traits can be used to examine which types of species perform well individually in mixtures, and which combinations perform well together. However, nature’s complexity introduces uncertainties, and it is not always clear which traits infer which functions, or how different functions influence species interactions.

Focusing on forest stands planted in global and European tree diversity experiments, I found that globally, forests with more tree species grew faster and were more productive, with gains levelling off after about five species. Some types of trees performed better than others: resource-acquisitive species, characterized by low wood density and nitrogen-rich leaves, thrived in diverse communities, while more conservative species were not proportionally disadvantaged. Across Europe, mixed-species forests stored more carbon in the topsoil than equivalent monocultures, especially in cooler and less fertile areas. Soil fungi also played a role, with greater fungal diversity often associated with increased soil carbon storage resulting from species mixing. Furthermore, I found that willow species uniquely influenced soil carbon accumulation and organic matter chemistry, and that these effects varied depending on whether willows were grown in mixture or monoculture. In experiments in Europe and Brazil, tree mixtures produced more woody biomass and leaf litter than monocultures, linked to changes in canopy cover and leaf economic traits.

As others and I have found, mixed-species forestry can simultaneously promote productivity, biodiversity, and resilience to environmental stressors, supporting both economic gain and climate change adaptation and mitigation. Species mixing does not necessarily entail a trade-off between ecological and economic benefits. The challenge lies in understanding species interactions within their environmental contexts well enough to optimize for specific values. In this thesis, I show that tree species mixtures can enhance large-scale productivity and carbon sequestration compared to monocultures, and that the success of these mixtures depends strongly on their functional composition and the environmental conditions in which they grow.

Populärvetenskaplig sammanfattning

Skogar är viktiga för människor och samhällen eftersom de tillhandahåller timmer, reglerar klimatet, vatten- och luftkvalitet, skyddar jord, stödjer biologisk mångfald, erbjuder platser för rekreation och spelar en nyckelroll i att minska och anpassa sig till effekterna av klimatförändringar. Hur skogar förvaltas är avgörande för vilka nyttor de ger, och att blanda olika trädarter istället för att odla dem var för sig är ett skötselalternativ som kan ge både ekologiska och ekonomiska vinster. Att använda trädslagsblandningar är inget nytt, men ett brett samhälleligt och akademiskt intresse är relativt nytt. Skogar, och därmed forskning rörande skog, är beroende av långsamma processer som sträcker sig över långa tidshorisonter, där nya utvecklingar kan vara flera decennier gamla. Sedan slutet av 1990-talet har ett ökande antal träddiversitetsexperiment etablerats världen över, och forskningsämnet fortsätter att växa tack vare ett fortsatt intresse.

Trots det växande antalet experiment och publikationer om blandskog kvarstår många frågor. Varför interagerar arter på olika sätt i olika sammanhang? Hur kan vi förstå dessa interaktioner tillräckligt väl för att tillförlitligt återskapa önskade effekter av trädslagsblandning? På grund av skogsekosystemens komplexitet har många studier fokuserat på specifika utfall under specifika omständigheter. Mitt mål i denna avhandling var att belysa en större del av helheten.

I detta arbete använde jag omfattande datamaterial från det växande nätverket av trädmångfaldsexperiment för att undersöka generella mönster i hur artblandningar påverkar ekosystemens funktion både ovan och under jord. Ett centralt verktyg i min analys var funktionella egenskaper: växters karaktärsdrag som kan hjälpa till att förutsäga hur arter presterar under olika förhållanden. Tack vare deras prediktiva förmåga kan funktionella egenskaper användas för att undersöka vilka typer av arter som individuellt presterar bra i blandningar, samt vilka kombinationer av arter som fungerar väl. Men naturens komplexitet introducerar osäkerheter, och det är inte alltid tydligt vilka egenskaper som förutsäger vilka funktioner eller hur olika funktioner påverkar artinteraktioner.

Med fokus på bestånd planterade i globala och Europeiska träddiversitetsexperiment fann jag att skogar med fler trädarter globalt sett växte snabbare och var mer produktiva, med effekter som planade ut efter cirka fem arter. Vissa trädtyper presterade bättre än andra: resurstillgängliga arter, kännetecknade av låg veddensitet och kväverika blad, trivdes i artrika samhällen, medan mer konservativa arter inte blev proportionellt negativt påverkade. I Europa lagrade blandade skogar mer kol i ytjorden än motsvarande monokulturer, särskilt i kallare och mindre bördiga områden. Marksvampar spelade också en roll, där högre svampmångfald ofta var kopplad till ökad kolinlagring i jorden till följd av trädslagsblandning. Vidare upptäckte jag att arter av *Salix* påverkade inlargringen av markkol och den kemiska sammansättningen av organiskt material på unika sätt, och att denna påverkan varierade beroende på om de växte i blandningar eller monokulturer. I experiment i Europa och Brasilien producerade trädblandningar mer vedbiomassa och lövförna än motsvarande monokulturer, kopplat till förändringar i krontäckning och bladegenskaper.

Som både jag och andra har visat kan blandskog samtidigt främja produktivitet, biologisk mångfald och resiliens mot miljöstress, vilket främjar både ekonomiska vinster och anpassning till samt mildrande av klimatförändringar. Trädslagsblandning behöver alltså inte innebära en avvägning mellan ekologiska och ekonomiska nyttor. Utmaningen ligger i att förstå interaktionerna mellan arter i sina miljömässiga sammanhang tillräckligt väl för att optimera för specifika värden. I denna avhandling visar jag att trädblandningar kan öka storskalig produktivitet och kolinlagring jämfört med monokulturer, och att framgången för blandningar i hög grad beror på deras funktionella sammansättning och den miljö de växer i.

Acknowledgements

First of all, a big thank you to my supervisors for providing this opportunity for learning, for your continuous input and for bearing with me through these years. Thank you also everyone at the Department of Crop Production Ecology and the Department of Ecology, who provided a friendly and collaborative place to work in. Thank you to Johannes for taking the time to consider my statistical approaches and for making sure they were not entirely crazy. Special mentions to Höök, who has shared a path with me for a long time. A big thank you to Chloe for showing me how to better write scientific text, to Fede for having all the answers and understanding how colors work, to Anika for the chess games, and to Janina and many others for the engaging fika conversations. Darwin, I hope you keep on boxing and kicking; boxkicking? Thanks also to James and Jonny for being good office mates. Thank you to Nisse and Eva for helping with the fieldwork among the willows. A big thanks to everyone in the TreeDivNet network for supplying and interpreting data, without you this would not even have been close to possible, and to the many co-authors whose perspectives improved the manuscripts and provided a source of learning. Thanks also to the MixForChange project and the other PhD students I worked alongside remotely. I gratefully acknowledge all funding sources, which supported many of my conferences, courses, and my research stay in Freiburg. Thank you also to everyone who made me feel welcome during my stay in Freiburg, especially Hernán, who was great for bouncing ideas with and challenging my wilder ones. And thanks to Ramona for the fun and (hopefully) successful shared manuscript. Finally, thank you to my friends and family, who reminded me that life extends beyond the scope of this thesis. Special thanks to my mom and Benne for your equally regular visits, and to Klara for creating the front cover of this thesis with only very unclear instructions.

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Variety and Site Drive *Salix* Mixture Effects on Soil Organic Matter Chemistry and Soil Carbon Accumulation

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Abstract: Soil organic matter (SOM) is essential for nutrient cycling and soil carbon (C) accumulation, both of which are heavily influenced by the quality and quantity of plant litter. Since SOM dynamics in relation to plant diversity are poorly understood, we investigated the effects of willow variety and mixture, and site on the soil C stocks, SOM chemical composition and thermal stability. Using pyrolysis-field ionization mass spectrometry (Py-FIMS), a method of stepwise thermal degradation in ultrahigh vacuum combined with soft ionization in a high electric field, followed by mass-spectrometric separation and detection of molecular ions, we analyzed SOM in the top 10 cm of soil from two 7-year-old experimental sites in Germany and Sweden. Monocultures and mixtures of two willow varieties (*Salix* spp.) belonging to different species were grown at the experimental plots. Overall, site had the strongest effect on SOM quality. The results showed significant variability across sites for willow identity and mixture effects on C accumulation and SOM chemistry. In the German site (Rostock), yearly soil C accumulation was higher ($p < 0.05$) for variety 'Loden' (1.0 Mg C ha^{-1} year^{-1}) compared to 'Tora' (0.5 Mg C ha^{-1} year^{-1}), whilst in the Swedish site (Uppsala), both varieties exhibited similar soil C accumulation rates of around 0.6 Mg C ha^{-1} year^{-1}. Willow variety identity significantly affected SOM quality at both sites, while mixing had minor effects. Our findings emphasize the significance of site-specific context and variety and species identity in shaping soil C accumulation in willow plantations.

Keywords: variety or species mixing; soil organic matter; carbon sequestration; chemical composition; thermal stability

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Citation: Jensen, J.; Fransson, P.; Baum, C.; Leinweber, P.; Eckhardt, K.-U.; Weih, M. Variety and Site Drive *Salix* Mixture Effects on Soil Organic Matter Chemistry and Soil Carbon Accumulation. *Forests* **2024**, *15*, 1339. https://doi.org/10.3390/f15081339

Academic Editor: Benjamin L. Turner

Received: 14 June 2024
Revised: 30 July 2024
Accepted: 30 July 2024
Published: 1 August 2024

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1. Introduction

Soils store more carbon (C) than both the atmosphere and all vegetation combined [1], thereby playing a critical role in terrestrial ecosystem carbon dioxide (CO_2) exchange [2], and in balancing atmospheric CO_2 emissions. Whether soils act as sinks or sources of CO_2 depends on the balance between photosynthesis, respiration and stabilization of C belowground, and changes in soil C stocks have the potential to impact atmospheric CO_2 levels and the global C budget [3]. Soil organic matter (SOM) comprises the largest active reservoir of terrestrial organic carbon [4], and plays a direct role in climate change mitigation [5–7]. However, the dynamics of SOM are complex and not fully understood [8], and an improved understanding of its formation and stabilization is crucial for developing sustainable approaches to enhance soil C sequestration.

The SOM consists of decomposing plant material and microbial-derived compounds varying in size, extent of degradation, accessibility, and residence time [9]. The chemical composition and stability of SOM controls the rate at which microbial communities process organic matter, thus governing the accumulation of soil C [10,11]. Since soil respiration is influenced by the soil microbial activity, a higher soil respiration rate could therefore reflect increased decomposition rates. In the present study, we use chemistry indicating SOM stability as a proxy of SOM quality. The stability of SOM is partly determined by its constituent molecules, some of which are more resistant to decomposition (e.g., lignin, phenols and suberin; [12,13]) than others (e.g., free fatty acids and peptides; [14,15]). Higher proportions of recalcitrant molecules contribute to more stable SOM, which is more likely to accumulate over time [16]. Climatic and edaphic factors further complicate SOM dynamics, as temperature and precipitation influence microbial activity and soil type, which can be instrumental for SOM stabilization [17–19].

There are many wet-chemical, spectrometric and spectroscopic analytical methods available to assess the quality of SOM, e.g., [20,21]. Pyrolysis-field ionization mass spectrometry (Py-FIMS) is a powerful analytical tool, with which biogenic marker substances can be associated with molecular compound classes derived from soil samples, thus providing a means of characterizing SOM chemical composition while also providing the possibility to assess the thermal stability of these same biogenic markers [11,22]. It reveals the strength of chemical bonds within molecules or between reactive mineral surfaces and organic molecules in response to thermal stress, thus providing a measure of resistance to microbial decomposition [11,13]. This data-rich method provides a high-resolution overview of the SOM chemical structure with the potential to elucidate responses of belowground processes to factors such as plant species identity and plant species mixing. SOM chemical composition and thermal stability are important aspects to consider when examining how aboveground vegetation influences the stability of SOM in different environments.

The quantity and quality of plant litter input can vary greatly between species and vegetation types [23,24]. Multiple studies have shown plant diversity to enhance soil C sequestration [25,26], often through increased aboveground biomass production through altered resource competition or facilitative plant–plant interactions, thus increasing the amount of organic matter supplied to the soil and therefore the accumulation of C [27–29]. However, the effects of species diversity on plant productivity are often highly context dependent [30,31]. Further, an increase in C storage with plant diversity can also result from longer persistence of plant litter due to slower decomposition [32]. Plant diversity, mainly studied in grasslands, but with evidence emerging from forest ecosystems, has been shown to affect SOM chemical diversity [33–35], microbial composition, activity and biomass [36,37], soil nutrient retention [38], and soil gas emissions [39]. Increased soil microbial biomass and consequently later necromass can make up more than half of SOC [40]. Plant diversity should therefore likely influence both SOM chemical composition and thermal stability, which could have major implications for SOM decomposition and ultimately ecosystem functioning [41–44]. Yet, the effects of plant diversity are not thoroughly explored in forest ecosystems, and especially the responses in SOM chemical composition and stability to tree species mixing remain poorly understood.

The cultivation of *Salix* spp. (willows) as a short-rotation coppice (SRC) has emerged as a promising approach to sustainably produce renewable biomass [45,46], with the largest cultivated areas found in China and Argentina, followed by Europe [47]. These production systems are characterized by short growth cycles of 2–5 years, after which the stems are harvested and shoots regrow rapidly from the stumps left in the soil [47]. In addition, willow SRC can serve as a model system for investigating plant diversity–productivity relationships [48], due to the fast growth and high phenotypic variability of willow species along with moderate-to-small phylogenetic contrasts. This enables the evaluation of subtle phenotypic differences on plant–plant interactions [49,50]. Different willow species and varieties can have a differential impact on belowground C dynamics and soil microbiota [51–53], and willow species or varieties grown in mixtures can differ from their monoculture counterparts in terms of nitrogen economy and productivity [50,54]. In the present study, we used two phenotypically distinct willow varieties belonging to different species grown both as monoculture stands and as mixtures. The aim of this study was to evaluate the effects of willow variety identity, mixture and site on soil C accumulation, SOM chemical composition and thermal stability using Py-FIMS methodology. We hypothesized the following: (i) willow variety identity affects soil C accumulation, SOM chemical composition and stability; (ii) willow variety mixtures accumulate similar amounts of soil C but differ in SOM chemical composition and stability compared to the equivalent monocultures at the same site; and (iii) site conditions modulate the effects of variety identity and mixture on soil C accumulation, SOM chemical composition and stability.

2. Materials and Methods

2.1. Experimental Design and Plant Material

Two experimental sites, one in Rostock, Germany (54°02′ N 12°05′ E), and one in Uppsala, Sweden (59°49′ N 17°39′ E), were planted with willow in a short-rotation coppice (SRC) system on former arable land in 2014. The two sites are part of the ECOLINK-Salix research trials (https://treedivnet.ugent.be/experiments/ECOLINKSalix.html (accessed on 12 July 2024)) as well as members of the global tree diversity network (TreeDivNet; [55]). Climatic conditions and soil properties differ between the two sites; notably, clay content is roughly 10 times higher in the Uppsala site compared to the Rostock site (Table 1).

Table 1. Site characteristics: soil group [56], topsoil (0–10 cm depth) properties measured in 2021 and climatic conditions during time since establishment at sites Rostock and Uppsala.

Site	Soil Group	pH	Bulk Density [g cm^{-3}]	Clay Content [%]	MAT [°C]	MAP [mg g^{-1}]
Uppsala	Vertic Cambisol	5.2	1.4	52	7.53	500
Rostock	Stagnic Cambisol	6.2	1.3	5	10.35	730

Two phenotypically distinct willow varieties belonging to different *Salix* species were used as stand components: ‘Loden’ (L; *S. dasyclados* Wimm.) and ‘Tora’ (T; *S. schwerinii x S. viminalis*). Generally, higher shoot biomass production is reported for ‘Tora’ than for ‘Loden’ [50,54], while leaf and fine root biomass production has been found to be higher for ‘Loden’ than for ‘Tora’ [57,58]. ‘Loden’ and ‘Tora’ also differ in terms of leaf chemistry and element stoichiometry [50,59], with [60] reporting weak effects of site, strong effects of variety and interaction effects between site and variety on leaf litter decomposability as measured by fraction of remaining biomass after incubation. Willows can form both ecto- and arbuscular mycorrhizal associations [61], but are generally more associated with ectomycorrhizal fungi [62]. In addition, [63] reported on greater ectomycorrhizal colonization of root tips belonging to *S. dasyclados* Wimm. than *S. viminalis* L., which are similar to ‘Loden’ (a *S. dasyclados* variety) and ‘Tora’ (a *S. schwerinii x S. viminalis* variety), respectively. In the present study, we use ‘Loden’ and ‘Tora’ in monoculture and the 2-component mixture. The willow varieties were planted in a randomized block design with 3 replicates for each monoculture (‘Loden’ and ‘Tora’) and mixture (‘Loden’:‘Tora’) for each site (i.e., 9 plots per site). All 9.6 × 9.6 m plots were planted in a hexagonal pattern with 12 rows, each row containing 12 plants at a distance of 0.8 m between neighboring plants, and further details can be found in [64].

2.2. Soil Sampling, Analyses and Measurements

Since the majority of *Salix* fine roots are found within the top 10 cm of soil [65,66], we focused our sampling efforts on this layer, assuming the most significant impact of *Salix* growth occurs here due to the turnover of fine roots and leaf litter. We collected nine soil samples per plot per site at experiment establishment in April 2014 and during the third cutting cycle in April 2021, using a soil auger (3 cm diameter). Subsamples were pooled per plot, dried at 40 degrees for 48 h and sieved (<2 mm). The concentrations of C and N were determined using a CN analyzer (Vario EL, Elementar Analysensysteme, Hanau, Germany). Soil pH was determined in 0.01 M $CaCl_2$ at a soil/:solution ratio of 1:2.5 (w/v). The C stocks (Mg ha^{-1}) were calculated for 2014 and 2021 by the following formula:

$$C_{stocks} = C_{org} * \rho d * depth \tag{1}$$

where C_{org} is the organic C concentration (g 100 g^{-1}) in the soil, ρd is the dry bulk density (g cm^{-3}), and *depth* is the soil sampling depth (10 cm). Yearly soil C accumulation (Mg C ha^{-1} $year^{-1}$) was calculated as the difference between 2021 and 2014 C stocks averaged per year. The determination of the dry bulk density (ρd) was based on the use of 250 cm^3 cores in 2014 and 2021 (ρd = dry weight [g]/volume [250 cm^3]). The soil cores were dried at 105 °C until a constant weight was achieved.

Double lactate-extractable phosphorus (P_{dl}), potassium (K_{dl}) and magnesium (Mg_{dl}) were determined after extraction of 0.6 g soil with 30 mL lactate solution [67]. The element concentrations in the extract were measured with inductively coupled plasma-optical emission spectroscopy (ICP-OES, Optima 8300, Perkin Elmer, Waltham, MA, USA). The lactate-extractable concentrations were considered to represent the plant-available fraction in soils [68]. C stocks and accumulation rates as well as P, Mg and K concentrations of soil samples from Uppsala and Rostock is represented in Supplementary Table S10.

Soil respiration was defined as CO_2 release from soil caused by respiration and was measured at 4-week intervals (8 times) during the growing season (April to October) for the year 2021 at the Uppsala site as a proxy for decomposition. Measurements were made using a portable infrared gas analyzer coupled to a 1296 cm^3 dark chamber in a closed air circuit (EgM-4 with SRC-1 probe type; PP Systems, Amesbury, MA, USA). The chamber was pressed firmly to the ground (avoiding weeds) for measurements in at least four different places per plot at each sampling occasion, evenly spread out with the intention to reflect the plot-level treatments. Due to cracking clay soil surfaces during dry summer months the sampling place varied between sampling occasions, ensuring a tight seal and avoiding cracks in the soil where large amounts of CO_2 was released. Respiration was typically monitored between 9:00 and 14:00 CET on cloudy to half-cloudy days after a recent rainfall if possible for ca 120 s per measurement and calculated as a function of the linear increase in CO_2 concentration in the chamber. Measurement quality was ensured by automatic baseline calibration by the 'auto-zero' option at least every 20 min and by keeping the start CO_2 concentration in the chamber at ambient level [69].

2.3. Pyrolysis-Field Ionization Mass Spectrometry (Py-FIMS)

SOM chemical composition and thermal stability were analyzed by pyrolysis-field ionization mass spectrometry (Py-FIMS) for samples from 2021 in three plots each for 'Loden', 'Tora' and 'Loden'/'Tora' plots from the Rostock site and from two plots each from the Uppsala site. About 3 mg of the air-dried, ground and homogenized samples were thermally degraded by pyrolysis in the ion source (emitter: 4.7 kV, counter electrode −5.5 kV) of a double-focusing Finnigan MAT 95. The samples were heated in a vacuum of 10^{-4} Pa from 50 °C to 700 °C, in temperature steps of 10 °C over a time period of 18 min. Between magnetic scans, the emitter was flash-heated to avoid residues of pyrolysis products. About 65 spectra were recorded for the mass range m/z 15 to 900. Biogenic marker signals (m/z) were assigned to nine relevant compound classes according to [21] (Table 2 and Table S8). All recorded marker signals (m/z) were combined to obtain the total ion intensity (TII) for each measurement. The difference in sample weight before and after pyrolysis provides a measure of "volatile matter" (VM) and is used to normalize sample ion intensities per mg sample weight. The hexoses/pentoses ratio is a measure of microbial- to plant-derived sugars [70] and is used as a measure of microbial contribution to SOM. Additionally, the ion intensities at each temperature step during pyrolysis was calculated separately for each of the about 65 single scans. The ion intensities of each compound class, plotted against the volatilization temperature, provided distinct thermograms that could be evaluated in terms of the thermal stability of compound classes. Examples of two Py-FYMS spectra with corresponding thermograms are represented in Supplementary

Materials S1 and S2 and Py-FI mass spectral data of soil samples from Uppsala and Rostock is represented in Supplementary Table S9.

Table 2. Pyrolysis-field ionization mass spectrometry (Py-FIMS) parameters and compound classes with associated biomolecules, as assigned by [21,71–74]. The marker signals (m/z) included in each compound class are represented in Supplementary Materials Table S8.

Py-FIMS Parameters	Explanations
Hexoses/pentoses	Ratio of microbial- to plant-derived sugars
TII	Total ion intensity (10^6 counts mg^{-1})
VM	Volatile matter in % (weight$_{\text{before pyrolysis}}$/weight$_{\text{after pyrolysis}}$)
CHYDR	Carbohydrates with pentose and hexose subunits
PHLM	Phenols and lignin monomers
LDIM	Lignin dimers
LIPID	Lipids, alkanes, alkenes, bound fatty acids, and alkylmonoesters
ALKYL	Alkylaromatics
NCOMP	Mainly heterocyclic N-containing compounds
PEPTI	Peptides (amino acids, peptides and aminosugars)
SUBER	Suberin
FATTY	Free fatty acids C_{16}–C_{34}

2.4. Statistical Analyses

All statistical analyses were conducted in R (version 4.3.0; [75]). SOM chemical composition for the two willow varieties in monoculture and mixture per study site was visualized using principal component analysis (PCA; function *rda* in package *vegan*; [76]). The PCA was performed on the relative ion intensities for the 9 Py-FIMS compound classes (Table 2). We used a principal component approach for the compound class data due to significant covariance between several of the compound classes. Principal component scores (PC1 and PC2; function *scores* in package *vegan*; [76]) were used as response variables in mixed-effects principal component regression models [77] to assess multivariate differences in SOM chemical composition between treatments. The robustness of the PCA performed on the compound classes was tested through comparison with an additional PCA performed directly on the Py-FIMS marker signals (m/z) (Supplementary Material Figure S1–S3).

The Shannon diversity index (H'), which accounts for both presence and relative abundance, was applied to our Py-FIMS biogenic marker signals (m/z) to quantify the chemical diversity of SOM (function *diversity* in package *vegan*; [76]):

$$H' = -\sum_{i=1}^{n} pi\, ln(pi) \tag{2}$$

where p_i is the proportion of relative ion intensity for marker signal (m/z) i, and n is the number of measured marker signals in a given sample.

The SOM thermal stability, here used as an indicator of resistance to microbial decomposition [21], was calculated for total ion intensity (TII) as well as for each compound class separately (Table 2). This was carried out following [78] by dividing the sum of ion intensities volatilized at high temperature (>400 °C) by ion intensities volatilized over the whole temperature range (50–650 °C).

Net diversity effects (NDE) of selected SOM properties were evaluated following [27]:

$$NDE\ (net\ diversity\ effect) = \frac{Observed - Expected}{Expected} \tag{3}$$

in which the observed values under variety mixtures are compared to the expected mixture values, calculated as the average values under their monoculture counterparts. Mixture effects are characterized as non-additive if significantly different from zero ($NDE \neq 0$) or additive if not (NDE = 0). To avoid any mixture effects being occluded by potential dominance effects, we applied weights to the expected mixture values based on their proportional basal area in the mixtures [29] (Supplementary Materials Table S1).

Responses in soil C accumulation, nutrient concentrations, Py-FIMS compound classes and SOM thermal stability were modeled using mixed-effects multiple linear regression models with the fixed effects of variety composition (‘Loden’, ‘Loden’:‘Tora’ and ‘Tora’), site (Rostock and Uppsala) and their interaction (function *lme* in package *nlme*; [79]). A block nested in the site was added to the model as a random effect to account for site-specific block effects, which were especially noticeable at the Rostock site. Due to different variance structures at our sites, site-specific variance weights were included in the model. Soil respiration was measured only at the Uppsala site and was modeled using a mixed effects multiple linear regression model in response to the fixed effects of variety composition and undergrowth ground cover (%). Block and plot nested in block were added as random effects to account for block effects and repeated measurements, respectively. Temporal autocorrelation between months was accounted for using an autoregressive correlation structure. For each response variable in the paper, the statistical significance of site, variety composition and their interaction was evaluated using analyses of variance (ANOVA; type = III, Kenward-Roger’s method, function *anova* in base R) and the results of these analyses are presented in Supplementary Materials Tables S2–S7. This was followed by pairwise comparisons of estimated marginal means using a Tukey adjustment (function *emmeans* in package *emmeans*; [80]). The function *contrast* from the *emmeans* package was used to examine specific variations across sites, varieties within sites, and varieties across sites, as well as the disparities between expected and observed mixture values within sites and observed mixture values across sites Estimated marginal means were used to calculate mean values due to the partially unbalanced nature of our dataset.

3. Results

3.1. Site Characteristics

The contents of soil C ($p = 0.004$), N ($p = 0.001$), K_{dl} ($p = 0.002$) and Mg_{dl} ($p = 0.011$) were significantly lower at the Rostock than Uppsala site (Table 3), while the C:N ratio and P_{dl} were similar between sites. No differences in the above characteristics were found between willow varieties grown in monoculture or mixture at either site.

Table 3. Soil chemical characteristics and soil respiration: estimated marginal means of topsoil (0–10 cm depth) soil C:N ratios, nutrient concentrations of C, N, K_{dl}, Mg_{dl} and P_{dl} as well as soil respiration for varieties ‘Loden’ and ‘Tora’ grown in monoculture and mixture at sites Rostock and Uppsala. Different letters indicate significant differences across sites (x–y) and within each site (a–b; $p < 0.05$, Tukey’s post hoc test).

Site	**Variety Composition**	**C:N**	**C [%]**	**N [%]**	**K_{dl} [mg g^{-1}]**	**Mg_{dl} [mg g^{-1}]**	**P_{dl} [mg g^{-1}]**	**CO_2 [g C m^{-2} h^{-1}]**
Rostock	‘Loden’	10.80 ^{xa}	1.26 ^{ya}	0.12 ^{ya}	9.99 ^{ya}	20.42 ^{ya}	4.40 ^{xa}	-
	‘Loden’:‘Tora’	10.63 ^{xa}	1.22 ^{ya}	0.11 ^{ya}	10.22 ^{ya}	21.06 ^{ya}	4.40 ^{xa}	-
	‘Tora’	10.22 ^{xa}	1.01 ^{ya}	0.10 ^{ya}	10.71 ^{ya}	21.96 ^{ya}	4.02 ^{xa}	-
Uppsala	‘Loden’	10.69 ^{xa}	1.89 ^{xa}	0.18 ^{xa}	22.23 ^{xa}	32.10 ^{xa}	4.27 ^{xa}	0.493 ^{a}
	‘Loden’‘Tora’	10.58 ^{xa}	1.58 ^{xa}	0.16 ^{xa}	23.62 ^{xa}	27.94 ^{xa}	5.04 ^{xa}	0.453 ^{a}
	‘Tora’	10.85 ^{xa}	1.90 ^{xa}	0.17 ^{xa}	19.89 ^{xa}	28.76 ^{xa}	3.60 ^{xa}	0.461 ^{a}

The total thermal stability of bulk SOM was similar across sites, but total ion intensity (TII; $p = 0.004$, hexoses:pentoses ratio ($p = 0.004$) and chemical diversity (H'; $p < 0.001$) were all significantly higher in Rostock than Uppsala (Table 4). Volatile matter was significantly higher in Uppsala than Rostock (VM; $p = 0.003$). In terms of compound classes, the Uppsala site had significantly higher relative abundances of carbohydrates (CHYDR; 5.0% TII, $p < 0.001$), phenols and lignin monomers (PHLM; 5.9% TII, $p < 0.001$), alkylaromatics (ALKYL; 3.5% TII, $p < 0.001$), N-compounds (NCOMP; 2.2% TII, $p < 0.001$) and peptides (PEPTI; 2.3% TII, $p = 0.001$), while lower relative abundances of lipids (LIPID; −1.7% TII, $p = 0.003$), suberin (SUBER; −0.2% TII, $p < 0.001$) and free fatty acids (FATTY; −0.5% TII, $p = 0.015$) were observed compared to the Rostock site.

Table 4. Py-FIMS parameters: estimated marginal means of TII (total ion intensity; 106 counts mg^{-1}) and total thermal stability of bulk SOM (ions volatilized > 400 °C/ions volatilized 50–650 °C), VM (volatile matter), H′ (SOM chemical diversity) and hexoses:pentoses (ratio of microbial- to plant-derived sugars) by site and by variety composition. Different letters indicate significant differences across sites (x–y) and within each site (a–b; $p < 0.05$, Tukey's post hoc test).

Site	Variety Composition	TII [10^6 Counts mg^{-1}]	Total Thermal Stability	Chemical Diversity [H′]	Hexoses: Pentoses	Volatile Matter
Rostock	'Loden'	53.3 ^{xa}	0.68 ^{xa}	6.71 ^{ya}	5.79 ^{xa}	2.83 ^{xa}
	'Loden':'Tora'	39.1 ^{xa}	0.72 ^{xa}	6.30 ^{ya}	5.73 ^{xab}	2.92 ^{xa}
	'Tora'	34.8 ^{xa}	0.77 ^{xa}	5.82 ^{ya}	5.67 ^{xb}	2.75 ^{xa}
Uppsala	'Loden'	14.8 ^{ya}	0.84 ^{xa}	14.66 ^{xa}	5.47 ^{ya}	1.89 ^{yb}
	'Loden':'Tora'	14.2 ^{ya}	0.82 ^{xb}	9.69 ^{xb}	5.45 ^{ya}	1.91 ^{yb}
	'Tora'	24.7 ^{ya}	0.83 ^{xab}	13.36 ^{xa}	5.53 ^{ya}	2.28 ^{ya}

3.2. *Effects of Willow Variety*

Soil C stocks measured at the establishment of the experiment in 2014 were similar across all plots within each site and averaged at 10.32 and 20.54 Mg C ha^{-1} for sites Rostock and Uppsala, respectively. Seven years after planting, yearly soil C accumulation rates measured at the Rostock site under 'Loden' (1.02 Mg C ha^{-1} $year^{-1}$) were significantly higher ($p = 0.004$) than under 'Tora' (0.54 Mg C ha^{-1} $year^{-1}$). Soil C accumulation rates measured at the Uppsala site were similar between 'Loden' (0.55 Mg C ha^{-1} $year^{-1}$) and 'Tora' (0.65 Mg C ha^{-1} $year^{-1}$). Furthermore, neither Loden nor Tora differed in C accumulation rates between sites (Figure 1).

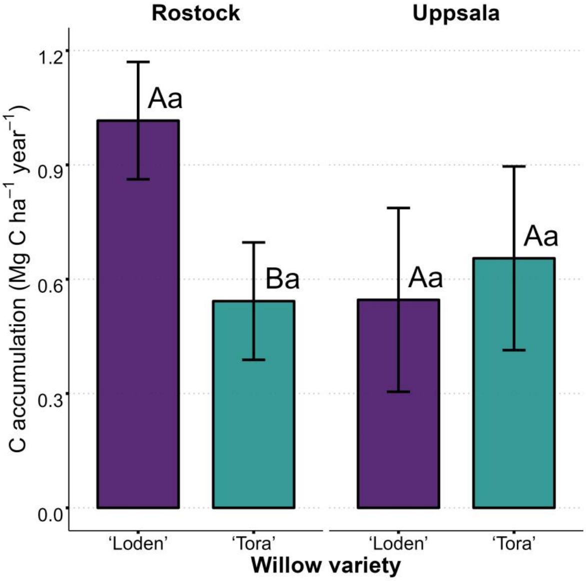

Figure 1. Soil C accumulation: estimated marginal means of topsoil (0–10 cm depth) C accumulation rates for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture at sites Rostock and Uppsala. Site-specific bulk densities 1.3 and 1.4 g cm^3 used in calculations of C stocks in Rostock and Uppsala, respectively. Different uppercase letters indicate significant pairwise differences between willow varieties within each site (A–B; $p < 0.05$). Different lowercase letters indicate significant pairwise differences for each willow variety between sites (a–b; $p < 0.05$). Standard errors are shown as error bars.

The SOM chemical composition differed between 'Loden' and 'Tora' ($p = 0.036$) and between the mixture and 'Tora' ($p = 0.043$) along PC1 at the Rostock site (Figure 2). No significant differences between 'Loden', 'Loden''Tora' or 'Tora' were found along PC1 at the Uppsala site, or along PC2 at either site. Principal component 1 (PC1) explained 92.4% of the variation in the 9 compound classes from Py-FI mass spectra (Table 2) of soil samples under the willow varieties in monoculture and mixture and was strongly associated ($p < 0.001$) with all nine compound classes. Principal component 2 (PC2) explained 3.7% of the variation and correlated with compound classes lignin dimers (LDIM), lipids (LIPID) and free fatty acids (FATTY) ($p < 0.05$).

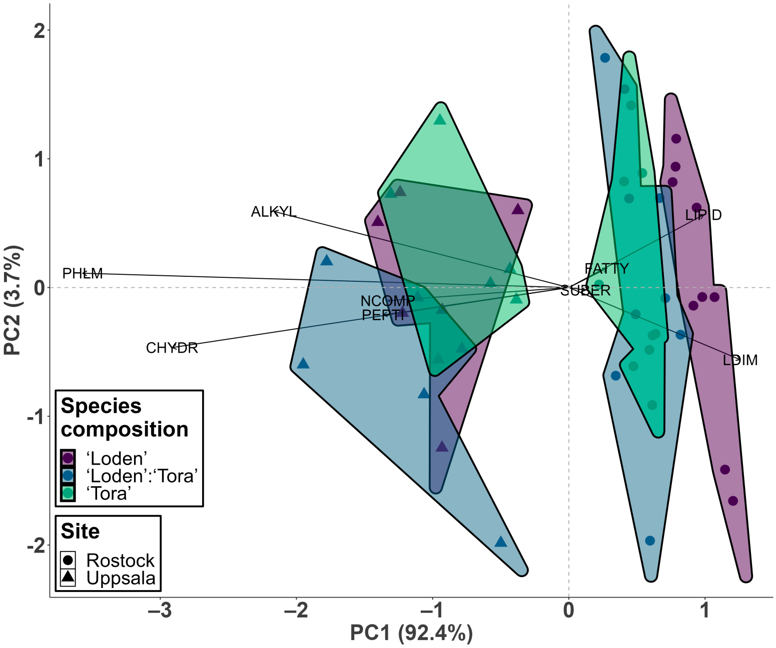

Figure 2. SOM chemical composition: principal components plot of the relative ion intensities (% TII) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0–10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala.

The SOM under 'Tora' exhibited significantly greater abundances of carbohydrates (CHYDR; 1.0% TII, $p = 0.015$), phenols and lignin monomers (PHLM; 1.8% TII, $p = 0.018$), N-compounds (NCOMP; 0.5% TII, $p = 0.017$), and peptides (PEPTI; 0.6% TII, $p = 0.026$), but significantly lower abundances of suberin (SUBER; −0.2% TII, $p = 0.014$) and free fatty acids (FATTY; −0.6% TII, $p = 0.014$), compared to SOM under 'Loden' at the Rostock site (Table 5). Conversely, at Uppsala, the abundance of lignin dimers (LDIM; 1.7% TII, $p < 0.001$) was significantly higher in SOM under 'Tora' than 'Loden', while peptides (PEPTI; −0.8% TII, $p < 0.001$) and free fatty acids (FATTY; −0.1% TII, $p = 0.004$) were significantly lower under 'Tora' compared to 'Loden'. Additionally, comparing SOM chemical composition under each willow variety between sites, 'Loden' cultivated in Uppsala showed significantly higher abundances of carbohydrates (CHYDR; 5.5% TII, $p = 0.003$), phenols and lignin monomers (PHLM; 7.3% TII, $p = 0.001$), alkylaromatics (ALKYL; 4.5% TII, $p = 0.002$), N-compounds (NCOMP; 2.6% TII, $p = 0.002$), and peptides (PEPTI; 2.8% TII, $p < 0.001$)

than 'Loden' cultivated in Rostock. In contrast, compound classes lignin dimers (LDIM; −2.6% TII, $p = 0.040$), lipids (LIPID; −2.0% TII, $p = 0.006$), suberin (SUBER; −0.31% TII, $p = 0.001$), and free fatty acids (FATTY; −0.71% TII, $p = 0.008$) were significantly lower under 'Loden' when cultivated in Uppsala compared to Rostock. For 'Tora', significant differences between sites included higher abundances of carbohydrates (CHYDR; 3.8% TII, $p = 0.010$), phenols and lignin monomers (PHLM; 4.5% TII, $p = 0.008$), alkylaromatics (ALKYL; 2.9% TII, $p = 0.009$), N-compounds (NCOMP; 1.5% TII, $p = 0.016$) and peptides (PEPTI; 1.4% TII, $p = 0.012$), in Uppsala compared to Rostock. Conversely, abundances of lipids (LIPID; −1.2% TII, $p = 0.037$) and suberin (SUBER; −0.11% TII, $p = 0.038$) were significantly lower in Uppsala compared to Rostock under 'Tora'.

Table 5. SOM chemical composition: estimated marginal means (± SE) of relative ion intensities (% TII) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0–10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture at sites Rostock and Uppsala. Different uppercase letters indicate significant pairwise differences between willow varieties within each site (A–B; $p < 0.05$). Different lowercase letters indicate significant pairwise differences for each willow variety between sites (a–b; $p < 0.05$).

Compound Classes	Rostock		Uppsala	
	'Loden'	'Tora'	'Loden'	'Tora'
CHYDR	4.0 (0.19) $^{\mathrm{Bb}}$	5.0 (0. 19) $^{\mathrm{Ab}}$	9.5 (0.82) $^{\mathrm{Aa}}$	8.8 (0.82) $^{\mathrm{Aa}}$
PHLM	9.9 (0.36) $^{\mathrm{Bb}}$	11.7 (0.36) $^{\mathrm{Ab}}$	17.2 (0.82) $^{\mathrm{Aa}}$	16.2 (0.82) $^{\mathrm{Aa}}$
LDIM	6.8 (0.64) $^{\mathrm{Aa}}$	7.1 (0.64) $^{\mathrm{Aa}}$	4.2 (0.59) $^{\mathrm{Bb}}$	5.9 (0.59) $^{\mathrm{Aa}}$
LIPID	10.3 (0.29) $^{\mathrm{Aa}}$	9.9 (0.29) $^{\mathrm{Aa}}$	8.4 (0.24) $^{\mathrm{Ab}}$	8.8 (0.24) $^{\mathrm{Ab}}$
ALKYL	13.3 (0.49) $^{\mathrm{Ab}}$	14.9 (0.49) $^{\mathrm{Ab}}$	17.8 (0.38) $^{\mathrm{Aa}}$	17.9 (0.38) $^{\mathrm{Aa}}$
NCOMP	1.6 (0. 10) $^{\mathrm{Bb}}$	2.1 (0.10) $^{\mathrm{Ab}}$	4.1 (0.36) $^{\mathrm{Aa}}$	3.6 (0. 36) $^{\mathrm{Aa}}$
PEPTI	3.6 (0.24) $^{\mathrm{Bb}}$	4.1 (0.24) $^{\mathrm{Ab}}$	6.4 (0.21) $^{\mathrm{Aa}}$	5.5 (0.21) $^{\mathrm{Ba}}$
SUBER	0.33 (0.03) $^{\mathrm{Aa}}$	0.16 (0.03) $^{\mathrm{Ba}}$	0.02 (0.01) $^{\mathrm{Ab}}$	0.05 (0.01) $^{\mathrm{Ab}}$
FATTY	0.87 (0.13) $^{\mathrm{Aa}}$	0.31 (0.13) $^{\mathrm{Ba}}$	0.17 (0.07) $^{\mathrm{Ab}}$	0.04 (0.07) $^{\mathrm{Ba}}$

Soil respiration, which was measured only at the Uppsala site, was similar across all variety compositions (Table 3). Chemical diversity (H') was significantly higher under 'Loden' compared to 'Tora' at the Rostock site ($p = 0.028$), with no difference at the Uppsala site (Table 4). The ratio of microbial- to plant-derived sugars (hexoses:pentoses), an indicator of microbial contribution to SOM, was significantly higher in SOM under 'Tora' compared to 'Loden' and the 'Loden':'Tora' mixture at the Uppsala site ($p = 0.021$ and $p = 0.026$, respectively). Total ion intensity (TII) was similar within sites, while total thermal stability was lower under 'Loden':'Tora' compared to 'Loden' ($p = 0.018$) only at the Uppsala site. Volatile matter (VM) was lower under 'Loden':'Tora' compared to both 'Loden' and 'Tora' at the Uppsala site ($p < 0.001$ and $p = 0.003$, respectively).

The thermal stability of compound classes lignin dimers (LDIM; $p = 0.047$), lipids (LIPID; $p = 0.030$), alkylaromatics (ALKYL; $p = 0.032$), suberin (SUBER; $p = 0.015$) and free fatty acids (FATTY; $p = 0.033$) were all significantly higher under 'Tora' than 'Loden' at the Rostock site (Table 6 and Figure 3). In contrast, at the Uppsala site, only suberin had a greater thermal stability under 'Tora' ($p < 0.001$), representing the sole compound class that consistently responded to variety identity across sites. Compound classes carbohydrates (CHYDR; $p = 0.004$), phenols and lignin monomers (PHLM; $p = 0.006$), alkylaromatics ($p = 0.022$), N-compounds (NCOMP; $p = 0.009$), and peptides (PEPTI; $p < 0.001$) were all significantly more stable under 'Loden' than 'Tora' at the Uppsala site (Table 6 and Figure 4). In terms of comparisons of SOM thermal stability under each willow variety between sites, 'Loden' cultivated in Uppsala showed significantly higher thermal stability of compound classes phenols and lignin monomers (PHLM; $p = 0.033$), lipids (LIPID; $p = 0.014$), alkylaromatics (ALKYL; $p = 0.038$) and N-compounds (NCOMP; $p = 0.022$) compared to 'Loden' cultivated in Rostock. For 'Tora', no significant differences in SOM thermal stability were found between the sites.

Table 6. SOM thermal stability: estimated marginal means (± SE) of thermal stability (ions volatilized > 400 °C/ions volatilized 50–650 °C) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0–10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture at sites Rostock and Uppsala. Different uppercase letters indicate significant pairwise differences between willow varieties within each site (A–B; $p < 0.05$). Different lowercase letters indicate significant pairwise differences for each willow variety between sites (a–b; $p < 0.05$).

Compound Classes	Rostock		Uppsala	
	'Loden'	'Tora'	'Loden'	'Tora'
CHYDR	0.32 (0.08) ^{Aa}	0.36 (0.08) ^{Aa}	0.60 (0.08) ^{Aa}	0.51 (0.08) ^{Ba}
PHLM	0.58 (0.06) ^{Ab}	0.67 (0.06) ^{Aa}	0.82 (0.05) ^{Aa}	0.77 (0.05) ^{Ba}
LDIM	0.88 (0.02) ^{Ba}	0.93 (0.02) ^{Aa}	0.95 (0.02) ^{Aa}	0.97 (0.02) ^{Aa}
LIPID	0.67 (0.04) ^{Bb}	0.80 (0.04) ^{Aa}	0.90 (0.03) ^{Aa}	0.90 (0.03) ^{Aa}
ALKYL	0.70 (0.04) ^{Bb}	0.80 (0.04) ^{Aa}	0.88 (0.04) ^{Aa}	0.87 (0.04) ^{Ba}
NCOMP	0.46 (0.07) ^{Ab}	0.53 (0.07) ^{Aa}	0.80 (0.06) ^{Aa}	0.68 (0.06) ^{Ba}
PEPTI	0.48 (0.07) ^{Aa}	0.54 (0.07) ^{Aa}	0.72 (0.06) ^{Aa}	0.64 (0.06) ^{Ba}
SUBER	0.76 (0.06) ^{Ba}	0.90 (0.06) ^{Aa}	0.88 (0.05) ^{Ba}	0.97 (0.05) ^{Aa}
FATTY	0.02 (0.01) ^{Ba}	0.07 (0.01) ^{Aa}	0.10 (0.07) ^{Aa}	0.12 (0.07) ^{Aa}

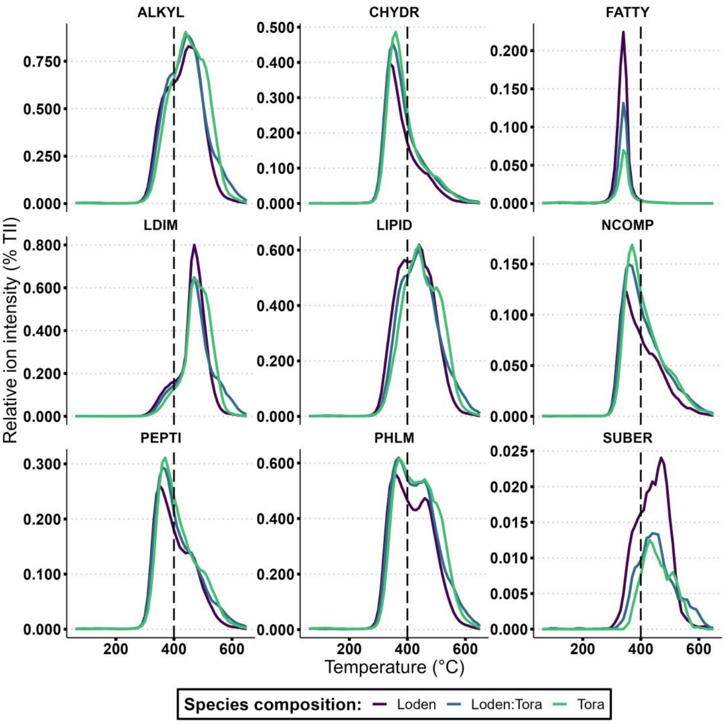

Figure 3. SOM thermal stability: thermograms showing ions volatilized under pyrolysis (0–650 °C) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0–10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and mixture at the Rostock site. Higher values of relative ion intensity indicate a greater abundance of specific compounds in the pyrolyzed SOM. The temperature at which compounds volatilize reflects their thermal stability, with ions volatilized over 400 °C being regarded as stable and ions volatilized under 400 °C being regarded as labile.

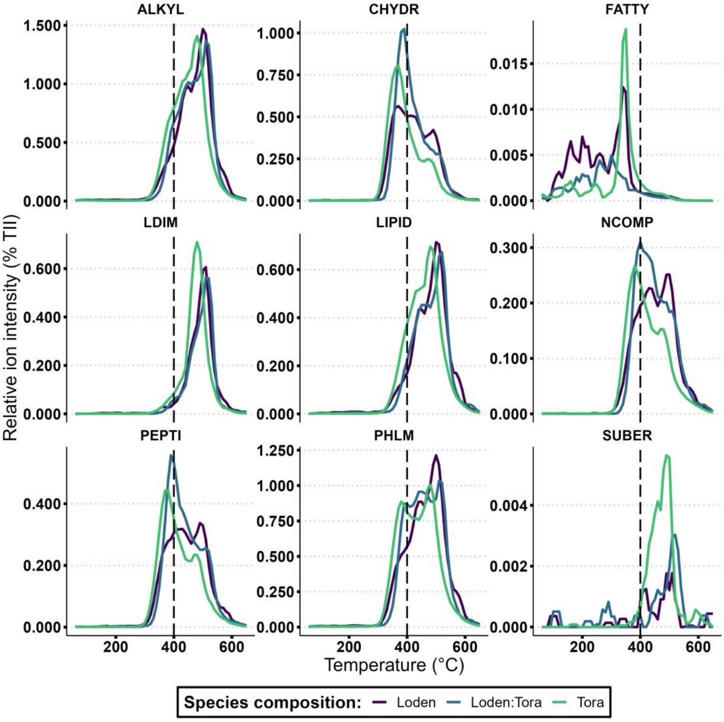

Figure 4. SOM thermal stability: thermograms showing ions volatilized under pyrolysis (0–650 °C) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0–10 cm depth) for the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and mixture at the Uppsala site. Higher values of relative ion intensity indicate a greater abundance of specific compounds in the pyrolyzed SOM. The temperature at which compounds volatilize reflects their thermal stability, with ions volatilized over 400 °C being regarded as stable and ions volatilized under 400 °C being regarded as labile.

At the Rostock site, the mean thermal stability of each compound class was as follows: lignin dimers > suberin > alkylaromatics > lipids > phenols and lignin monomers > peptides > N-compounds > carbohydrates > free fatty acids (Figure 3).

At the Uppsala site, the mean thermal stability of each compound class was as follows: lignin dimers > lipids > suberin > alkylaromatics > phenols and lignin monomers > N-compounds > peptides > carbohydrates > free fatty acids (Figure 4).

3.3. *Effects of Variety Mixing*

Expected values of yearly soil C accumulation in mixtures, as based on basal area weighted and averaged monoculture values, were similar to the observed mixture values at either site (Figure 5). Expected and observed soil C accumulation in mixtures were 0.75 and 0.98 Mg C ha^{-1} year^{-1}, respectively, at the Rostock site, and 0.61 and 0.16 Mg C ha^{-1} year^{-1}, respectively, at the Uppsala site. At the Rostock site, observed mixture values were found to be significantly higher than at the Uppsala site ($p = 0.046$).

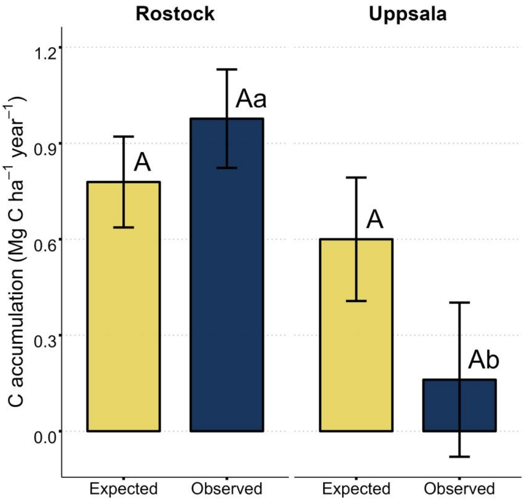

Figure 5. Soil C accumulation: estimated marginal means of expected and observed topsoil (0–10 cm depth) C accumulation rates at sites Rostock and Uppsala. Site-specific bulk densities 1.3 and 1.4 g cm^3 used in calculations of C stocks in Rostock and Uppsala, respectively. Expected values represent the basal area weighted and averaged mean values of the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and observed values represent the mean values of 'Loden' and 'Tora' grown in mixture. Different uppercase letters indicate significant pairwise differences between expected and observed mixture values within each site (A–B; $p < 0.05$). Different lowercase letters indicate significant pairwise differences for observed mixture values between sites (a–b; $p < 0.05$). Standard errors are shown as error bars.

Expected SOM chemical composition in mixtures, as based on basal area weighted and averaged monoculture values, were mostly similar to the observed mixture values (Table 7). Significant non-additive diversity effects were found for lignin dimers (LDIM) and peptides (PEPTI) at the Uppsala site, where lignin dimer abundance was reduced under mixtures (NDE = −18.3%, $p < 0.001$) compared to monocultures and peptide abundance was elevated under mixtures compared to monocultures (NDE = 18.2%, $p < 0.001$).

Table 7. SOM chemical composition: estimated marginal means (± SE) of expected and observed relative ion intensities (% TII) of nine compound classes: CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER and FATTY in Py-FI mass spectra (for abbreviations, see Table 2), as well as net diversity effect (NDE; Equation (3)) in topsoil (0–10 cm depth) at sites Rostock and Uppsala. Expected values represent the basal area weighted and averaged mean values of the *Salix* varieties 'Loden' and 'Tora' grown in monoculture and observed values represent the mean values of 'Loden' and 'Tora' grown in mixture. Asterisks indicate significant pairwise differences between expected and observed values within each site (*** = $p < 0.001$, n.s. = not significant).

Compound Classes	**Rostock**			**Uppsala**		
	Expected	**Observed**	**NDE**	**Expected**	**Observed**	**NDE**
CHYDR	4.6 (0.14)	5.0 (0.19)	9.2% n.s.	9.0 (0.62)	10.6 (0.82)	17.1% n.s.
PHLM	11.0 (0.26)	11.6 (0.36)	5.8% n.s.	16.5 (0.63)	17.4 (0.82)	5.7% n.s.
LDIM	7.0 (0.62)	6.6 (0.64)	−5.6% n.s.	5.4 (0.59)	4.4 (0.59)	−18.3% ***
LIPID	10.1 (0.23)	9.9 (0.29)	−1.9% n.s.	8.6 (0.20)	8.0 (0.24)	−7.2% n.s.
ALKYL	14.2 (0.35)	14.6 (0.49)	2.8% n.s.	17.8 (0.29)	17.6 (0.38)	−1.0% n.s.
NCOMP	1.9 (0.07)	2.1 (0.25)	10.2% n.s.	3.8 (0.27)	4.5 (0.23)	20.1% n.s.
PEPTI	3.9 (0.22)	4.1 (0.24)	4.0% n.s.	5.8 (0.20)	6.8 (0.21)	18.2% ***
SUBER	0.23 (0.03)	0.20 (0.03)	−14.8% n.s.	0.04 (0.01)	0.03 (0.01)	−18.0% n.s.
FATTY	0.55 (0.10)	0.52 (0.13)	−6.5% n.s.	0.08 (0.07)	0.13 (0.07)	59.4% n.s.

Comparable to SOM chemical composition, SOM thermal stability was mostly similar between the expected and observed mixture values for most compound classes, though some significant non-additive mixture effects were found, but only at the Uppsala site (Table 8 and Figure 4). There, the stability of both compound classes ALKYL (NDE = −0.9%, $p = 0.036$) and suberin (SUBER; NDE = −22.7%, $p < 0.001$) was lower under mixtures compared to monocultures.

Table 8. SOM thermal stability: estimated marginal means (± SE) of expected and observed thermal stability (ions volatilized > 400 °C/> 0 °C) of nine compound classes: CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER and FATTY in Py-FI mass spectra (for abbreviations, see Table 2), as well as the net diversity effect (NDE; Equation (3)) in topsoil (0–10 cm depth) at sites Rostock and Uppsala. Expected values represent the basal area weighted and averaged mean values of varieties 'Loden' and 'Tora' grown in monoculture and observed values represent the mean values of 'Loden' and 'Tora' grown in mixture. Asterisks indicate significant pairwise differences between expected and observed values within each site (*** = $p < 0.001$, * = $p < 0.05$, n.s. = not significant).

Compound Classes	**Rostock**			**Uppsala**		
	Expected	**Observed**	**NDE**	**Expected**	**Observed**	**NDE**
CHYDR	0.34 (0.08)	0.36 (0.08)	3.3% n.s.	0.54 (0.08)	0.53 (0.08)	−1.0% n.s.
PHLM	0.63 (0.05)	0.63 (0.06)	−1.0% n.s.	0.78 (0.05)	0.78 (0.05)	0.3% n.s.
LDIM	0.91 (0.02)	0.91 (0.02)	−0.6% n.s.	0.96 (0.02)	0.95 (0.02)	−1.5% n.s.
LIPID	0.74 (0.04)	0.74 (0.04)	−0.7% n.s.	0.90 (0.03)	0.90 (0.03)	0.4% n.s.
ALKYL	0.76 (0.04)	0.74 (0.04)	−2.0% n.s.	0.87 (0.04)	0.86 (0.04)	−0.9% *
NCOMP	0.48 (0.06)	0.50 (0.07)	−0.2% n.s.	0.71 (0.06)	0.74 (0.06)	3.55% n.s.
PEPTI	0.52 (0.07)	0.50 (0.07)	−2.5% n.s.	0.67 (0.07)	0.67 (0.06)	0.4% n.s.
SUBER	0.84 (0.05)	0.83 (0.06)	−1.8% n.s.	0.99 (0.05)	0.76 (0.05)	−22.7% ***
FATTY	0.05 (0.01)	0.04 (0.01)	−19.8% n.s.	0.12 (0.05)	0.15 (0.07)	30.8% n.s.

4. Discussion

4.1. Effects of Site-Specific Environmental Conditions

Our study used two experimental sites with distinct climatic and edaphic circumstances, which provided a platform to investigate how local conditions modulate the influence of willows on SOM quality. Our results showed that the interaction between plants and the investigated soil properties is strongly influenced by local site conditions, where soil C accumulation, SOM chemical composition and thermal stability responded differently to both variety identity and mixture across sites (confirming Hypothesis 3). Temperature, moisture and especially clay content, which differed between the two study sites, are widely documented as strong modifiers of decomposition rates [23,81], and microbial dynamics [82–84]. Therefore, we expected the lower temperatures and precipitation levels as well as higher clay content in Uppsala to contribute to lower SOM decomposition rates compared to Rostock. In the present study, this is partly supported by the lower ratio of microbial- to plant-derived sugars (hexoses:pentoses) found in Uppsala compared to Rostock, indicating lower microbial contribution to SOM [70,85]. Additional supporting evidence for lower decomposition rates in Uppsala compared to Rostock comes from a previous study on the same willow SRCs [60], showing slower leaf litter decomposition rates for monocultures and higher fractions of remaining N (immobilization of N) in mixtures in Uppsala compared to Rostock, though with only minor effects of climate. However, the highest accumulation of soil C was found under 'Loden' in Rostock, where we expected a higher decomposition rate compared to Uppsala. This discrepancy between likely outcomes based on literature evaluations and results may be explained by the generally greater biomass production at the Rostock site [64], leading to a greater litter input to the soil. Additionally, more recalcitrant compounds such as lipids and lignin dimers were more abundant at the Rostock site, possibly contributing to SOM formation [86,87].

4.2. Effects of Willow Variety

In the present study, we demonstrated that the influence of willow SRC on soil C accumulation and SOM chemistry strongly depended on willow variety (confirming Hypothesis 1). After seven years of growth, the net average annual C accumulation in the topsoil (0–10 cm depth) was consistently positive across all experimental plots, with C accumulation rates ranging from 0.06 to 1.29 Mg C ha^{-1} $year^{-1}$. These values were comparable to mean soil C accumulation values documented under willow SRC for 'Loden' (0.73 Mg C ha^{-1} $year^{-1}$) and 'Tora' (0.65 Mg C ha^{-1} $year^{-1}$) near the Uppsala site over a 17-year period in [51]. In the site with more climatically favorable growth conditions (Rostock), 'Loden' had a higher C accumulation rate compared to 'Tora', whilst both varieties accumulated similar soil C amounts at the site with less climatically favorable growth conditions (Uppsala). A greater C accumulation under 'Loden' could be due to a higher fine root biomass production compared to 'Tora', as reported by [57] at the Rostock site. Furthermore, at the Rostock site, 'Loden' also had higher abundances of suberin compared to 'Tora', a compound primarily derived from roots [88]. This suggests a higher fine root biomass production under 'Loden' at the Rostock site, thus in line with the findings of [57]. Interestingly, the difference in C accumulation between 'Loden' and 'Tora' in Rostock was similar to what [51] reported in a site near Uppsala after 17 years of growth. It is therefore plausible that, in the future (e.g., after an additional 10 years), we will also see a significantly greater soil C accumulation under 'Loden' than 'Tora' in the site with less favorable growth conditions (Uppsala). The difference in C accumulation between 'Loden' and 'Tora' in Rostock could also depend on differences in SOM chemistry, or results in different stability of the accumulated SOM. A fertilization experiment in central Sweden, using mid-infrared spectroscopy and pyrolysis–gas chromatography–mass spectrometry (GC/MS) for their analysis, also observed a different SOM chemical composition between willow varieties 'Loden' and 'Tora' [89]. At the Rostock site, we found more chemically diverse SOM under 'Loden' compared to 'Tora', which may have contributed to a decreased decomposition and a subsequently promoted C accumulation for 'Loden' [4,90]. Enhanced SOM chemical diversity under 'Loden' compared to 'Tora' has also been reported in a recent study [89]. The relative enrichment of monomeric lignin building blocks under 'Tora' at the Rostock site, which can be explained by an advanced lignin decomposition [15], also supports enhanced decomposition in 'Tora' plots. Further, 'Tora' plots at the Rostock site displayed higher overall thermal stabilities of compound classes, suggesting higher decomposition rates as the more labile fractions of plant litter SOM would be decomposed first [11], leaving more recalcitrant molecules behind. A final potential explanation to the differences in C accumulation between 'Loden' and 'Tora', in addition to differential biomass production and decomposition rates, can depend on the interaction between mycorrhizal and saprotrophic fungi. Since 'Loden' is more dependent on the ectomycorrhizal association compared to 'Tora' [57,63] the saprotrophic activity under 'Loden' may have been suppressed as per the Gadgil effect [91]. The Gadgil effect implies suppression of saprotrophic activity in the presence of increased ectomycorrhizal colonization due to competition between the two functional groups and assimilate transfer from the host plant.

4.3. Effects of Variety Mixing

In the present study, we found no effect of variety mixing on soil C accumulation (confirming part of Hypothesis 2), which is consistent with the findings of [92–94]. Since previous investigations of mixed-species willow plantations with 'Loden' and 'Tora' have found no indication of aboveground over-yielding [64,95], which is considered one of the main mechanisms of increased soil C sequestration in mixtures [25,96], this may explain the lack of response. However, even without increased plant productivity, 'Loden'/'Tora' mixtures have been shown to affect other belowground processes such as soil phosphorus (P) cycling [57], e.g., through promoting alkaline phosphatase activity in P-deficient soils in mixtures compared to monocultures [95], and to increase endophytic root colonization [57] when compared to their monoculture counterparts. We detected some significant effects of variety mixing on SOM chemical composition and thermal stability (confirming the second part of Hypothesis 2). At the Uppsala site, the detected effects of variety mixing on SOM chemical composition were found in the compound classes of lignin dimers and peptides, which revealed significantly higher and lower abundances, respectively, in variety mixtures compared to equivalent monocultures. Elevated levels of lignin decomposition in mixtures as a response to litter diversity is a possible explanation for these findings [87], which might be based on the higher general decomposition activity as revealed for the P cycling [57]. Since lignin is a rather stable fraction of SOM, lower lignin levels in mixtures could reduce SOM stability and decrease the long-term C sequestration in mixtures. Even so, the absence of effects of variety mixing on soil C accumulation and the presence of only some effects on SOM chemistry suggest that mixed willow cultivation does not greatly impair SOM quality or climate change mitigation potential compared to equivalent monoculture plantations at the same location. However, an increased decomposition of lignin in the mixtures in Uppsala could also indicate a decreased SOM formation. Finally, soil respiration, which is largely based on microbial activity in the soil, can reflect increased decomposition rates when respiration rates are higher. However, we did not find any difference in soil respiration between the treatments in the present study.

5. Conclusions

Our results highlight the complexity of plant–soil interactions and the challenges they present during interpretation. Despite the complex nature of our results, our study revealed that willow variety or species identity could have a significant impact on soil C accumulation, SOM chemical composition and thermal stability. Willow variety 'Loden' showed higher soil C accumulation rates compared to 'Tora' at the Rostock site, while both varieties had similar rates at the Uppsala site. SOM under 'Tora' showed a generally higher thermal stability then under 'Loden' at the Rostock site, while the opposite was true at the Uppsala site. We found no evidence for non-additive effects of willow variety mixtures on soil C accumulation, but some non-additive effects on SOM chemical composition and thermal stability were observed at the Uppsala site. This suggests that variety or species mixtures can be used in multifunctional plantations without greatly compromising soil C accumulation or SOM quality, as they mainly exhibit values similar to their monoculture counterparts. Significant interactions between willow variety and site conditions have important implications for the management of willow SRC plantations. The selection of willow varieties or species for willow SRC plantations needs to consider the context dependency of their expression under specific site conditions. Further research should investigate the environmental factors influencing the effects of tree species on soil chemistry.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15081339/s1, Figure S1: Py-FIMS spectrum and thermogram for SOM under 'Tora' at the Uppsala site; Figure S2: Py-FIMS spectrum and thermogram for SOM under under 'Loden':'Tora' at the Uppsala site; Figure S3: PCA using Py-FI marker signals (m/z) instead of compound classes; Table S1: Basal area weights used for calculating net diversity effects (NDE); Table S2: Soil chemical characteristics: results of two-way ANOVAs for soil C:N ratios nutrient concentrations and soil respiration; Table S3: Py-FIMS parameters: results of two-way ANOVAs for various SOM properties; Table S4: Soil C accumulation: results of a two-way ANOVA of topsoil C accumulation rates; Table S5: Principal component regression: results of two-way ANOVAs for principal components (PC1 and PC2) derived from the relative ion intensity (% TII) of nine compound classes in topsoil; Table S6: SOM chemical composition: results of two-way ANOVAs for the relative ion intensity (% TII) of nine compound classes in Py-FI mass spectra in topsoil; Table S7: SOM thermal stability: results of two-way ANOVAs for the thermal stability of nine compound classes in Py-FI mass spectra in topsoil; Table S8: Py-FI marker signals (m/z) included in each compound class; Table S9: Py-FI mass spectral data of soil samples from Uppsala and Rostock; Table S10: C stocks and accumulation rates as well as P, Mg and K concentrations in topsoil.

Author Contributions: Conceptualization: J.J., P.F., C.B., P.L. and M.W.; methodology, J.J.; formal analysis, J.J.; investigation, J.J. and K.-U.E.; resources, C.B. and P.L.; data curation, K.-U.E.; writing—original draft preparation, J.J.; writing—review and editing, P.F., C.B., P.L. and M.W.; visualization, J.J.; supervision, P.F., C.B. and M.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research received funding from FORMAS (The Swedish Research Council for Environment, Agricultural sciences and Spatial Planning) for the MixForChange project [grant number 2020-02339]. The establishment and management of the field trial was funded by grants from the Swedish Energy Agency [project numbers 36654-1, 36654-2]. Part of the soil analyses was funded by Deutsche Forschungsgemeinschaft (DFG) [project number BA 1494/9-1]. Petra Fransson was supported by the Swedish Research Council FORMAS [grant number 2016-01107].

Data Availability Statement: Data are available in the Supplementary Materials; further inquiries can be directed to the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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Suppelementary Material

Table S1. Basal area weights for varieties 'Loden' and 'Tora' in species mixtures 'Loden':'Tora' at sites Rostock and Uppsala used for calculating net diversity effects (NDE; equation 3).

Site	Variety	Basal area weights
Rostock	'Loden'	0.427558
Rostock	'Tora'	0.572442
Uppsala	'Loden'	0.302752
Uppsala	'Tora'	0.697248

Table S2. Soil chemical characteristics: results of two-way ANOVAs for soil C:N ratios, nutrient concentrations of C, N, K_{dl}, Mg_{dl} and P_{dl} as well as soil CO_2 respiration for the Salix varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and *p*-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
C:N	(Intercept)	734.03	1	<0.001
	Site	0.04	1	0.850
	Variety composition	1.80	2	0.406
	Site:variety composition	1.61	2	0.447
C	(Intercept)	246.72	1	<0.001
	Site	13.73	1	<0.001
	Variety composition	8.42	2	0.015
	Site:variety composition	3.70	2	0.157
N	(Intercept)	262.50	1	<0.001
	Site	21.13	1	<0.001
	Variety composition	3.00	2	0.223
	Site:variety composition	2.65	2	0.266
K_{dl}	(Intercept)	35.91	1	<0.001
	Site	20.30	1	<0.001
	Variety composition	0.11	2	0.947
	Site:variety composition	1.40	2	0.498
Mg_{dl}	(Intercept)	113.53	1	<0.001
	Site	13.04	1	<0.001
	Variety composition	0.32	2	0.850
	Site:variety composition	1.49	2	0.474
P_{dl}	(Intercept)	137.34	1	<0.001
	Site	0.03	1	0.858
	Variety composition	0.75	2	0.688
	Site:variety composition	1.16	2	0.561
CO2 respiration	(Intercept)	1.47	1	0.225
	Variety composition	0.15	2	0.926
	Grass cover	0.78	1	0.377

Table S3. Py-FIMS parameters: results of two-way ANOVAs for TII (total ion intensity; 106 counts mg^{-1}) and total thermal stability of bulk SOM (ions volatilized > 400 °C / ions volatilized 50-650 °C), VM (volatile matter), H′ (SOM chemical diversity) and hexoses:pentoses (ratio of microbial- to plant-derived sugars) for the Salix varieties ‘Loden’ and ‘Tora’ grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and *p*-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
TII	(Intercept)	111.12	1	<0.001
	Site	41.15	1	<0.001
	Variety composition	8.26	2	0.016
	Site:Variety composition	14.12	2	0.001
Total thermal stability	(Intercept)	180.40	1	<0.001
	Site	5.07	1	0.024
	Variety composition	6.34	2	0.042
	Site:Variety composition	7.39	2	0.025
Chemical diversity	(Intercept)	27926.60	1	<0.001
	Site	14.23	1	<0.001
	Variety composition	4.36	2	0.113
	Site:Variety composition	6.86	2	0.032
Hexoses:pentoses	(Intercept)	549.45	1	<0.001
	Site	33.68	1	<0.001
	Variety composition	1.82	2	0.403
	Site:Variety composition	14.12	2	0.001
Volatile matter	(Intercept)	70.44	1	<0.001
	Site	51.54	1	<0.001
	Variety composition	1.92	2	0.382
	Site:Variety composition	34.44	2	<0.001

Table S4. Soil C accumulation: results of a two-way ANOVA of topsoil (0-10 cm depth) C accumulation rates for the Salix varieties ‘Loden’ and ‘Tora’ grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and p-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
C accumulation (Mg C ha^{-1} $year^{-1}$)	(Intercept)	43.50	1	<0.001
	Site	2.70	1	0.100
	Variety composition	19.20	2	<0.001
	Site:Variety composition	9.00	2	0.011

Table S5. Principal component regression: results of two-way ANOVAs for principal components (PC1 and PC2 in Figure 2) derived from the relative ion intensity (% TII) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0-10 cm depth) for the Salix varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and *p*-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
PC1	(Intercept)	114.98	1	<0.001
	Site	81.27	1	<0.001
	Variety composition	16.17	2	<0.001
	Site:Variety composition	5.23	2	0.073
PC2	(Intercept)	0.00	1	0.967
	Site	0.00	1	0.969
	Variety composition	0.09	2	0.958
	Site:Variety composition	1.39	2	0.499

Table S6. SOM chemical composition: results of two-way ANOVAs for the relative ion intensity (% TII) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0-10 cm depth) for the Salix varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and *p*-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
CHYDR	(Intercept)	441.20	1	<0.001
	Site	43.20	1	<0.001
	Variety composition	17.90	2	<0.001
	Site:Variety composition	2.90	2	0.240
PHLM	(Intercept)	770.80	1	<0.001
	Site	66.20	1	<0.001
	Variety composition	15.10	2	0.001
	Site:Variety composition	5.00	2	0.081
LDIM	(Intercept)	113.30	1	<0.001
	Site	8.90	1	0.003
	Variety composition	1.90	2	0.388
	Site:Variety composition	14.50	2	0.001
LIPID	(Intercept)	1261.90	1	<0.001
	Site	28.30	1	<0.001
	Variety composition	2.20	2	0.332
	Site:Variety composition	4.20	2	0.125
ALKYL	(Intercept)	735.80	1	<0.001
	Site	51.60	1	<0.001
	Variety composition	6.30	2	0.043
	Site:Variety composition	3.90	2	0.145
NCOMP	(Intercept)	232.90	1	<0.001
	Site	47.00	1	<0.001
	Variety composition	15.70	2	<0.001
	Site:Variety composition	4.80	2	0.091
PEPTI	(Intercept)	223.30	1	<0.001
	Site	78.50	1	<0.001
	Variety composition	11.40	2	0.003
	Site:Variety composition	67.00	2	<0.001
SUBER	(Intercept)	94.50	1	<0.001
	Site	75.40	1	<0.001
	Variety composition	15.00	2	0.001
	Site:Variety composition	18.50	2	<0.001
FATTY	(Intercept)	48.50	1	<0.001
	Site	24.70	1	<0.001
	Variety composition	14.10	2	0.001
	Site:Variety composition	8.80	2	0.012

Table S7. SOM thermal stability: results of two-way ANOVAs for the thermal stability (ions volatilized > 400 °C / ions volatilized 50-650 °C) of nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY in Py-FI mass spectra (for abbreviations, see Table 2) in topsoil (0-10 cm depth) for the Salix varieties 'Loden' and 'Tora' grown in monoculture and mixture at sites Rostock and Uppsala. The table lists the Chi-square values (Chisq), degrees of freedom (df), and *p*-values for the fixed effects of Site, Variety composition, and their interaction (Site:Variety composition). Significance of parameters is indicated by $p < 0.05$.

Response variable	Model parameter	Chisq	df	*p*-values
CHYDR	(Intercept)	15.70	1	<0.001
	Site	6.60	1	0.010
	Variety composition	2.10	2	0.346
	Site:Variety composition	14.80	2	0.001
PHLM	(Intercept)	105.10	1	<0.001
	Site	10.30	1	0.001
	Variety composition	6.30	2	0.042
	Site:Variety composition	14.30	2	0.001
LDIM	(Intercept)	1382.30	1	<0.001
	Site	4.70	1	0.030
	Variety composition	6.90	2	0.032
	Site:Variety composition	1.80	2	0.409
LIPID	(Intercept)	234.50	1	<0.001
	Site	17.50	1	<0.001
	Variety composition	9.10	2	0.011
	Site:Variety composition	8.80	2	0.012
ALKYL	(Intercept)	268.30	1	<0.001
	Site	9.20	1	0.002
	Variety composition	8.90	2	0.012
	Site:Variety composition	10.60	2	0.005
NCOMP	(Intercept)	46.80	1	<0.001
	Site	13.20	1	<0.001
	Variety composition	2.50	2	0.292
	Site:Variety composition	13.70	2	0.001
PEPTI	(Intercept)	48.80	1	<0.001
	Site	6.30	1	0.012
	Variety composition	2.70	2	0.260
	Site:Variety composition	14.40	2	0.001
SUBER	(Intercept)	191.20	1	<0.001
	Site	2.60	1	0.109
	Variety composition	13.20	2	0.001
	Site:Variety composition	32.20	2	<0.001
FATTY	(Intercept)	3.20	1	0.073
	Site	1.30	1	0.258
	Variety composition	8.70	2	0.013
	Site:Variety composition	0.30	2	0.841

Table S8. Py-FI marker signals (*m*/*z*) for nine compound classes; CHYDR, PHLM, LDIM, LIPID, ALKYL, NCOMP, PEPTI, SUBER, FATTY (for abbreviations, see Table 2).

Compound class	Py-FI marker signals (*m*/*z*)
CHYDR	60, 61, 72, 82, 84, 96, 98, 110, 112, 114, 126, 132, 144, 162, 163
PHLM	94, 108, 110, 122, 124, 138, 140, 150, 152, 154, 164, 166, 168, 178, 180, 182, 194, 196, 208, 210, 212
LDIM	246, 260, 270, 272, 274, 284, 286, 296, 298, 300, 310, 312, 314, 316, 326, 328, 330, 340, 342, 356
LIPID	202, 216, 230, 244, 256, 258, 270, 272, 284, 286, 298, 300, 312, 314, 326, 328, 340, 342, 354, 368, 380, 382, 394, 396, 408, 410, 422, 424, 438, 452, 466, 480, 494, 508, 522, 536, 550, 564, 578, 592, 606, 620, 634, 648, 662, 676, 704, 718, 732, 746
ALKYL	92, 106, 120, 134, 142, 148, 156, 162, 170, 176, 184, 190, 192, 198, 204, 206, 218, 220, 232, 234, 246, 260, 274, 288, 302, 316, 330, 344, 358, 372, 386
NCOMP	67, 79, 81, 93, 95, 103, 109, 111, 117, 123, 137, 139, 153, 161
PEPTI	58, 59, 70, 73, 74, 75, 84, 87, 91, 97, 115, 120, 129, 135, 167, 185, 203, 243, 276
SUBER	432, 446, 460, 474, 488, 502, 516, 530
FATTY	256, 270, 278, 280, 282, 284, 298, 312, 326, 340, 354, 368, 382, 396, 410, 424, 438, 452, 466, 480, 494, 508

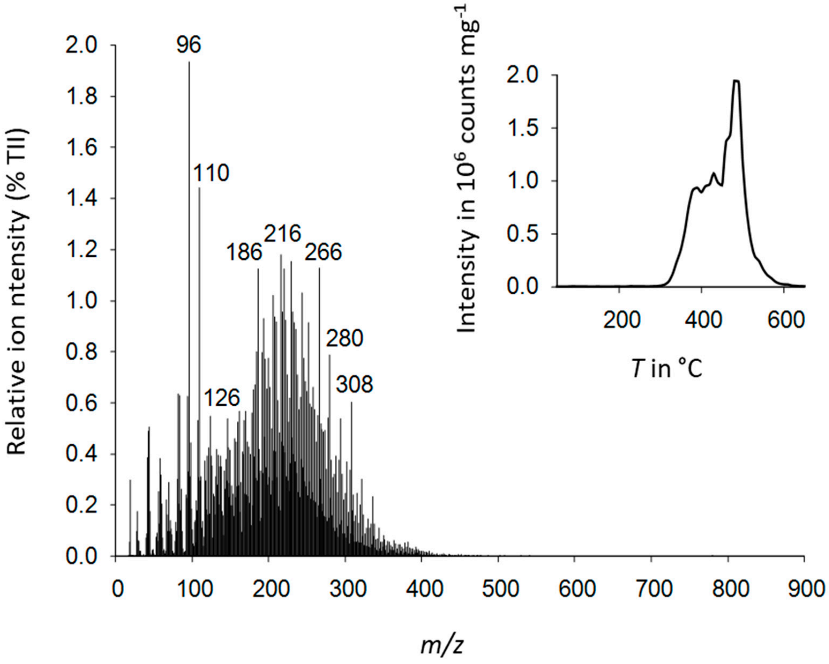

Figure S1. Py-FIMS spectrum with the intensities (% of total ion intensity (TII)) of mass peaks (*m*/*z*) and thermogram (upper right) for soil organic matter from a plot of *Salix* variety 'Tora' at the Uppsala site.

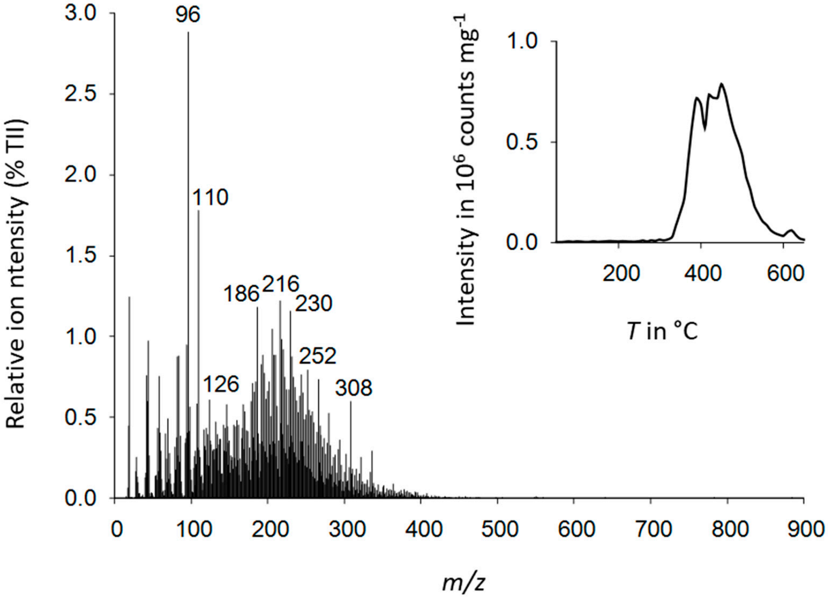

Figure S2. Py-FIMS spectrum with the intensities (% of total ion intensity (TII)) of mass peaks (*m*/*z*) and thermogram (upper right) for soil organic matter from a plot of *Salix* variety mixture 'Loden':'Tora' at the Uppsala site.

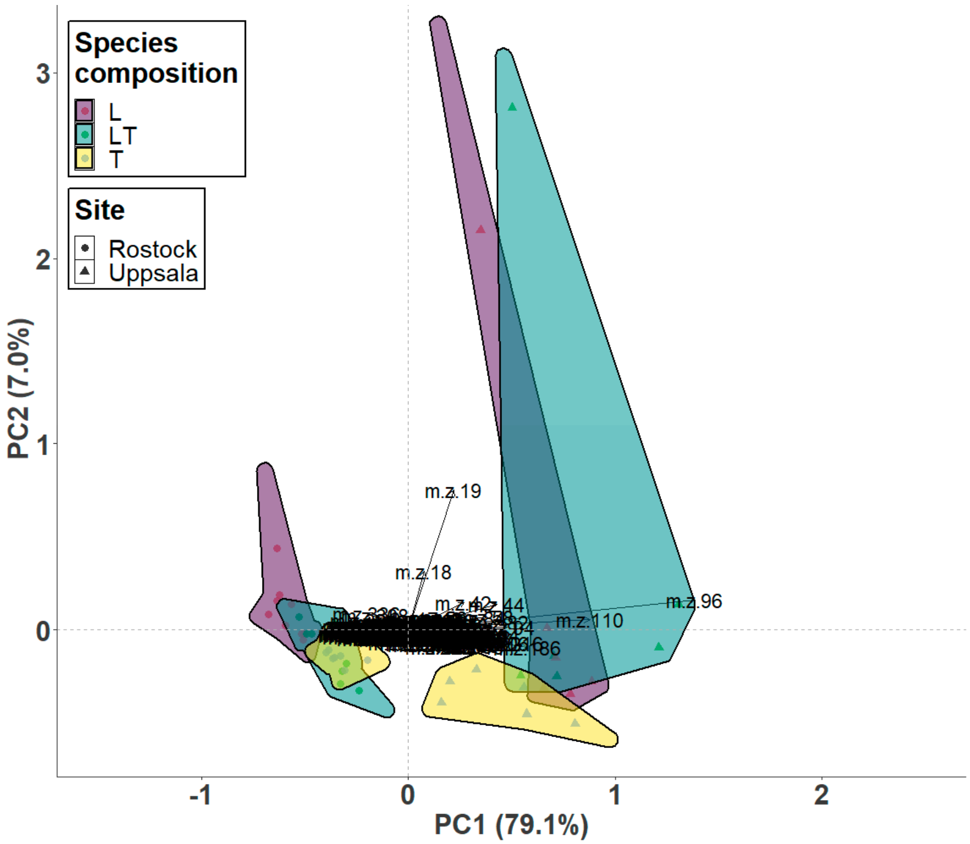

Figure S3. Principal component analysis (PCA) using Py-FI marker signals (*m*/*z*) instead of compound classes.

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DOCTORAL THESIS NO. 2025:41

Mixed-species forestry is emerging as a promising alternative to monocultures and this thesis examines the large-scale effects of tree species mixing on forest productivity and carbon sequestration. Although outcomes vary, greater species diversity generally enhances both, with certain environments and combinations of functionally distinct species proving particularly beneficial. These findings support the use of tree species mixtures as a robust and adaptable management option in the face of a changing climate.

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ISSN 1652-6880
ISBN (print version) 978-91-8046-476-5
ISBN (electronic version) 978-91-8046-526-7