

Does alley-cropping benefit soil biodiversity and nutrient cycling functions in temperate agroecosystems?

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Abstract

Temperate alley-cropping is anticipated to enhance soil biodiversity, nutrient-use efficiency, and carbon sequestration on croplands. However, alley-cropping's effects on soil biodiversity and organic matter vary among systems and the mechanistic underpinnings remain poorly understood, impeding effective design and management. Here, alley-cropping's impacts on two processes central to soil organic matter formation and stability were examined: litter decomposition and mineral-associated organic matter formation. As soil fauna are central to carbon and nutrient cycling, yet their contributions in alley-cropping systems are largely overlooked, this thesis also assessed how faunal biodiversity and faunal-mediated litter decomposition respond to alley-cropping.

Using field- and laboratory-based approaches, soil meso- and macro-faunal biodiversity, litter decomposition, and soil organic matter stabilisation were assessed in paired alley-cropping and sole-cropping systems at five arable farms in England, United Kingdom. Measurements taken in tree rows, crop alley edges, and crop alley centres tested whether tree-row effects extended into crop alleys.

Alley-cropping increased faunal abundance, order richness, and QBS-ar scores, and tree rows supported distinct communities with more epigeous, litter-dwelling, and disturbance-sensitive taxa. Litter decomposition was also higher in tree rows and crop alley edges relative to sole-cropping, but faunal-mediated decomposition was unaffected by alley-cropping. Greater decomposition potential did not translate into more organic matter formation. Tree-row soils accumulated less mineral-associated organic matter than those from arable production zones and experienced more litter-derived C and N losses. Soil biodiversity and functioning were also strongly influenced by soil type and agronomic management.

Findings from this thesis show that alley-cropping can enhance soil faunal biodiversity and stimulate litter decomposition, both in tree rows and adjacent crop alleys. However, increased decomposition in mature or mineral-saturated systems may promote litter-derived carbon and nitrogen losses rather than formation of stable organic matter, underscoring the importance of considering system and soil properties when evaluating the long-term benefits of alley-cropping.

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If you've made it this far, hats off to you, only another 82,000 words to go (give or take)!

Author's declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references.

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Experimental chapters 3–5 presented in this thesis are intended for publication. Earlier versions of two chapters have been previously submitted for publication and are available as pre-prints. Full details are provided in Table 0. I designed the experiments, carried out the practical work, analysed the data, and produced the first draft of each paper. Co-authors were involved in project conception, advised on methodological design and data analysis, and commented on initial and subsequent drafts. NB contributed substantially to litter analyses in Chapter 4.

Table 0: Details of scientific articles associated with experimental chapters 3–5.

Chapter	Paper title	Intended Journal	Status	Co-authors	Pre-print
3	Tree rows alter the biodiversity and biological quality of soil fauna in temperate alley-cropping systems	Soil Use and Management	In review	Mark E. Hodson ¹ ; Roy Neilson ² ; Alexa Varah ³	Evans et al. 2025b
4	Alley-cropping and endogean soil fauna promote litter decomposition in temperate agroecosystems	Pedobiologia	In review	Alexa Varah; Roy Neilson; Navneet Basran ⁴ ; Mark E. Hodson	Evans et al., 2025a
5	Tree rows reduce mineral-associated organic matter formation from applied litter in temperate alley-cropping systems	Plant and Soil	Ready to submit	Mark E. Hodson; Alexa Varah; Eric Paterson ⁵ ; Roy Neilson	

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Author contributions

Beth Evans was responsible for conceptual development of the thesis, funding and resource acquisition, project administration, methodological development, investigation and data curation, validation, visualisation, and writing and editing of all original and subsequent versions of individual manuscripts and the thesis. As PhD supervisors, Alexa Varah, Mark E. Hodson, and Roy Neilson contributed to project conceptualisation, funding and resource acquisition, methodological development, project administration, supervision, and review of original and subsequent drafts of individual chapters and the thesis. Navneet Basran contributed heavily to data curation and investigation of the original research article presented in Chapter 4. Eric Paterson contributed to methodological development, resource acquisition, and review and editing of the original research article presented in Chapter 5.

Table of acronyms

Acronym	Description
AC	Alley-cropping, the practice of growing crops between parallel tree rows
AICc	Corrected Akaike Information Criterion
Al	Soil exchangeable Aluminium concentration (mg kg ⁻¹)
AMF	Arbuscular mycorrhizal fungi
BAM	Basidiomycete fungi
BD	Soil bulk density (g cm ⁻³)
C	Carbon
Ca	Soil exchangeable Calcium concentration (mg kg ⁻¹ , unless otherwise specified)
CEC	Soil cation exchange capacity (meq 100 g ⁻¹)
CN	Soil carbon-to-nitrogen ratio
Crop _{div}	Temporal crop diversity, the number of major crops grown from 2021–2024
db-RDA	Distance-based redundancy analysis
DOM	Dissolved organic matter
EA-IRMS	Elemental analysis-isotope ratio mass spectrometry
EMI	Ecomorphological index, as defined by the QBS-ar index
Fe	Soil exchangeable iron concentration (mg kg ⁻¹)
f-POM	Fine particulate organic matter (53–250 µm)
ICP-OES	Inductively coupled plasma optical emission spectrometry
K	Soil exchangeable potassium concentration (mg kg ⁻¹ , unless otherwise specified)
LM	Linear model
LMM	Linear mixed-effects model
LOGO-CV	Leave one group out cross validation
Manage	Agronomic management style, conventional or organic
MAOM	Mineral-associated organic matter (< 53 µm)
MC _{avg}	Average soil moisture content across all sampling periods (g 100 g ⁻¹)
MC _{low}	Lowest soil moisture content measured across all sampling periods (g 100 g ⁻¹)
MC _{high}	Highest soil moisture content measured across all sampling periods (g 100 g ⁻¹)
MC _{range}	Difference between MC _{low} and MC _{high} (g 100g ⁻¹)
Mg	Soil exchangeable magnesium concentration (mg kg ⁻¹ , unless otherwise specified)
Mn	Soil exchangeable manganese concentration (mg kg ⁻¹)
N	Nitrogen
Na	Soil exchangeable sodium concentration (mg kg ⁻¹)
o-POM	Occluded particulate organic matter, protected inside soil aggregates
P	Phosphorus
PCoA	Principal coordinates analysis
PERMANOVA	Permutational multivariate analysis of variance, a non-parametric multivariate statistical permutation test
POM	Particulate organic matter (> 53 µm)
SBQ	Soil biological quality, as determined via the QBS-ar Index
SC	Sole-cropping, the practice of growing crops without integrated semi-natural features such as tree rows
SIMPER	Similarity percentages, a statistical method which identifies which taxa or variables contribute most to community dissimilarities
SOC	Soil organic carbon
SOM	Soil organic matter (g 100 g ⁻¹ , when presenting experimental results)
TC	Soil total carbon content (g kg ⁻¹)
Temp	Soil temperature at 10 cm depth.
Temp _{avg}	Average soil temperature measured across all sampling periods (°C)
Temp _{low}	Lowest soil temperature measured across all sampling periods (°C)
Temp _{high}	Highest soil temperature measured across all sampling periods (°C)
Temp _{range}	Difference between temp _{low} and temp _{high} (°C)
TN	Soil total nitrogen content (g kg ⁻¹)
UVS	Understory vegetation strip, the strip of perennial vegetation below tree rows
WEOM	Water-extractable organic matter, a water-soluble fraction of soil organic matter

1 Introduction

1.1 Background

1.1.1 Soil degradation in the European Union and United Kingdom

Soils are the largest terrestrial reservoir of C (Lal, 2018), a major store of N (Almaraz et al., 2025), and host to a substantial proportion of global biodiversity (Anthony et al., 2023). As such, they are central to European (EU-27 + UK) strategies addressing climate change, nutrient pollution, and biodiversity loss (Luna Juncal et al., 2023; Panagos et al., 2022, 2025). For example, the EU intends to harness an additional topsoil C sequestration potential of 150–350 Mt CO₂ year⁻¹ to balance residual emissions of 500–600 Mt CO₂-eq year⁻¹ and offset the declining European forest biomass sink (Bellassen et al., 2022). More broadly, improving soil health has been positioned as a cross-cutting enabler of climate action, biodiversity conservation, water quality enhancement, food and nutritional security, and rural economic resilience (Department for Environment, Food, and Rural Affairs, 2025; Panagos et al., 2022).

Increasing soil organic matter (SOM) is fundamental to achieving multifunctionality (van Rijssel et al., 2025) and realising the full potential of soils to address global challenges (Environment Agency, 2019; Panagos et al., 2024). Yet widespread soil degradation, estimated to cost €40.9–72.7 billion year⁻¹ (Panagos et al., 2025), continues to drive SOM losses (Panagos et al., 2024), contributing to average declines in soil C of 0.04–0.4 t ha⁻¹ yr⁻¹ (Bellassen et al., 2022; De Rosa et al., 2024) and exacerbating N surpluses (Batool et al., 2022; Eastman et al., 2023). In response, the EU aims to have all soils in a healthy condition by 2025 (Directive (EU) 2025/2360) and England has committed to bringing 60% of agricultural soils into sustainable management by 2030 (Department for Environment, Food and Rural Affairs, 2025a). The UK is also a signatory to the ‘4 per 1000’ initiative, pledging to increase C stocks in agricultural, grassland, and forest soils by 0.4 % annually.

Intensively managed cropland soils are particularly vulnerable to SOM losses (De Rosa et al., 2024) because they receive limited organic inputs and experience frequent disturbance which disrupts aggregates (Edlinger et al., 2023; Li et al., 2023), increases aeration and SOM decomposition (Erickson, 1982), and impacts the soil biodiversity underpinning C and N cycling (de Graaff et al., 2019; de Vries et al., 2013; Tsiafouli et al., 2015). These processes suppress SOM accumulation and diminish long-term C and N storage (Fließbach et al., 2007; Grandy and Robertson, 2007). Given that croplands cover 26% of the UK’s land area (Department for Environment, Food and Rural Affairs, 2025b) and hold 21% of Europe’s soil

C (Andrés et al., 2022), transitioning to agronomic systems that protect and enhance SOM by reducing disturbance, supporting diverse and continuous organic inputs to soils (Li et al., 2023; Ortega et al., 2024; Wood and Bradford, 2018), reducing reliance on mineral fertilisers (Demay et al., 2023), and promoting soil biodiversity (Banerjee et al., 2016) are essential for sustaining soil biodiversity and multifunctionality. For example, cropland soil organic carbon (SOC) stocks in Great Britain increased by $0.17 \text{ t ha}^{-1} \text{ year}^{-1}$ between 2019–22 and were speculated to be driven by reductions in conventional tillage and straw removal (Bentley et al., 2025). Agricultural management strategies to increase the size and persistence of SOM stocks on European croplands which are also multifunctional can additionally support long-term food and nutritional security, facilitate rural development, and improve the natural environment.

Europe has responded to this clear need for a new agricultural paradigm by initiating a transition towards more sustainable forms of farming. Facilitated by policies such as the European Green Deal and Farm to Fork Strategy, this transition aims to create food systems which are “fair, healthy, and environmentally friendly” (COM(2020) 381) by rewarding farmers for practices which reduce emissions, protect natural resources, and improve soil health. The UK is undergoing a similar agricultural transition, shifting away from land-based subsidies to a model of public money for public goods. England, specifically, has introduced policies which compensate farmers for sustainable farming practices, wildlife habitat creation and protection, and in some cases wider landscape restoration (Department for Environment, Food & Rural Affairs, 2025a). Of critical importance to the UK’s agricultural transition are multifunctional systems which balance food production with environmental improvements, climate change resilience, and economic security. Alley-cropping agroforestry represents one such promising approach.

1.1.2 Agroforestry’s role in Europe’s agricultural transitions

Agroforestry is a traditional multifunctional land management practice which was widespread in the Europe, including the UK, prior to the industrialisation of agriculture (Mosquera-Losada et al., 2012; Smith, 2010). Trees and shrubs were incorporated into landscapes to provide diverse benefits from crop production and windbreaks to field demarcation and shade for livestock (Smith, 2010). However, removal of trees from farmland was encouraged by neoliberal agricultural policies in the 19th and 20th centuries to pave the way for agricultural mechanisation and efficiency, leading to the simplified agricultural landscapes we see in many areas of Europe today (Smith, 2010). Now, agroforestry accounts for only ~3.3% of the UK’s total agricultural area and < 10 % of the EU’s utilised agricultural area (den Herder et al., 2017).

Today, agroforestry systems are again widely regarded as multifunctional land use systems, but through a modern lens: in addition to supporting diversified food production, agroforestry systems are considered able to simultaneously address major environmental challenges such as biodiversity loss (Kletty et al., 2023), climate change (Mosquera-Losada et al., 2018) and soil nutrient imbalances (Raj et al., 2024; Schmidt et al., 2021). Agroforestry's potential as a cornerstone nature-based solution has been increasingly recognised in EU and UK policy spanning soils, biodiversity, climate change, and agriculture and food security (Mosquera-Losada et al., 2023; Olave et al., 2025). For example, the EU Soil Strategy for 2030 states that agroforestry provides “many benefits for soil health and climate adaptation” (COM/2021/699 final), while England's Environmental Improvement Plan 2025 has committed to increase the area of both silvoarable and silvopastoral agroforestry systems (Department for Environment, Food and Rural Affairs, 2025a).

Several regions of Europe have been identified as hotspots for agroforestry establishment, including several target areas in the UK (Landaverde et al., 2025). Areas of the UK which have a high concentration of mechanised arable agriculture, such as the East of England and Midlands, may particularly benefit from alley-cropping due to the vulnerability of croplands to soil erosion and organic matter losses (Graves et al., 2015). Cropland soils in the East of England and Midlands are also at an elevated risk from climate change adverse effects such as flooding, heatwaves, and droughts (Arnell et al., 2021) which reduce soil biodiversity and exacerbate organic matter losses (Abebaw and Feleke, 2026; Leal Filho et al., 2023). These issues are likely to be further compounded by loss of soil biodiversity and biological functions across most of England (Orgiazzi et al., 2016), which are essential to maintaining soil structure and nutrient cycles (Briones, 2018). Consequently, the potential for alley-cropping to yield positive outcomes for farmers, food systems, and the environment in these regions is high, explaining why the East of England has been identified as a target area for agroforestry in the Land Use Framework for England (Department for Environment, Food & Rural Affairs, 2026).

Despite its potential, uptake of agroforestry, and particularly silvoarable systems, across Europe remains low. From 2012–2022, the area of silvoarable agroforestry in the EU-27 declined by 53.6% (Rubio-Delgado et al., 2025). In England, public support for agroforestry is strong (Felton et al., 2023; Tindale et al., 2025) and farmers report a broad awareness of associated benefits (Felton et al., 2023). Additionally, several mature alley-cropping systems are established in the East of England and Midlands (Figure 1.1), providing essential opportunities for peer-to-peer learning and knowledge exchange to accelerate adoption (Hood

et al., 2025). Still, willingness from farmers in east and south-eastern England to establish new systems within the next five years is limited due to perceived financial risks and concerns around agroforestry's compatibility with existing farm operations represent key barriers to adoption (Felton et al., 2023).



Figure 1.1. Two example alley-cropping systems at farm S2.

Alley-cropping, a modern form of agroforestry characterised by the production of crops and/or livestock between parallel rows of trees, may be uniquely positioned to benefit farmers in the intensive farming landscapes of western Europe due to its compatibility with mechanised systems, flexibility in design, and relatively low input requirements (Quinkenstein et al., 2009; Wolz et al., 2018b). The close integration of trees with crops in alley-cropping systems can improve land-use efficiency compared to other agricultural systems whilst maximising benefits to crops (e.g., climate buffering, improved nutrient cycling, drought resilience) and the environment (e.g., biodiversity gains, reduced soil erosion, SOM accumulation) (Wolz et al., 2018b). However, there remain significant knowledge gaps regarding the impact of alley-cropping on ecosystem services and aspects of human well-being (Castle et al., 2022), thus limiting the availability of information to support alley-cropping policy or establishment in promising regions both in England and more broadly.

1.1.3 Soil biodiversity and organic matter in temperate alley-cropping systems

Evidence from temperate regions shows a generally positive, though inconsistent, influence of alley-cropping on soil biodiversity (Kletty et al., 2023; Marsden et al., 2020; Beule et al., 2022b, 2025). Effects on SOC are similarly heterogeneous. Ivezić et al. (2022) reported that temperate alley-cropping can alter SOC by a factor of 0.5–1.7 (median ≈ 1.0), consistent with estimated C sequestration rates of $0.36 \pm 1.05 \text{ t C ha}^{-1} \text{ year}^{-1}$ for the 0–40 cm soil layer (Mayer et al., 2022). As such, alley-cropping can reduce as well as increase SOC even many years after establishment, due to enhanced SOM decomposition (Ivezić et al., 2022). Furthermore, under

projected future climate scenarios, alley-cropping is predicted to reduce, but not prevent, SOC losses at 0–23 cm depth (Giannitsopoulos et al., 2025). Increases in concentrations of N, P, K, Ca, and Mg have also been observed in alley-cropping compared to sole-cropping systems, especially in surface horizons (Beuschel et al., 2020; D’Hervilly et al., 2021; Guillot et al., 2019, 2021; Pardon et al., 2017), and in some cases within as little as four years of establishment (Clivot et al., 2020). Again, outcomes vary, with a negligible (Lu et al., 2015) or negative influence of alley-cropping on soil nutrients detected in some studies (Andrianarisoa et al., 2016).

Uncertainty remains regarding the mechanisms underpinning observed changes in soil biodiversity and SOM (e.g., decomposition of litter and SOM, rhizodeposition, nutrient pumping, SOM stabilisation) and the circumstances under which alley-cropping results in SOM losses. Further investigation of organic matter dynamics within temperate alley-cropping systems is needed to clarify how tree rows influence SOM formation, turnover, and nutrient retention under current and future climate scenarios. Such insights are crucial for assessing alley-cropping’s potential role in biodiversity conservation and efforts to achieve C neutrality, adapt to climate change, and stay within critical environmental thresholds (Fontaine et al., 2024; Schulte-Uebbing et al., 2022), as well as to optimise alley-cropping systems to achieve these goals. Furthermore, given the context-dependent nature of alley-cropping outcomes, region-specific studies are needed across the EU-27 and UK to inform evidence-based policy development and decision-making. This thesis therefore aimed to evaluate, under UK conditions, alley-cropping’s potential to enhance soil biodiversity in croplands and influence two key processes involved in SOM accumulation and persistence: litter decomposition and SOM stabilisation.

1.2 Thesis outline

This PhD thesis consists of six chapters, including three experimental chapters (Chapters 3–5). The contents of each chapter are described briefly below, excluding this introductory chapter. Detailed hypotheses for each experiment are given within the relevant chapters.

Chapter 2 is a literature review contextualising the thesis, providing an overview of alley-cropping’s effects on litter decomposition and SOM dynamics. This chapter first summarises the fundamental and complex role that soil organisms play in litter decomposition and SOM dynamics. The chapter then synthesises current knowledge on the effects of temperate alley-cropping on soil biodiversity, litter decomposition, SOM mineralisation, and organic matter

stabilisation by mineral association or occlusion within soil aggregates. Finally, this chapter highlights limitations and knowledge gaps pertaining to our current understanding of soil biodiversity and decomposition within temperate alley-cropping systems, outlining four key questions that this thesis aims to address.

Chapter 3 describes an assessment of soil biodiversity and biological quality carried out at five commercial alley-cropping systems in Nottinghamshire, Cambridgeshire, and Suffolk. Soil meso- and macro-fauna were taken from paired alley-cropping and sole-cropping fields at three distances (0, 3, and 13 m) along linear transects running perpendicular to tree rows. This allowed sampling of the tree row, crop alley edge, and crop alley centre. This set-up was mimicked in sole-cropping systems. Sampling was undertaken in Spring 2023, Autumn 2023, and Spring 2024. In the laboratory, larger specimens were removed from samples by hand and preserved in 80 % industrial methylated spirit before extraction of meso-fauna using Berlese Tullgren funnels. Soil fauna were identified to taxonomic orders and a biological quality score was generated for each sampling point following the QBS-ar Index. Soil samples taken in Autumn 2023 were analysed for texture, bulk density, pH, organic matter content, total C, total N, cation exchange capacity, and concentrations of exchangeable Al, Ca, Fe, K, Mg, Mn, and Na. At each sampling event, soil temperature was measured in the field and moisture content was calculated in the laboratory. Environmental variables, meso- and macro-faunal biodiversity (abundance, taxonomic richness, and composition), and soil biological quality were compared between alley-cropping and sole-cropping systems, as well as between transect positions within both agricultural systems. Farm-specific responses of soil faunal biodiversity to alley-cropping were also investigated.

Chapter 4 investigates the effects of alley-cropping on litter decomposition rates and the contribution of soil meso- and macro-fauna to litter decomposition. In Autumn 2023, following the experimental design outlined in Chapter 3, litter bags containing *Phleum pratense* shoot material were buried at 10 cm depth for 16 weeks, after which ash-free mass loss was calculated. At each sampling point, two litter bags were buried: one which permitted access only to soil microorganisms and one which also permitted access to soil meso- and macro-fauna via 1 cm holes. Ash-free mass loss between bags with and without holes was compared to determine the contribution of soil meso- and macro-fauna to litter decomposition. Litter decomposition and soil meso- and macro-faunal decomposition activity were compared between alley-cropping and sole-cropping systems and transect positions within agricultural systems. The influence of soil physicochemical variables on litter decomposition, and farm-

specific responses to alley-cropping, were also investigated. The contamination of litter bags with mineral soils and pre-existing soil organic matter is detailed in Appendix A.

Chapter 5 investigates the impact of alley-cropping on SOM formation and persistence through a controlled laboratory experiment. This chapter adopts the simple and widely accepted contextualisation of SOM as two functionally distinct fractions with different persistence times in soil: particulate organic matter (POM; > 53 μm , shorter residence times) and mineral-associated organic matter (MAOM; < 53 μm , stable SOM). In Spring 2024, samples were taken from paired alley-cropping and sole-cropping systems following the experimental design described in Chapter 3. Dual-labelled (^{13}C = 3.82 atom%, ^{15}N = 4.14 atom%) *Lolium perenne* shoot material was added to soil samples and incubated for 28 days in controlled conditions. Following this, samples were separated into POM and MAOM using particle size fractionation. The enrichment of fractions with litter-derived ^{13}C and ^{15}N was determined via elemental analysis-isotope ratio mass spectrometry. Litter decomposition and MAOM formation were compared between alley-cropping and sole-cropping systems and transect positions within agricultural systems. As for Chapters 3 and 4, the influence of soil physicochemical properties on SOM dynamics and farm-specific responses to alley-cropping were investigated.

Chapter 6 concludes by summarising the key findings of each experimental chapter and examining how they have answered the research questions posed at the end of Chapter 2. This chapter also explores the relationships present between soil biodiversity and nutrient cycling functions measured over the experimental chapters, addresses the limitations of the work performed, and provides suggestions for future research undertaken in temperate alley-cropping systems.

A conceptual diagram (Figure 1.2) demonstrates how each chapter relates to the research questions posed in Chapter 2, as well as to each other.

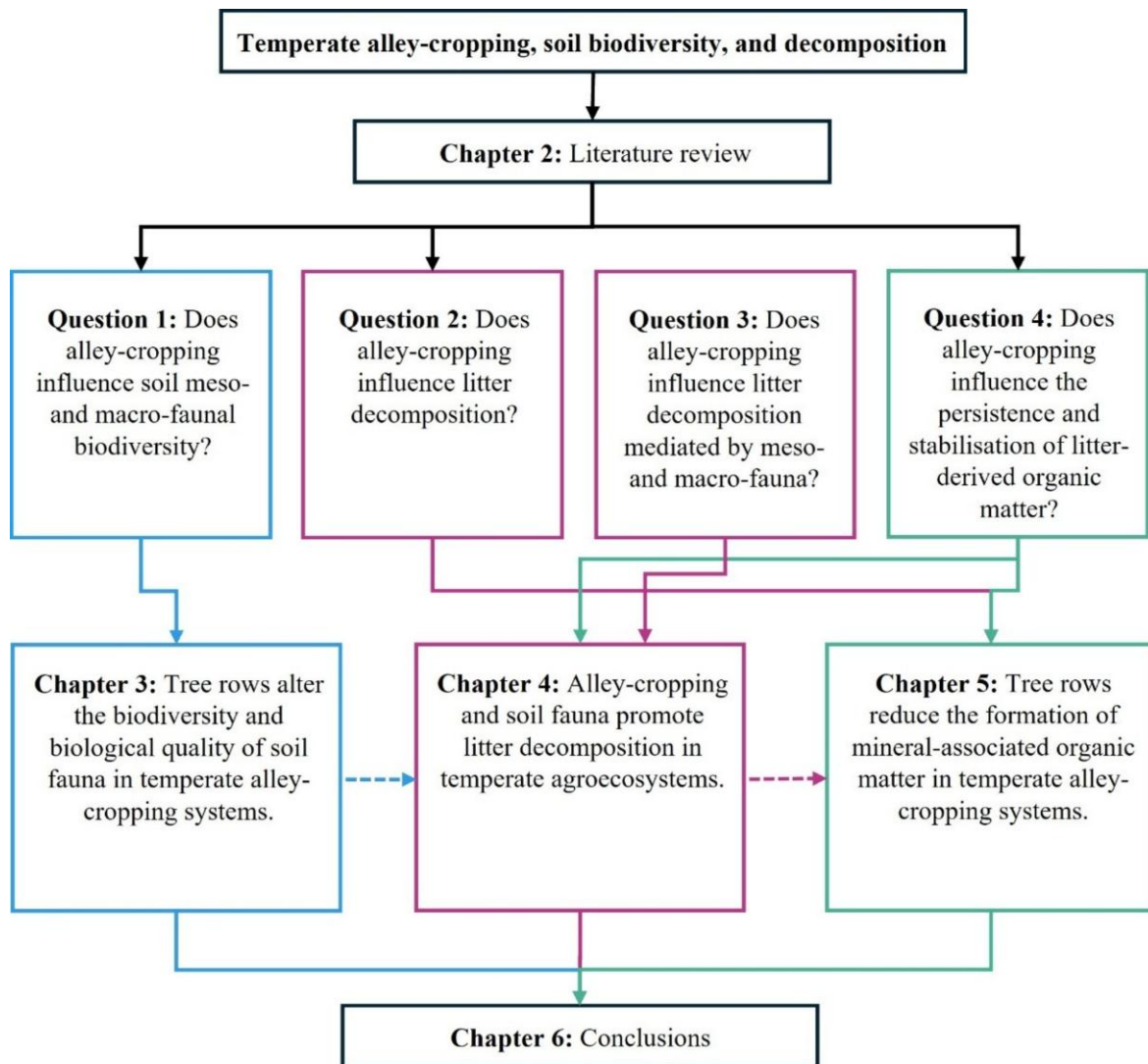


Figure 1.2. A conceptual diagram demonstrating how each thesis chapter addresses the research questions posed at the end of Chapter 2, as well as how they connect to each other. Chapter titles provide a brief summary of their key findings. Dashed lines indicate that data from one chapter was included in additional analyses at the end of another.

2 Alley-cropping, soil biodiversity, and decomposition: A literature review

2.1 Scope of the review

This review examines current knowledge on the effects of temperate alley-cropping on soil biodiversity and organic matter decomposition. In ecology, decomposition is commonly defined as the transformation of complex dead organic material to simpler organic and inorganic forms (Findlay, 2021), yet conceptual boundaries vary across the literature. In some studies, decomposition is assessed primarily through loss of litter mass or litter-derived C and N (e.g., Contos et al., 2024; Wachendorf et al., 2020). For clarity, this review adopts a process-based perspective, considering organic matter transformation from the macromolecular to the molecular scale. Specifically, it evaluates the influence of alley-cropping on litter decomposition, SOM mineralisation and immobilisation, and accumulation of SOM within persistent pools.

Given the central role of soil biota in regulating decomposition processes (de Graaff et al., 2015; Handa et al., 2014), this review first synthesises evidence on how soil organisms contribute to litter breakdown, SOM mineralisation, and organic matter stabilisation. It then explores the theoretical mechanisms by which alley-cropping may influence soil microbial and faunal communities and the previously outlined decomposition processes, whilst evaluating empirical evidence from temperate alley-cropping systems. In doing so, this review establishes the foundation for the wider thesis, which provides an in-depth assessment of how alley-cropping influences soil meso- and macro-faunal biodiversity, litter decomposition, and litter-derived SOM stabilisation in UK conditions.

2.2 Soil biota and decomposition

Decomposition is regulated by complex interactions between diverse soil biota and their biotic and abiotic environment (Nielsen et al., 2011, Paul, 2016). Soil microbes are the primary agents of decomposition (Bardgett and van der Putten, 2014), secreting extracellular enzymes which break down complex organic molecules into simpler compounds or inorganic nutrients. Although quantification of their contributions to decomposition has proved challenging due to rapid microbial succession during decomposition and a scarcity of experiments addressing the full range of decay stages (Maillard et al., 2024), they are estimated to be responsible for up to 90 % of litter decomposition (Swift et al., 1979) and their community structure affects the decay mode of litter (Khan et al., 2025; Whalen et al., 2024). The presence of soil microbes can also

substantially increase plant acquisition of nutrients from SOM (Hestrin et al., 2019), highlighting their role in SOM decomposition.

Soil fauna contribute substantially to litter decomposition in temperate regions, increasing mass loss by 8.4–21 % in forests (Burtis et al., 2024; García-Palacios et al., 2013; Lin et al., 2019) and substantially increasing litter decomposition rates in agroecosystems (Cassani et al., 2021; Castro-Huerta et al., 2015; Chassain et al., 2021). Soil fauna directly contribute to litter decomposition by fragmenting and consuming organic matter. In temperate regions, faunal litter-feeders are estimated to consume 100 % and 79 % of annual litter inputs to soils to grasslands and forests, respectively (Heděnc et al., 2022), incorporating a small proportion (5–50 %) into their biomass (Frouz, 2018). Comminution by soil fauna increases the decomposability of organic matter for soil microorganisms by increasing surface area, releasing cell contents, and preconditioning in the gut (Frouz, 2018). Leaching from litter can also increase during faunal processing, enhancing the spatial accessibility of litter-derived organic matter for microorganisms.

Soil fauna also indirectly influence litter and SOM decomposition by creating spatial and temporal “hot spots/moments” of microbial activity (Kuzyakov and Blagodatskaya, 2015) by releasing carbon-rich compounds from organic matter or microbial biomass (Angst et al., 2024; Frouz, 2018). Furthermore, grazing by soil fauna can alter density-dependent microbial decomposition functions (Peng et al., 2022a), activate microbes during gut passage (Briones, 2018), and inoculate organic matter (Filser et al., 2016; Grandy et al., 2016), facilitating microbial decomposition (Gesisen et al., 2021). Soil fauna can additionally modify soil structure to maintain favourable conditions (e.g., moisture content, oxygen availability) for microbial decomposition, as well as translocate organic matter where it is accessible to endogean organisms (Briones, 2018; Frouz, 2018). The contribution of soil fauna to litter decomposition tends to decline with increasing experiment duration (Chassain et al., 2021; Garcia-Palacios et al., 2023; Li et al., 2024b), highlighting their importance in stimulating early-stage decomposition of fresh litter through fragmentation, microbial activation, and consumption of labile compounds. However, the impact of soil fauna on litter decomposition is context-dependent (Burtis et al., 2024), with some studies reporting a negative effect (Kampichler and Bruckner, 2009; Njoroge), potentially due to suppression of microbial activity (Bradford et al., 2002; Kampichler and Bruckner, 2009).

The complementary activities of diverse soil organisms means that soil biodiversity plays a central role in organic matter decomposition (Nielsen et al., 2011, Paul, 2016). Increases in

microbial and faunal diversity consistently enhance litter breakdown (Peng et al., 2022a, 2023), while biodiversity losses reduce decomposition and respiration (de Graaff et al., 2015) and make ecosystem functions such as litter decomposition more sensitive to environmental stress (Beaumelle et al., 2020). Globally, declines in functional diversity of soil microbes and fauna slow carbon and nitrogen cycling (Handa et al., 2014), with microbes and fauna being more closely related to plant tissues decomposition and C respiration, respectively (de Graaff et al., 2015). Furthermore, the composition and metabolic activity of soil biota determine the proportion of SOM which is respired or incorporated into stable SOM fractions (e.g., MAOM) (Paul, 2016).

While evidence shows that soil biota enhance the decomposition of litter and SOM, they are also key agents in SOM stabilisation. Faunal processing can reduce the decomposability of organic matter by changing its chemistry and structure, enriching it with lignin or forming insoluble phenol-protein complexes that resist microbial degradation (Frouz, 2018). Faunal consumption can additionally restrict microbial access to organic matter, either by creating anoxic soil environments or via aggregate formation during gut passage (Frouz, 2018). Similarly, decomposers, such as arbuscular mycorrhizal (AMF) fungi and filamentous bacteria, can enhance aggregate formation and occlusion of SOM (de Goede et al., 2025; Helfrich et al., 2015). Movement of litter to mineral soils via processes such as bioturbation can further slow decomposition due to reduced soil temperature variability and oxygen availability, and thus microbial activity (Kirschbaum et al., 2021). Perhaps most importantly, microbial enzymes catalyze key reactions involved in humus and stable SOM formation (Paul, 2016) and microbial turnover itself forms a key pathway for the formation of stable SOM (Cotrufo et al., 2015). Soil fauna may accelerate SOM stabilisation by creating microhabitats which facilitate the increase, and subsequent die-off, of microbial biomass, or themselves releasing ingested microbial necromass (Frouz et al., 2003), in areas with a high proportion of mineral particles (Angst et al., 2024).

Overall, decomposition appears to be regulated by the complex interactions between diverse soil biota and their biotic and abiotic environment. However, the influence of soil biota on organic matter decomposition varies widely, as does the relative contribution of different groups. Microbial and faunal decomposition are shaped by several factors working at multiple spatial scales, including climate (Garcia-Palacios et al., 2013; Wall et al., 2008), vegetation composition (Peng et al., 2022a; Zhang et al., 2024), litter quality and palatability (Canessa et al., 2021; Córdova et al., 2018), and soil properties such as temperature, moisture content, pH,

C:N ratio, and N availability (Peng et al., 2022a; Raza et al., 2023; Simpson et al., 2012). Therefore, organic matter decomposition dynamics on arable land are likely to be substantially altered by the introduction of tree rows, due to changes in organic matter inputs, soil biodiversity, and microclimatic conditions.

2.3 Alley-cropping and soil biodiversity

The introduction of tree rows into temperate arable landscapes can substantially alter soil biodiversity (Kletty et al., 2023). Tree rows and understory vegetation strips (UVS) increase above-ground plant diversity in arable systems (Boinot et al., 2019a), thereby enhancing the quality and diversity of above- and below-ground resources accessible for soil organisms and expanding the range of available soil micro-habitats (Cardinael et al., 2018, 2019; Swieter et al., 2022; Pardon et al., 2017). The inherent spatial and temporal complexity of alley-cropping creates a heterogeneous mosaic of resources and niches that favour the diversification and coexistence of soil organisms (Boinot et al., 2019b; Korboulewsky et al., 2016), enhancing functional diversity (Santos et al., 2022).

Tree rows typically experience less disturbance (e.g., tillage, application of agrochemicals) than cropped areas, providing permanent breeding, nesting, and overwintering habitat for soil fauna (Cardinael et al., 2019; Pardon et al., 2019), and acting as a refuge for disturbance-sensitive taxa (Boinot et al., 2019b). By physically stabilising soils (Zhu et al., 2020) and modifying microclimatic conditions (Jacobs et al., 2022), tree rows can buffer soils and their inhabitants against climatic extremes (e.g., drought, temperature fluctuations) (de Vries et al., 2012) and physical degradation (e.g., erosion, flooding) (Judson et al., 2025; Torralba et al., 2016). More favourable soil conditions may in turn facilitate movement, feeding, and reproduction (Guillot et al., 2019; Udawatta et al., 2014).

The extensive root and canopy systems of trees can introduce spatial gradients in vegetation composition (Oelbermann et al., 2006; Swieter et al., 2022), microclimatic conditions (Jacobs et al., 2022; Sutterlütti et al., 2023), and resource availability (Dulac et al., 2025; Guillot et al., 2021; Pardon et al., 2017) over alley-cropping fields. Consequently, the benefits of alley-cropping for soil biodiversity may spill over into neighbouring crop alleys.

2.3.1 Soil microorganisms

Extensive research has investigated how temperate alley-cropping influences soil microbial communities in arable systems (Kletty et al., 2023). Two recent comprehensive reviews synthesise more than 20 years of research on this topic (Beule et al., 2022b, 2025). Their key

conclusions were: (i) tree rows typically increase microbial biomass and both taxonomic and functional diversity compared to the arable areas (Beuschel et al., 2019; Beule et al., 2020; Guillot et al., 2021), and increases can occur in subsoils as well as topsoils (Beule et al., 2022a); (ii) microbial taxa exhibit differential responses to alley-cropping, often resulting in compositional shifts which favour soil fungi and Gram(-) bacteria (Beule et al., 2022b); (iii) changes to microbial communities are commonly confined to tree rows (Beuschel et al., 2019), but spatial gradients extending into the crop alley have been reported in some systems (Luo et al., 2022); (iv) responses vary across systems and studies due to differing sampling approaches and factors such as system maturity, plant species composition, management; and (v) outcomes depend strongly on the method to assess microbial communities. Despite these trends, some studies have reported a negligible (Bardhan et al., 2013; Furze et al., 2017) or negative (Bainard et al., 2011; Sun et al., 2018) effect of alley-cropping on soil microbial communities.

Recent studies in Germany provide further support for the findings of the reviews by Beule et al. (2022b, 2025). Alley-cropping systems exhibited greater bacterial and fungal abundance and higher microbial biomass C compared to sole-cropping systems (Giray et al., 2025; Vaupel et al., 2023; Veldkamp et al., 2023), and in some cases the crop alley (Vaupel et al., 2023), whereas microbial biomass N showed the opposite trend (Veldkamp et al., 2023). Phospholipid fatty acid analysis showed increased fungal biomarkers and decreased bacterial biomarkers under tree rows compared with crop alleys, representing a shift in community composition towards fungi (Giray et al., 2024). Tree rows were particularly beneficial for Basidiomycete fungi, whereas AMF demonstrated a decline in tree rows compared to crop alleys at most sites (Giray et al., 2024). Tree rows also demonstrated a unique composition of soil fungi, whereas communities in crop alleys and sole-cropping systems overlapped substantially (Vaupel et al., 2023). Significant differences in soil microbial communities between tree rows and the crop alley reduced the spatial homogeneity of soil microbial communities relative to sole-cropping (Vaupel et al., 2025), but few studies reported a strong gradient in soil microbial biodiversity in relation to tree rows. However, Giray et al. (2024) identified a small but significant decline in the ratio of gram(-):Firmicutes at Dornburg and Forst with increasing distance from the tree row, a pattern which could not be explained by available data (Giray et al., 2024).

Recent investigations of soil microbial communities within temperate alley-cropping systems have largely substantiated findings from previous research demonstrating the capacity for tree rows to increase microbial abundance and diversity, as well as introduce compositional changes which favour soil fungi. However, strong site effects on the influence of alley-cropping were

reported in many studies (Beule et al., 2025; Giray et al., 2024), which are likely attributable to differences in local pedo-climatic conditions, alley-cropping system configurations, and management practices. For example, Sun et al. (2018) observed that the response of microbial biomass to poplar tree rows was dependent on whether alley-cropping was combined with organic agriculture. Bainard et al. (2011) reported that alley-cropping with conifer spruce reduced AMF diversity compared to sole-cropping, whereas this was not the case for other tree species. Furthermore, despite the substantial research effort dedicated to microorganisms, functionally important groups such as archaea and protists have been largely neglected (Beule et al., 2025), leaving us with an incomplete understanding of how alley-cropping impacts microbial communities.

2.3.2 *Soil fauna*

In a global review, Marsden et al. (2020) reported that silvoarable agroforestry generally has a positive effect on soil faunal biodiversity compared to sole-cropping systems. Although most studies in the review considered tropical systems and did not focus exclusively on alley-cropping, their findings largely align with those from temperate alley-cropping systems (Beule et al., 2025). A comprehensive review of literature studying soil fauna in temperate cropland agroforestry also identified a predominantly positive effect of alley-cropping on soil faunal density and diversity (Beule et al., 2025). Numerous studies have reported a higher abundance or diversity of macro-invertebrates (including earthworms, slugs, beetles, woodlice, millipedes, centipedes, and arachnids) in tree rows compared to crop alleys (Boinot et al., 2019b; D'Hervilly et al., 2020, 2022; Pardon et al., 2019, 2020; Price and Gordon, 1998; Ramón et al., 2012), and sole-cropping control systems (Staton et al., 2021) or both (Cardinael et al., 2019; Griffiths et al., 1998; Matevski et al., 2024; Thevathasan and Gordon, 2004; Vaupel et al., 2023). A recent meta-analysis of soil biological health in silvo-arable systems in Western Europe also reported an increase in the abundance of earthworms and litter-feeding macrofauna in the 0–30 cm soil layer (De Clerck et al., 2025).

Marsden et al. (2020) found no consistent effect of tree rows on soil fauna in crop alleys. Among the studies listed above, only five reported significantly greater soil faunal biomass or biodiversity in crop alleys, relative either to a sole-cropping control (Cardinael et al., 2019; Griffiths et al., 1998; Matevski et al., 2024) or a distance further into the crop alley (D'Hervilly et al., 2020; Matevski et al., 2024; Vaupel et al., 2023). Where positive effects in the crop alley were reported, they typically occurred within 1.5 m of tree rows (Park et al., 1994; Vaupel et al., 2023), likely reflecting spatial gradients in tree-mediated microclimatic changes and above-

/below-ground biomass inputs (Jacobs et al., 2022; Swieter et al., 2022). Still, gradual declines in earthworm (D'Hervilly et al., 2022; Vaupel et al., 2023) and spider (Matevski et al., 2024) biodiversity in crop alleys has been reported, substantiating findings from boundary-planted fields which revealed that the activity density of some macro-fauna declines with distance from tree rows (Pardon et al., 2019, 2020). Furthermore, higher earthworm and spider biodiversity in the centre of the crop alley compared to sole-cropping controls (Cardinael et al., 2019; Griffiths et al., 1998; Matevski et al., 2024) demonstrates that the influence of tree rows can extend well into the cropped zone, particularly in mature systems. Together, these findings reveal that tree rows can enhance soil faunal biodiversity in the crop alley, but we are far from having a comprehensive understanding of how tree rows influence the spatial distribution of the full range of faunal taxa and functional groups on alley-cropping fields.

Soil faunal responses to alley-cropping vary markedly among taxa and functional groups. Tree rows appear to consistently benefit detritivores and disturbance-sensitive taxa (Boinot et al., 2019b; D'Hervilly et al., 2022), whereas responses of predatory arthropods are mixed (Martin-Chave et al., 2019; Pardon et al., 2019, 2020). Furthermore, several taxa, including Chilopoda, Coleoptera, Dermaptera, and Hemiptera, have exhibited negligible responses to alley-cropping (D'Hervilly et al., 2022) or were more abundant in crop alleys than in tree rows (Boinot et al., 2019b). Even within higher resolution taxa, responses to alley-cropping are divergent. Earthworms exhibit compositional shifts from anecics to endogeics between tree rows and crop alleys (D'Hervilly et al., 2020, 2021); functional groups of spiders exhibit starkly different responses to alley-cropping, with forest specialists (as opposed to open habitat specialists and generalists) experiencing the greatest benefits (Matevski et al., 2024); and species-specific responses occur in Carabid beetles (Richard et al., 2020). These heterogeneous responses reflect a high level of functional diversity within soil faunal taxa and caution against assuming uniform responses across taxa or functional groups.

To date, research has disproportionately focussed on epigeous macrofauna, whereas soil micro-fauna (e.g., nematodes, rotifers, tardigrades) and endogean arthropods, including many meso-fauna, remain severely understudied (Kletty et al., 2023). Marsden et al. (2020) similarly noted substantial bias; in their review, soil macro-fauna were considered in 7.5 times and 3.8 times more publications than soil meso- and micro-fauna, respectively. The few publications studying soil meso-fauna in temperate alley-cropping systems addressed only a subset of higher-level taxa, focussed predominantly on changes in abundance, and reported mixed responses to alley-cropping. Whereas Acari, Collembola, Pseudoscorpion (Boinot et al., 2019b) and Diplura

(Ramón et al., 2012) abundance has been reported to increase in tree rows compared to the arable crop alley, Doblas-Miranda et al. (2014) reported a significantly lower species density of oribatid mites in alley-cropping compared to sole-cropping. Two further studies, undertaken in Hungarian and Polish shelterbelt systems, found that compared to adjacent cropland, tree rows increased Acari density (Olejniczak, 2007), soil biological quality (determined using the QBS-ar index, which incorporates microarthropods) (Szigeti et al., 2022), and Collembola abundance and richness (Szigeti et al., 2022), and altered Collembola community structure (Szigeti et al., 2022). However, Olejniczak (2007) identified no clear spatial relationship for Acari or Collembola in relation to tree rows, and the density of both groups appeared to increase at 15 m compared to 0.5 m into the cultivated field.

Overall, temperate alley-cropping systems show predominantly positive effects on soil faunal density and biodiversity (Beule et al., 2025). However, the existing literature has several limitations. Due to the limited research undertaken on soil meso- and micro-fauna (Kletty et al., 2023; Marsden et al., 2020), this statement largely applies to soil macro-fauna. Extrapolating macrofaunal patterns to other size groups is poorly supported (Wu and Wang, 2019), necessitating further study of neglected groups. Even within macro-faunal studies, few have comprehensively sampled the full range of taxa present in alley-cropping systems (i.e., surface-dwelling and endogean), even at a coarse taxonomic resolution (but see Boinot et al., 2019b; D'Hervilly et al., 2022; Ramón et al., 2012). Although arguably not the intention of these studies, the consequence of this fragmented sampling, and consideration of a limited number of biodiversity indices in individual studies, is that existing work tells us more about taxon-specific rather than whole-community responses to alley-cropping. Furthermore, the studied systems are highly varied, demonstrating different tree-crop combinations, maturity levels, configurations (e.g., alley widths and orientations), management practices, land-use histories, and local pedo-climatic conditions, which moderate the influence of tree rows below-ground communities (Boinot et al., 2020; Olejniczak, 2007; Price and Gordon, 1998; Thevathasan and Gordon, 2004). Identifying generalisable patterns across studies, which also employ different methodologies (e.g., spatio-temporal sampling design), is thus challenging.

2.4 Alley-cropping and decomposition

The decomposition of plant litter is a fundamental process in carbon and nutrient cycling within temperate agroecosystems. Globally, an estimated 60 Pg C year⁻¹ is transferred to soils through decomposition (Lal, 2018), approximately 11 % of the C stored in live vegetation (Lal, 2018).

SOM formed through litter decomposition sustains belowground energy fluxes (Potapov, 2022) and is an important source of plant nutrients (Cotrufo et al., 2015).

Alley-cropping may substantially influence litter decomposition through its effects on soil microclimate, litter quality, and soil biotic communities. As discussed in Section 2.4, tree rows typically support a higher density, abundance, and diversity of soil decomposers and detritivores (Beule et al., 2022b, 2025). Where this increase in biodiversity translates to higher biological activity, it could enhance the fragmentation, mixing, and chemical breakdown of litter and its incorporation into SOM (de Graaff et al., 2015; Nielsen et al., 2011). Improved soil structure and moisture content can further facilitate decomposer activity and access to litter by increasing pore connectivity and maintaining microsites with adequate moisture and aeration (Hao et al., 2025; Negassa et al., 2015). For example, Beuschel et al. (2019) found that continuous delivery of organic material which is both more diverse and chemically complex, as well as a higher connectivity of soil pores under trees, resulted in fungal communities which were more abundant, dominated by saprotrophic and ectomycorrhizal species, and accompanied by higher enzymatic activity. Tree rows also modify soil microclimates, often increasing humidity (Jacobs et al., 2022) and soil moisture content (Judson et al., 2025) whilst stabilising soil temperatures (Quinkenstein et al., 2009; Jacobs et al., 2022). In settings where decomposition is constrained by drought stress, thermal extremes, or surface exposure, more favourable and stable microclimates can facilitate microbial and faunal activity.

In addition, fine-root turnover, rhizodeposition, and litterfall from trees rows and UVS can stimulate decomposer communities through priming mechanisms by supplying labile C or by alleviating stoichiometric limitations on decomposition through enhanced nutrient availability. Mixed litters, characteristic of systems combining trees, herbaceous vegetation, and arable crops, can increase decomposition rates relative to their constituent parts (Zhang et al., 2023). When this occurs, the more labile substrate is assumed to provide the nutrients required to break down the more recalcitrant substrate, although this effect is not consistent (Porre et al., 2020). Higher SOM and concentrations of exchangeable cations (e.g., Ca^{2+}) accumulated from organic inputs have the additional benefit of buffering soils against pH changes which can disturb decomposer communities (Rousk et al., 2009). Through these mechanisms, alley-cropping can potentially enhance the decomposition of organic matter relative to sole-cropping.

2.4.1 *Catabolic potential*

Alley-cropping tree rows can influence potential soil enzyme activities involved in microbial respiration and SOM turnover (e.g., arylsulfatase, dehydrogenase, glucosaminidase, leucine aminopeptidase, N-acetyl- β -glucosaminidase, phosphatase, protease, tyrosine-aminopeptidase) (Beule et al., 2022b). Enzyme activities are generally higher in tree rows than in crop alleys (Beuschel et al. 2019; Mungai et al. 2005; Udawatta et al. 2008, 2009; Weerasekara et al., 2016) and microbial communities in tree rows often exhibit a broader substrate-utilisation capacity (Beuschel et al., 2019; Mungai et al., 2005). However, responses vary across enzymes and depend on sampling location, depth, and timing (Beule et al., 2022a; Clivot et al., 2020; Mungai et al., 2005). For example, Beuschel et al. (2019) identified a significant increase in the activity of multiple soil enzymes in the 0–5 cm soil layer, but not in the 5–20 cm soil layer. Several studies have also reported negligible effects of alley-cropping on specific enzymes (e.g., arylsulfatase, glucosidase, N-acetyl- β -glucosaminidase, phosphatase, protease) (Clivot et al., 2020; Udawatta et al., 2008, 2009, 2014). In some cases, limited effects may reflect system immaturity (Clivot et al., 2020), whereas in others alley-cropping may simply have a limited impact on potential enzyme activity.

While increases in potential enzyme activity suggest greater catabolic potential in tree rows, substrate-induced respiration (SIR) provides evidence of active microbial processing of easily metabolised substrates. SIR assessments in temperate alley-cropping systems have typically shown higher activity in tree rows compared to crop alleys (Beuschel et al., 2019; Mettauer et al., 2022; Mungai et al., 2005) or reference sole-cropping systems (Guillot et al., 2021) across a range of substrates. Similarly, basal respiration, arising from SOM mineralisation (Creamer et al., 2014), has been reported to increase under arable alley-cropping compared to sole-cropping (Lee and Jose, 2003), and in tree rows compared to the crop alley (Mettauer et al., 2022). Where microbial communities have been quantified alongside soil respiration, increased respiration appears to reflect higher metabolic intensity rather than a functional shift in microbial catabolic profiles (Mettauer et al., 2022). Overall, the existing literature largely demonstrates an increase in catabolic potential in temperate alley-cropping relative to sole-cropping systems.

2.4.2 *Litter decomposition*

Few studies have quantified litter decomposition in temperate alley-cropping systems and their results are inconsistent. Using bait lamina to assess litter fragmentation and consumption in a Mediterranean alley-cropping system, Mettauer et al. (2022) identified similar decomposition

activity in tree rows and crop alleys. Although bait lamina underestimate microbial decomposition activity (Gestel et al., 2003), these findings align with litter bag experiments from other temperate systems (O'Connor et al., 2025; Oelbermann et al., 2006; Sutterlütty et al., 2024).

Earlier litter bag studies in temperate alley-cropping systems have reported no differences in decomposition of crop residues or leaf litter between crop alleys and a sole-cropping reference (Oelbermann et al., 2006) and are supported by several recent publications (Moran-Rodas et al., 2025; O'Connor et al., 2025; Sutterlütty et al., 2024). In an application of the Tea Bag Index at an experimental alley-cropping system in Germany, O'Connor et al. (2025) found few differences in decomposition between tree rows and a sole-cropping control system, except at 100 cm depth where rooibos mass loss was lower in tree rows. Variation in litter decomposition was primarily explained by SOM, soil mineral N, and fine root biomass within tea bags (O'Connor et al., 2025). In an 11-year-old grassland alley-cropping system, Sutterlütty et al. (2024) also reported no consistent effect of alley-cropping on litter decomposition, which varied between years and over the growing season. Instead, litter decomposition increased under higher grass swards, potentially due to elevated humidity that promotes microbial activity. Similarly, Moran-Rodas et al. (2025) detected no consistent influence of alley-cropping on litter decomposition, though decomposition was higher in tree rows than in crop alleys and sole-cropped controls at one experimental site in a specific year. This is perhaps surprising when, as discussed in Section 2.4.1, tree rows often demonstrate higher catabolic potential than arable crop areas.

In contrast, several studies have identified a significant effect of alley-cropping on litter decomposition. At the same site studied by Oelbermann et al. (2006), Wotherspoon et al. (2014) reported a lower mass loss of soybean stalk residues, buried at 15–20 cm depth, in the crop alley (68 %) than in the sole-cropping system (71 %), although leaf residues did not differ. Using a combination of stable isotope and litter bag techniques at five alley-cropping systems in Germany, Wachendorf et al. (2020) revealed that residue breakdown was greater under tree rows than all positions in the crop alley. Following a similar approach at an experimental arable alley-cropping system in Germany, Giray et al. (2025) reported greater loss of maize-derived C and N in tree rows compared to 4.5 m into the crop alley. Enhanced litter decomposition in alley-cropping systems may partly reflect elevated activity of several enzymes involved in the breakdown of fresh litter and woody biomass (e.g., β -glucosidase, β -xylosidase, phosphatase) in alley-cropping relative to sole-cropping systems (Clivot et al., 2020) or in tree rows

compared to crop alleys (Beuschel et al., 2019; Mungai et al., 2005; Udawatta et al., 2008). However, this cannot be confirmed, as previous studies have not quantified soil biodiversity or biological activity alongside litter decomposition measurements.

Despite the central role of soil organisms to litter decomposition (de Graaff et al., 2015; Handa et al., 2014), little attention has been given to identifying their contribution or linking soil biodiversity to litter decomposition in temperate alley-cropping systems. No alley-cropping studies have used exclusion experiments to isolate size-class contributions to litter decomposition, and only one has jointly measured soil biodiversity (within litter bags or ambient communities) and litter decomposition using the same spatio-temporal design (Giray et al., 2025). However, although Giray et al. (2025) quantified bacterial and fungal gene abundances in litter bags and soil, they didn't explore their relationship with litter decomposition. Moreover, only two studies (Giray et al., 2025; Wachendorf et al., 2020) investigated the fate of applied litter once it left the litter bags, even though this knowledge is crucial to our understanding of C and nutrient dynamics within alley-cropping systems. Their findings indicate that although litter C and N losses increased in tree rows, more litter-derived C and N were incorporated into underlying soil (Giray et al., 2025; Wachendorf et al., 2020), suggesting that enhanced decomposition in tree rows may simultaneously increase C and N losses (via leaching or gaseous emissions) and SOM formation.

Taken together, current evidence does not allow formation of clear conclusions as to whether alley-cropping increases or decreases litter decomposition and SOM formation relative to sole-cropping, either in tree rows or crop alleys. Studies, a large proportion of which were concentrated in Germany, differed in a number of ways which could have contributed to the inconsistent findings, including litter bag mesh size (Kampichler and Bruckner, 2009; Xie, 2020), litter substrate (García-Palacios et al., 2016; Li et al., 2024b; Sauvadet et al., 2017), incubation depth (O'Connor et al., 2025), experiment duration (García-Palacios et al., 2013), local pedo-climatic conditions (García-Palacios et al., 2013; Li et al., 2024b; Tan et al., 2021; Wall et al., 2008), agroforestry system characteristics (Fujii et al., 2018), and agricultural management (Sutterlütti et al., 2024). A key limitation present in the reviewed literature is a lack of appropriate spatial comparisons and controls. Some studies did not include a suitable sole-cropping reference system (Mettauer et al., 2022; Sutterlütti et al., 2024; Wachendorf et al., 2020) while others lacked sampling in both tree rows and crop alleys of alley-cropping systems (O'Connor et al., 2025; Oelbermann et al., 2006; Wotherspoon et al., 2014). More decomposition experiments conducted in temperate alley-cropping systems will be necessary

to confirm the findings presented here, identify potential drivers of reported decomposition dynamics (e.g., soil and above-ground biodiversity, soil microclimatic conditions, soil physicochemical properties), and quantify the influence of site- and experiment-specific factors on the responses of litter decomposition to alley-cropping.

2.4.3 SOM mineralisation

Enhanced litter decomposition represents an opportunity for soil C sequestration only if litter-derived products are incorporated into SOM with a long persistence time in soils, which is ultimately determined by mineralisation rates. Mineralisation, or the transformation of SOM into simpler, inorganic compounds, is a complex function involving several processes (e.g., amination, ammonification, nitrification, and dissimilatory nitrate reduction) driven by soil micro-organisms and their extracellular enzymes (Wu et al., 2024). Mineralisation is a central process in C and nutrient cycling in agricultural systems which underpins agricultural productivity by dictating the availability of plant-available nutrients (Hood et al., 2003). Rates of SOM mineralisation will also determine C and nutrient losses via gaseous emissions, runoff, and leaching.

2.4.3.1 SOC mineralisation

SOC mineralisation in temperate alley-cropping systems has largely been assessed via soil CO₂ effluxes. Many studies have reported higher CO₂ emissions in tree rows relative to crop alleys (Medinski et al., 2015; Peichl et al., 2006; Wotherspoon et al., 2014) or sole-cropping reference systems (Baah-Acheamfour et al., 2016), with similar trends reported for CH₄ (Gauthier et al., 2016). These increases align with evidence of elevated catabolic potential in alley-cropping soils (Beule et al., 2022b) and may reflect more favourable soil conditions for catabolic activity and/or the priming effect of fresh C inputs from tree rows (Kuzyakov et al., 2000). Fresh C inputs have been shown to stimulate mineralisation of older SOM in subsoils (Fontaine et al., 2007), potentially contributing to observed reductions in soluble SOC below 70 cm in an 18-year-old Mediterranean alley-cropping system (Cardinael et al., 2015). These findings contrast with literature reporting reduced CH₄ emissions (Veldkamp et al., 2023) and greater SOC sequestration (Ivezic et al., 2022; Mayer et al., 2022; Veldkamp et al., 2023) in temperate alley-cropping compared to sole-cropping systems.

A meta-analysis reported generally positive SOC accumulation in temperate alley-cropping systems relative to sole-cropping (0.21 and 0.15 t C ha⁻¹ year⁻¹ for topsoils and subsoils, respectively) (Mayer et al., 2022). This potential can be attributed to high organic inputs from

trees and herbaceous vegetation (Mayer et al., 2022), as well as reduced surface erosion and leaching (Judson et al., 2025; Torralba et al., 2016; Veldkamp et al., 2023), which may offset CO₂ losses. Moreover, both laboratory and field experiments have demonstrated that alley-cropping tree rows can reduce soil CO₂ effluxes compared to crop alleys (Franzluebbers et al., 2017; Medinski et al., 2015) or sole-cropping reference systems (Cardinael et al., 2020). For example, in a laboratory experiment using soils from a Mediterranean alley-cropping system, decomposition of both SOC and SIC in the 0–10 cm layer was lower in soils from tree rows than from crop alleys and sole-cropping controls (Cardinael et al., 2020).

Reduced CO₂ effluxes from alley-cropping systems may result from increased POM recalcitrance due to the contribution of “lower quality” litter (i.e., high C:N ratio and lignin content, low nutrient availability) by trees and UVS (Cardinael et al., 2015, 2018), which has a lower mineralisation rate and higher accumulation efficiency in MAOM compared to higher quality litters (Córdova et al., 2018; Zheng et al., 2024). Despite higher potential catabolic activity, alley-cropping tree rows can also exhibit greater microbial C-use efficiency compared to arable crop areas (Nii-Annang et al., 2009; Beuschel et al., 2019; D’Hervilly et al., 2021; Guillot et al., 2021), resulting in more SOC being allocated to microbial growth (immobilisation). This is consistent with increases in labile SOM and microbial biomass reported in tree rows relative to arable crop areas (Beule et al., 2022b; Cardinael et al., 2020; Medinski et al., 2015). As microbial residues constitute a major formation pathway for stable SOM such as MAOM or occluded POM (o-POM) (Cotrufo et al., 2015), immobilisation of SOC could increase its residence time in soil where remineralisation is limited.

2.4.3.2 *SON mineralisation*

Investigations of SON mineralisation in temperate alley-cropping systems have quantified net and gross rates of ammonification and nitrification, the two major stages of the mineralisation process. Application of ion exchange membranes as part of an integrative assessment of soil health in a Mediterranean alley-cropping system revealed that NO₃⁻ and NH₄⁺ exchange was higher in tree rows compared to the crop alley, suggesting enhanced ammonification and nitrification in tree rows (Mettauer et al., 2022). Nitrification potential of tree rows was also reported to be 1.5 times higher than at two distances into crop alleys (1.5 and 10 m) at an 8-year-old alley-cropping system in southwestern France (Mettauer et al., 2024). Similarly, young trees in an experimental alley-cropping system increased soil NH₄⁺ content in topsoils, potentially reflecting enhanced SOM mineralisation in tree rows (Rufin et al., 2025). Using a ¹⁵N pool dilution approach, Lang et al. (2019) demonstrated that tree rows increased gross rates

of ammonification compared to crop alleys. Furthermore, N mineralisation rates in a Danish combined food and energy system ($108 \text{ kg ha}^{-1} \text{ year}^{-1}$) exceeded those of an arable sole-cropping system ($64 \text{ kg ha}^{-1} \text{ year}^{-1}$), in both tree rows ($196 \text{ kg ha}^{-1} \text{ year}^{-1}$) and crop alleys ($121 \text{ kg ha}^{-1} \text{ year}^{-1}$) (Ghaley et al., 2014b). Through innovative use of root barriers (Allen et al., 2005) or removal of leaf litter from crop alleys (Thevathasan and Gordon, 1997), increases in SON mineralisation in crop alleys, and especially near tree rows, has been linked to the presence of tree roots and leaf biomass.

Enhanced SON mineralisation is likely associated with an increase in microbial activity (Beule et al., 2022b), which could increase N losses via leaching or N_2O emissions. Although this has been reported in some alley-cropping systems (Kim et al., 2016; Veldkamp et al., 2023), alley-cropping frequently reduces both the concentration of N in run-off and leachate (Kim and Isaac, 2022; Wolz et al., 2018a) and soil N_2O effluxes (Beaudette et al., 2010; Franzluebbers et al., 2017; Luo et al., 2022; Shao et al., 2022; Wolz et al., 2018a). This may reflect greater microbial immobilisation of NH_4^+ in alley-cropping relative to sole-cropping, as observed in tree rows compared to crop alleys by Lang et al. (2019). As discussed for SOC, microbial immobilisation may facilitate the protection of N in MAOM or occluded POM (o-POM). Tree rows can also mitigate N losses by (i) capturing N which has leached beyond the crop rooting zone, remains outside of crop growth periods, or is surplus to crop requirements, reducing N availability for denitrification (Kim and Isaac, 2022), and (ii) improving soil structure and aeration via roots, fungal hyphae, and soil fauna, thereby regulating soil microclimates and reducing pulses of N_2O release (Chen et al., 2016).

2.4.3.3 *Summary for SOM mineralisation*

Current evidence does not reveal a consistent effect of temperate alley-cropping on SOM mineralisation. Alley-cropping can stimulate or suppress mineralisation depending on system maturity (Rufin et al., 2025), tree species (Franzluebbers et al., 2017), soil texture (Franzluebbers et al., 2017; Luo et al., 2022). Although not tested in their experiment, Franzluebbers et al. (2017) also speculated that alley-cropping's effect on SOM mineralisation was dependent on agricultural management, edaphic properties (e.g., soil C and N content), and climate. In short, responses are highly context-specific and governed by resource supply and accessibility to microbes.

Soil GHG fluxes are inherently variable and sensitive to spatio-temporal sampling design (Veldkamp et al., 2023). For example, Medinski et al. (2015) reported that elevated CO_2 in tree rows occurred only during warmer months, and this trend reversed in cooler months (Medinski

et al., 2015). Such temporal dynamics may be missed in laboratory incubations (e.g., Cardinael et al., 2020) or inadequately replicated field studies. Reliance on CO₂ effluxes and net NH₄⁺/NO₃⁺ changes, as has largely been the case for alley-cropping studies, provides only partial insight into SOM mineralisation, as they don't reveal the responses of specific mineralisation processes (e.g., ammonification, mineralisation, nitrification) to alley-cropping. Moreover, research has centred on C and N, largely neglecting other nutrients such as P (but see Scott and Condon, 2003).

2.4.4 SOM stabilisation

SOM persistence in soil is enhanced by associations with minerals and physical protection within aggregates. To assess SOM accrual, persistence, and responses to disturbance, a simple conceptualisation has been widely adopted which divides SOM into two functionally distinct fractions with different turnover times: POM and MAOM (Cotrufo and Lavelle, 2022). POM comprises partially degraded, complex plant and fungal-derived compounds which are vulnerable to disturbance and have a mean residence time in soils of years to decades. MAOM consists of single molecules or microscopic fragments of organic matter sorbed directly to minerals (direct sorption pathway) formed from microbial residues (microbial pathway) (Angst et al., 2021). Mineral association, either as chemical or physical bonds, protects SOM from decomposition and increases its residence time in soil from decades to millennia (Lavelle et al., 2020). Both POM and MAOM may be occluded within soil aggregates (Angst et al., 2017), further increasing their persistence in soils (John et al., 2005; Meyer et al., 2011, 2024). Consequently, increasing o-POM or MAOM represents a pathway to longer-lasting SOM retention (Lavelle et al., 2020).

Alley-cropping has the potential to enhance MAOM formation through both direct sorption and microbial pathways. As discussed in Section 2.4, alley-cropping tree rows are often associated with more abundant and diverse detritivore and decomposer communities compared to arable crop areas (Beule et al., 2022b, 2025). Associated increases in catabolic potential (Beule et al., 2022b) may increase litter decomposition (Giray et al., 2025; Wachendorf et al., 2020; Wotherspoon et al., 2014) and POM breakdown, generating light molecular weight products (e.g., dissolved organic matter or DOM) and microbial necromass, particularly fungal residues (Klink et al., 2022), that can bind to mineral surfaces (Angst et al., 2024). Greater initial respiration rates have been shown to promote accumulation of C and N in clay-sized MAOM via microbial pathways (Cyle et al., 2016). Higher microbial C-use efficiency in alley-cropping systems (Guillot et al., 2021) would further shift substrate C investment in biomass

and by-products rather than CO₂, enhancing precursor supply for MAOM formation. This may explain why the multifunctionality of microbial traits, which supports a wider substrate use diversity, has previously been demonstrated to promote SOM formation and stability (Whalen et al., 2024).

Aside from promoting MAOM formation, alley-cropping tree rows may enhance the persistence of POM and MAOM through (i) organic N additions to soils (Pardon et al., 2017) which alleviate the need for microbial N mining from SOM (Turner et al., 2017), (ii) formation of more stable micro- and macro-aggregates within which POM and MAOM is physically protected (Baah-Acheamfour et al., 2014; Udawatta et al., 2008, 2014), and (iii) enhanced mineral weathering in response to afforestation (Lafleur et al., 2013), which can increase the availability of binding sites for SOM. However, it is also possible that, through priming effects (Jilling et al., 2021), alleviation of nutrient limitations (Zheng et al., 2024), and greater live root and rhizosphere activity (Pierson et al., 2021), microbial decomposition of POM and destabilisation of MAOM is stimulated by tree rows and UVS. Thus, alley-cropping may both stabilise and destabilise SOM depending on context

Empirical studies directly quantifying MAOM and o-POM in temperate alley-cropping systems are scarce. Tree rows commonly exhibit higher labile SOM (Medinski et al., 2015) and POM (Mungai et al., 2006b) than arable crop areas. Mungai et al. (2006b) reported that, in one of two studied alley-cropping systems, subsoil POM-C was two- to three-fold higher in tree rows than crop alleys (Mungai et al., 2006b). Evidence of changes to o-POM and MAOM, as well as the C and N concentration of POM and MAOM, in temperate alley-cropping systems, however, is more variable.

In an 18-year-old walnut-based Mediterranean alley-cropping system, tree rows showed higher C concentrations in POM (< 50 µm) and in silt- and sand-sized MAOM fractions (2–20 and 20–50 µm) in the top 0–10 cm than crop alleys and sole-cropping controls (Cardinael et al., 2015). C concentration of clay-sized (< 2 µm) MAOM was also higher in tree rows compared to crop alleys, but not sole-cropping controls (Cardinael et al., 2015). At the same site three years later, Guillot et al. (2021) also reported higher C concentrations of all SOM fractions (coarse and fine POM, o-POM, and MAOM, free and occluded light fractions) in tree rows compared to crop alleys (to 6.5 m distance), with exceptions close to tree rows (1–2 m) for POM and the occluded light fraction. (Guillot et al., 2021).

By contrast, Clivot et al. (2020) reported no significant difference in concentrations of MAOM-N between crop alleys (2.5 m distance) and sole-cropping controls at an experimental alley-cropping system in northeastern France. On post-mining soils in Germany, alley-cropping increased the concentration of o-POM-C over time relative to sole-cropping soils, but MAOM-C declined in both tree rows and crop alley soils as the system matured (Kanzler et al., 2021). Furthermore, in 4-year-old poplar and robinia-based alley-cropping systems, the humification index of water-extractable organic matter (WEOM) increased with distance from tree rows, suggesting reduced formation of complex SOM near tree rows (Sun et al., 2017).

Current evidence indicates that alley-cropping can increase SOM storage in stable fractions within tree rows, and in some cases into adjacent crop alleys, compared to sole-cropping. However, responses are inconsistent across systems, reflecting the importance of farm- and field-scale properties on SOM dynamics. SOM availability for o-POM or MAOM formation is influenced by system maturity (Ivezic et al., 2022) and local pedo-climatic conditions (e.g., existing soil C) (Franzluebbers et al., 2017). Litter quality and root traits (e.g., mycorrhizal or ectomycorrhizal associations), which are dependent on the composition of alley-cropping trees and UVS, also influence MAOM formation and stability (Beidler et al., 2023). Where alley-cropping systems do increase SOM, MAOM formation is dependent on the existing saturation levels of minerals (Georgiou et al., 2025). Midwood et al. (2021) demonstrated that where there is limited mineral weathering of parent material (and presumably MAOM saturation), most newly accumulated C from woody perennial crops is present as POM. Although in some temperate agroecosystems no upper limit for MAOM formation has been detected (Begill et al., 2023), mineralogical C saturation levels vary widely across temperate regions (Georgiou et al., 2022), constraining the capacity for MAOM accrual in some landscapes.

2.5 Alley-cropping, soil biodiversity, and decomposition: The knowledge gaps

The literature demonstrates that alley-cropping can influence soil biodiversity and decomposition processes. However, a consistent pattern emerging across studies is the high degree of variability in the direction and magnitude of these effects. Alley-cropping systems differ markedly in their composition (e.g., tree species, understory vegetation, crop rotations), structural design (e.g., tree maturity, density, orientation, and spacing), and management of tree rows and crop alleys. Additionally, each system is embedded within a distinct landscape context, characterised by a unique climate, geomorphology, land-use history, and landscape composition. These sources of variation mean that few widely generalisable trends can currently be drawn. As such, a key aim of this thesis is to generate UK-specific evidence on

how alley-cropping affects soil biodiversity and decomposition, to better inform policy development and land-management decisions.

Although research in temperate alley-cropping systems has increased substantially in recent years, the focus of this research is skewed towards certain soil taxa and functions (Beule et al., 2025; Kletty et al., 2023). As highlighted in Section 2.3, soil meso- and micro-fauna (Kletty et al., 2023; Marsden et al., 2020), as well as important groups of soil microorganism (Beule et al., 2025), remain severely understudied, despite their central roles in soil functioning. There is also limited research that considers soil biotic communities, rather than focussing on a few key target taxa (Kletty et al., 2023). Functional assessments of soils are similarly scarce (Kletty et al., 2023), particularly studies directly quantifying faunal-mediated processes (Marsden et al., 2020). While numerous studies have examined SOC accumulation and soil CO₂ and N₂O effluxes in alley-cropping systems, relatively few have investigated the underlying processes regulating these patterns, such as litter decomposition and SOM stabilisation. These knowledge gaps limit our ability to design, manage, and optimise temperate alley-cropping systems to enhance SOM formation, soil fertility, and long-term soil C storage.

From these observations, four key questions therefore arise which are subsequently addressed in Chapters 3–5:

- 1) Does alley-cropping influence soil meso- and macro-faunal biodiversity?
- 2) Does alley-cropping influence litter decomposition?
- 3) Does alley-cropping influence the decomposition activity of soil meso- and macro-fauna?
- 4) Does alley-cropping influence the persistence and stabilisation of litter-derived organic matter?

3 Tree rows alter the biodiversity and biological quality of soil fauna in temperate alley-cropping systems

3.1 Abstract

Alley-cropping has the potential to mitigate the detrimental effects of intensive agricultural practices (e.g., sole-cropping) on functionally critical soil fauna. However, major gaps exist in our understanding of how tree rows impact understudied faunal groups or the biodiversity of faunal communities. To address this, the impacts of alley-cropping on soil meso- and macro-faunal biodiversity relative to sole-cropping were assessed across five commercial farms in England, United Kingdom.

Linear/linear mixed-effects models revealed that, relative to sole-cropping, alley-cropping increased soil faunal abundance by 107.0 fauna ($\pm 30.6_{SE}$, $p < 0.001$), richness by 1.8 taxa ($\pm 0.50_{SE}$, $p = 0.002$), and QBS-ar scores by 22.1 points ($\pm 5.1_{SE}$, $p < 0.001$). Alley-cropping also drove compositional shifts ($p = 0.001$) characterised by higher abundances of dominant taxa and greater occurrences of rare taxa representing multiple life strategies and levels of sensitivity to disturbance. Changes relative to sole-cropping were greatest in tree rows but evident at 1.5 m into crop alleys for all metrics excluding abundance. Higher biodiversity in tree rows was partially attributed to increases in soil K, total N, and moisture content ($p < 0.05$). Soil type, crop diversity, and soil C:N ratio also influenced faunal biodiversity ($p < 0.05$).

Overall, alley-cropping supported more biodiverse soil faunal communities, including disturbance-sensitive taxa. These findings highlight alley-cropping's potential for soil biodiversity conservation in temperate arable systems and provide novel insights into responses of previously overlooked meso-faunal and endogean groups. Further research is needed to substantiate these findings, particularly on the mechanistic drivers of biodiversity gains.

3.2 Introduction

Widespread soil degradation (Právělie et al., 2024) driven by agricultural intensification (Geisen et al., 2019; Jeffery and Gardi, 2010; Tibbett et al., 2020) has placed soil faunal communities, and their associated ecosystem services (e.g., soil structure formation, carbon transformations, nutrient cycling, and the regulation of biological populations) (Briones, 2018; Culliney, 2013; Turbé et al., 2011), at risk across large areas of Europe (Gardi et al., 2013; Orgiazzi et al., 2016). Intensification subjects soil fauna to direct mortality from agronomic disturbance (physical and chemical) (Betancur-Corredor et al., 2022; Beaumelle et al., 2023; Roger-Estrade et al., 2010), intolerable shifts in soil environments (de Graaff et al., 2019;

Phillips et al., 2024; Tsiafouli et al., 2015), and the loss of semi-natural features (e.g., forest patches) and the diverse, high-quality, and, perhaps most importantly, undisturbed habitats and resources that accompany them (D'Hervilly et al., 2020; Mamabolo et al., 2024; Smith et al., 2008b). This has resulted in marked declines in soil faunal abundance, diversity (de Graaff et al., 2019; Lavelle et al., 2022; Tsiafouli et al., 2015), biological quality (Mantoni et al., 2021), and connectivity (Creamer et al., 2016) within intensive systems, ultimately leading to shifts in functional composition (de Graaff et al., 2019; Thiele-Bruhn et al., 2012; Yin et al., 2020).

The consequences of soil faunal biodiversity loss for agricultural soil functioning are substantial (de Graaff et al., 2019; de Vries et al., 2013), threatening food security and farmer livelihoods (El Mujtar et al., 2019; Kopittke et al., 2019), as well as efforts to address the negative outcomes of soil degradation (e.g., emissions, pollution, and flooding) beyond the farm gate (de Ruiter et al., 2005; Kraamwinkel et al., 2021). Transitioning to structurally complex agroecosystems that restore degraded soils is therefore critical (British Ecological Society, 2025; Köninger et al., 2022). Alley-cropping, a modern agroforestry practice in which crops and/or livestock are produced between parallel tree rows, is one promising candidate. Alley-cropping has gained recognition among policymakers and farmers as a multifunctional system (Veldkamp et al., 2023) capable of improving soil health without compromising farmer livelihoods (Quinkenstein et al., 2009; Wolz et al., 2018), while contributing to EU Green Deal targets to restore high-diversity landscape features on at least 10% of agricultural land by 2030 (European Environment Agency, 2025). However, these benefits depend largely on its effects on soil biodiversity, including soil fauna.

Alley-cropping has been reported to exert a largely positive, though highly variable, influence on soil fauna (Beule et al., 2025; Marsden et al., 2020). The spatial and temporal heterogeneity introduced by tree rows naturally favours faunal diversification and coexistence (Boinot et al., 2019b; Korboulewsky et al., 2016; Santos et al., 2022). Tree rows and UVS also provide permanent, diverse, and relatively undisturbed habitat and resources for soil fauna within otherwise harsh intensive landscapes (Boinot et al., 2019b; Cardinael et al., 2019; Pardon et al., 2019), as well as buffer soil fauna against soil degradation and climatic extremes by stabilising soil profiles (Zhu et al., 2020) and beneficially modifying soil microclimates (Jacobs et al., 2022). Benefits can even extend into crop alleys through root and canopy effects (Pardon et al., 2017; Sutterlüttich et al., 2023). Despite this promise, clear evidence that tree rows promote soil faunal biodiversity on arable farmland, rather than benefit a limited subset of faunal taxa,

remains scarce (Vandendriessche et al., 2025). Indeed, several important knowledge gaps persist regarding the impact of alley-cropping on soil fauna.

To date, research on soil fauna within temperate alley-cropping systems has focussed disproportionately on epigeal macro-fauna (e.g., Cardinael et al., 2019; D'Hervilly et al., 2020; Matevski et al., 2024; Pardon et al., 2019), with soil micro- and meso-fauna, as well as endogeal arthropods, receiving far less attention (De Clerck et al., 2025; Kletty et al., 2023). In a review of 45 temperate silvoarable studies, only three addressed endogeal soil arthropods (Park et al., 1994; D'Hervilly et al., 2020,2022) compared to the 17 addressing epigeal arthropods, earthworms, and gastropods (Kletty et al., 2023). Globally, macro-fauna featured in 7.5 and 3.8 times more publications than meso- and micro-fauna, respectively (Marsden et al., 2020). Given soil faunal size classes respond differently to changes in plant communities and soil properties (Malica et al., 2022; Wu and Wang, 2019), macro-faunal trends cannot be reliably extrapolated to smaller, less mobile, and more soil-adapted taxa. Indeed, the few assessments of soil meso-fauna in temperate alley-cropping systems have yielded inconsistent findings (Boinot et al., 2019b; Doblas-Miranda et al., 2014; Ramón et al., 2012). Whole-community assessments are also lacking. Few alley-cropping studies have sampled the full range of faunal taxa (i.e., full size classes or both surface-dwelling and endogeal fauna) even at coarse taxonomic resolution (but see D'Hervilly et al., 2022; Ramón et al., 2012), limiting our understanding of faunal community responses to alley-cropping, especially across varying pedo-climatic contexts, management regimes, and system configurations (Boinot et al., 2022).

The narrow taxonomic scope of many studies partly reflects the extensive labour and expertise required to identify diverse soil faunal taxa (Marsden et al., 2020). The QBS-ar Index offers a practical alternative, evaluating arthropod communities using class- or order-level identifications alongside ecomorphological traits reflecting level of soil adaptation (Menta et al., 2018). While successfully applied across various agroecosystems (Menta et al., 2018), the QBS-ar Index has rarely been used within temperate alley-cropping systems (but see Gavinelli et al., 2024), potentially because the index's performance, including its reference values for healthy soils, requires validation in more international contexts (Gallese et al., 2025). If demonstrated to be effective at capturing the impacts of alley-cropping on soil faunal biodiversity, wider application of the QBS-ar Index in temperate alley-cropping research could facilitate larger-scale, taxonomically broader evaluations of soil fauna.

Here, we investigated alley-cropping's impacts on soil meso- and macro-faunal biodiversity in commercial arable agroecosystems in England, United Kingdom. We measured the abundance,

taxonomic (order) richness, biological quality (QBS-ar Index), and composition of soil meso- and macro-fauna in tree rows and crop alleys compared to sole-cropping systems. We hypothesised that (i) soil faunal abundance, taxonomic richness, and biological quality would be greater under alley-cropping than sole-cropping; (ii) increases in soil faunal biodiversity would be restricted to tree rows due to frequent soil disturbance in crop alleys; (iii) tree rows would support a distinct faunal composition differentiated by the presence of uncommon, disturbance-sensitive taxa; and (iv) QBS-ar scores would reflect similar but more clearly elucidated patterns than taxonomic richness.

3.3 Methods

3.3.1 Study sites

Five farms across three English counties were sampled (Figure 1A). At each farm, paired arable fields were sampled: one with linear tree rows (alley-cropping) and one without (sole-cropping) (Figure 1B). Farms were selected based on being under typical arable management, tree rows planted more than five years prior to the start of the experiment, and available paired alley-cropping and sole-cropping fields with comparable management histories and soil textures. Paired fields were managed in the same way, excluding S1, where fields followed the same crop rotation but had different crops at the time of sampling, and thus experienced differing disturbance regimes (Table 3.1). Furthermore, in 2021, the alley-cropping field at farm S2 was planted with spring wheat whereas the sole-cropping field was placed in ley. However, these fields usually follow the same crop rotation.

All farms utilised a combination of herbal leys and crop residue retention to manage their soil fertility. Soils at farm C1 were ploughed and mole drained every five years, with subsoiling undertaken as required. Red and white clover ley was chopped and mulched to maintain soil fertility. C2 soils were ploughed and tine cultivated and weeded annually in spring. Farm N1 transitioned to organic farming in September 2023. Prior to this, both experimental fields were under minimum tillage (undertaken prior to drilling of crops) and treated with liquid nitrogen, compound fertiliser, and Glyphosate as required. After September 2023, experimental fields remained under minimum tillage and fertility was managed by application of cattle manure every three years, but no manure was applied prior to sampling in Spring 2024. At S1, fields were ploughed prior to the sowing of cereals. As the alley-cropping field remained under a ley mixture for the duration of the experiment, it was not ploughed. Sheep grazing typically occurred on both experimental fields when under an herbal ley mixture, but sheep had not been

grazed on either field in the period 2021–2024. At farm S2, soils were ploughed as needed to relieve soil compaction.

Table 3.1. Characteristics of paired alley-cropping ('AC') and sole-cropping fields ('SC') at five farms in England, United Kingdom.

	C1	C2	N1	S1	S2
Region	Cambridgeshire	Cambridgeshire	Nottinghamshire	Suffolk	Suffolk
Crops ¹ (2021–2024)	ww-ao-ly-ly	ao-ao-ao-ao	ly-ww-sw-sc	AC: sc-wb-ly-ly SC: ly-ly-sw-wb	AC: sw-ly-ly-ly SC: ly-ly-ly-ly
Crop diversity	3	1	3	3	AC: 2 / SC: 1
Management type ²	O	O	CO	O	O
Soil type ³	9	27	8	18	18
Soil texture ⁴	Silty clay	Sandy clay loam	Sandy clay	Clay/sandy clay	Clay/sandy clay
Year established	2015	2008	2015	2014	2000
Tree row orientation ⁵	N-S	N-S	N-S	N-S	N-S
Tree diversity ⁶	25 species	1 species	5 species	6 species	3 species
Tree density (ha ⁻¹)	58	85	75	138	64
Tree row width (m)	4	3	4	6 (double row)	5
Intra-row (m)	4	3	3	3	6
Alley width (m)	24	24	24	24	15

¹ Four most recent crops in the rotation provided. Crop rotation: 'ao' = autumn oats, 'ly' = fertility-building ley, 'sc' = secondary cereal (e.g., spelt or rye grass), 'sw' = spring wheat, 'ww' = winter wheat, 'wb' = wheat + beans. Bold letters indicate the crop(s) grown at the time of sampling in 2023 and 2024.

² Management type: 'O' = organic, 'C' = conventional.

³ Soil type according to the Soilscores Viewer online soil reporting tool hosted by Cranfield University (Cranfield Soil and Agrifood Institute, 2025): '8' = "slightly acid loamy and clayey soils with impeded drainage", '9' = "lime-rich loamy and clayey soils with impeded drainage", '18' = "slowly permeable seasonally wet slightly acid but base-rich loamy and clayey soils", and '27' = "fen peat soils".

⁴ Soil texture determined by feel according to Thien (1979).

⁵ Tree row orientation: 'N' = north, 'S' = south.

⁶ Tree species information can be found in Table 3.A.1.

3.3.2 Experimental design

Soil samples were taken from paired alley-cropping and sole-cropping fields at each farm. Space-for-time substitution was used (e.g., Cardinael et al., 2015; Judson et al., 2025); given the similar aspect, soil type, and management history of paired alley-cropping and sole-cropping systems, sole-cropping systems were assumed to represent the baseline state for alley-cropping systems. Three linear transects were established on each experimental field, along which three sampling points (0, 3, and 13 m) which in alley-cropping systems equated to: (i) 1.5 m into tree rows from the edge of the UVS (AC0); (ii) 1.5 m into crop alleys from the edge of the UVS (AC3); and (iii) the centre of crop alleys, which was 11.5 m into crop alleys for all farms, excluding S2 where it was 7.5 m (AC13) (Figure 3.1B). The transect spacing was replicated in sole-cropping fields (SC0, SC3, and SC13). As the influence of tree rows on soils was expected to be greater with proximity and on the side shielded from prevailing westerly winds (Donat et al., 2023; Jacobs et al., 2022), transects were established one metre to the north

of a tree and ran perpendicular from the eastern side of the tree row (Figure 3.1B). Transects were established a minimum of 30 m from the field edge to minimise edge effects. The same sampling design (i.e., the spacing and orientation of transects) was replicated on sole-cropping fields to determine whether observed spatial trends in litter decomposition were driven by tree rows or spatial autocorrelation of soil properties. Sampling in tramlines was avoided due to the expected impact of compaction on soil fauna (Carlesso et al., 2019).

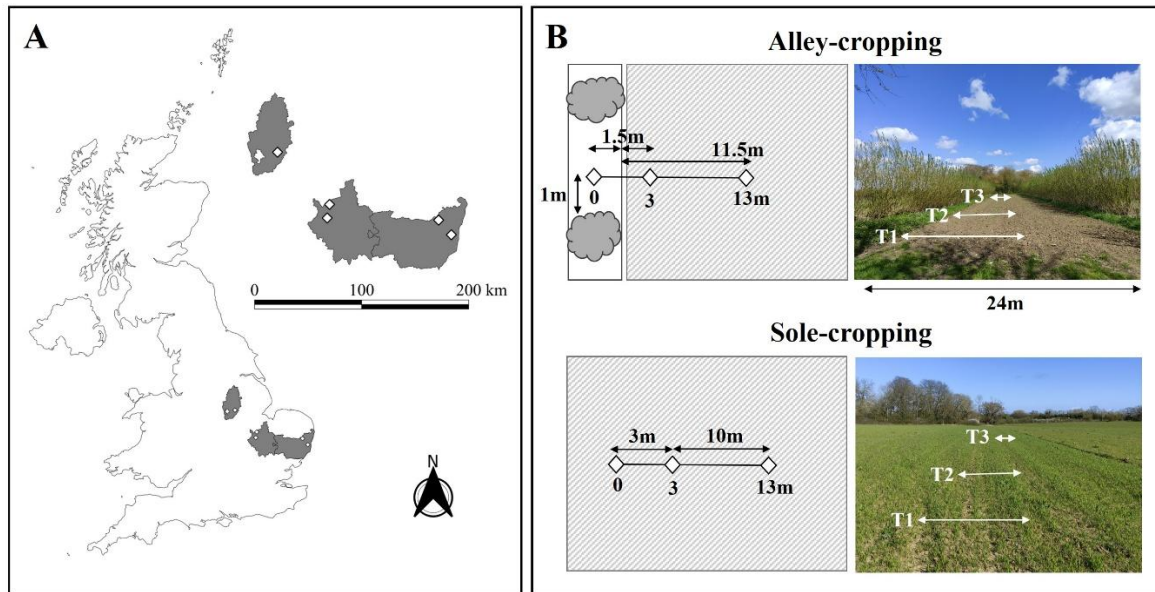


Figure 3.1. Sampling locations and experimental design. (A) Location of five arable farms in England, United Kingdom. The English counties of Nottinghamshire (left), Cambridgeshire (centre), and Suffolk (right) are represented by grey polygons. The locations of sampled farms are indicated by white diamonds. (B) Schematic representation of the experimental design on paired alley-cropping and sole-cropping fields at each farm. Transects are denoted by black lines, with individual sampling points represented by diamonds positioned at three distances (m) along the transect. In alley-cropping systems, transect positions were located as follows: 0m = within the tree row, 1.5 m in from the edge of the understory vegetation strip or UVS,); 3m = 1.5 m into the crop alley from the edge of UVS; 13m = in the crop alley centre, which was 7.5 m or 11.5 m from the edge of the UVS depending on alley width. Each experimental system contained three transects (T). UK map created using QGIS software (QGIS Development Team, 2025).

This sampling design aligns with recommendations that alley-cropping studies include replicated measurements in tree rows, multiple distances in the crop alley, and in a sole-cropping control (Beule et al., 2025; Kletty et al., 2023). The design was not intended to characterise the spatial distribution of soil meso- and macro-faunal biodiversity across alley-cropping fields, but rather to identify whether tree rows had any effect on the crop alley and if so, whether that extended to the centre of the crop alley. A sampling point was positioned at 1.5 m into the tree row, specifically, as the greatest influence of tree rows on soil properties is typically observed within 2 m (Park et al., 1994; Vaupel et al., 2023). That many previous alley-cropping studies have employed a similar design (Cardinael et al., 2019; Judson et al., 2025; Mettauert et al., 2024; Sun et al., 2017) also facilitates future data synthesis.

3.3.3 *Arthropod sampling*

Arthropod samples were collected by taking one intact soil core (8 cm diameter x 15 cm depth) from each sampling point on three separate occasions: once in spring 2023 (April–May), once in autumn 2023 (November–December), and once in spring 2024 (March–May). Cores were secured in sealed plastic bags and stored at 3–5 °C for a maximum of 48 h before processing. Samples were hand-sorted to extract larger specimens before transfer to Berlese-Tullgren funnels, an indirect extraction method which utilises a temperature, moisture and light gradient to drive organisms out of the soil and into a collection pot (Smith et al., 2008a). Samples were exposed to the light of a 40-W bulb positioned 10 cm above the soil for 5–12 days, until moisture was no longer visible on the inside of the funnel. All soil fauna collected were preserved in 80 % industrial methylated spirit until identification. Specimens were identified to order-level according to Barber (2008), Dallimore and Shaw (2013), Tilling (2014), and provisional keys for the identification of British soil mites (Shepherd and Crotty, unpublished) and Diplopods (Lee, unpublished). Protura, of which two orders are present in Britain, were identified to class-level resolution due to a lack of available taxonomic expertise. Organisms from the same sampling point across sampling events were amalgamated to form 90 composite samples for further analysis.

3.3.4 *Calculation of soil biological quality*

The QBS-ar Index was used to determine the influence of alley-cropping on soil biological quality (SBQ) (Menta et al., 2018; Parisi et al., 2005). First, specimens were categorised into taxonomic groups by class or order. Then, within each taxonomic group, specimens were allocated an ecomorphological index (EMI) score based on their level of adaptation to the soil environment, on a scale of 1 (low adaptation) to 20 (high adaptation) (Menta et al., 2018; Parisi et al., 2005). According to the QBS-ar Index, specimens were allocated an EMI score of 1, 2, 4, 5, 6, 8, 10, 15, or 20 following a biological form approach, where the presence or form of specific physical characteristics for a given taxa indicated which score should be allocated (see Menta et al., 2018 for full details). Using Collembola as an example, a specimen with scarcely-developed appendages and no pigmentation, ocelli, or furca (adapted to living in soil) would be given an EMI score of 20, whereas a specimen with complex pigmentation, ocelli, well-developed appendages, and a furca (adapted to live on the soil surface) would be given an EMI score of 1 or 2 depending on their size (if > 2 mm, EMI score = 1). Larvae and adults of holometabolous insects were considered separately (i.e., counted as separate groups with different potential EMI scores) due to their differing ecological roles and soil adaptation levels

(Menta et al., 2018). Finally, a soil biological quality score was generated for each sampling point by adding together the highest EMI score recorded for every taxonomic group present in the composite sample.

3.3.5 *Soil physicochemical analysis*

Soil communities demonstrate localised assemblages which are highly influenced by fine-scale patterns in soil properties (Nielsen et al., 2015). Consequently, the following physical and chemical soil parameters were measured at each sampling point to help explain observed patterns in soil fauna: temperature (Temp, °C), moisture content (MC, g H₂O 100 g⁻¹), bulk density (BD, g cm⁻³), texture, pH, organic matter content (SOM, g 100 g⁻¹), cation exchange capacity (CEC, meq 100g⁻¹), total carbon (TC, g kg⁻¹), total nitrogen (TN, g kg⁻¹), C:N ratio, and concentrations of exchangeable Al, Ca, Fe, K, Mg, Mn, and Na (mg kg⁻¹). Soil temperature and moisture content were measured at each sampling event (details below); the remaining soil properties were determined from a soil core (8 cm diameter x 15 cm depth) collected in November 2023 from 10 cm to the left of each sampling point. Analyses were conducted on thoroughly mixed, air-dried, 2 mm-sieved samples, unless stated otherwise.

Soil temperature was measured at a depth of 10 cm using a digital thermometer (Hanna Instruments EN-13485 Checktemp® Pocket). Soil moisture content was determined following the method of ISO 11465 (ISO International Organization for Standardization, 1993). Soil bulk density was calculated using the volumetric cylinder method of ISO 11272 (International Organization for Standardization, 2017). Bulk density was calculated by dividing the soil dry weight by the original sample volume. Soil texture was determined by feel (Thien, 1979). Organic matter content (g 100 g⁻¹ oven-dry soil) was calculated by loss-on-ignition overnight at 350°C (Ayub and Boyd, 1994). For pH analysis, 10 g soil were mixed with 25 mL of deionised water and shaken for 15 minutes on an end-over-end shaker at 25 rpm. Samples were left to settle for 15 mins before measurement using a Thermo Orion Star A111 pH meter calibrated to pH 4.0, 7.0 and 10.0 buffers (Ministry of Agriculture, Fisheries and Food, 1986).

Cation exchange capacity was measured using the BaCl₂ method (Hendershot and Duquette, 1986). Exchangeable Ca, Mg, K, Na, Al, Fe, and Mn in the samples were measured in the 0.1 M BaCl₂ extract by inductively coupled plasma-optical emission spectroscopy (ICP-OES) (Thermo iCAP 7000). For calculation of CEC, instrumental accuracy was determined as 106-122 % through analysis of Merck ICP multi-element standard solution IV at a concentration of 0.25 mg L⁻¹. Precision, determined through duplicate analysis of 10 % samples (Gill and

Ramsey, 1997) was: 2.1 %, Mn, 32.9 % Fe, 0.7 %, Mg, 0.8 %, Ca, 25.2%, Al, 7.1 %, Na, and 7.5 %, K. Detection limits were determined by ten repeat analyses of a calibration blank (Walsh, 1997). All procedural blanks were below the detection limit of the ICP-OES. Concentrations below the detection limit were set to a consistent value (detection limit / square root of two) for statistical analysis (Croghan and Egeghy, 2003). Fe and Al were not included in further analysis due to low instrumental accuracy (44 %) and sample concentrations (< 7 % of samples above detection limit), respectively. Total C and N were determined by elemental analysis (Elementar Vario EL Cube) on soil oven-dried at 40 °C for 48 h and ground to < 200 µm using a Retsch MM200 ball mill. Quality control data for measurement of soil carbon and nutrient concentrations are available in Table 3A.2.

3.3.6 Data analysis

3.3.6.1 Abundance, taxonomic richness, and SBQ

To address hypotheses (i) and (ii), linear (abundance, SBQ) or linear mixed-effects models (taxonomic richness) were applied to investigate the influence of agricultural system (alley-cropping vs sole-cropping), transect position (0, 3, or 13 m), and their interaction on soil faunal biodiversity (Models 1–3). As high spatial variation was observed in sole-cropping, alley-cropping transect positions were also compared with the average for sole-cropping across transect positions (Models 4–6). Farm-level characteristics (Table 3.1) and soil physicochemical properties (Table 3.B.1) which may have influenced soil faunal biodiversity or the effect of alley-cropping on soil fauna were considered during model selection. However, reduced models were used to quantify the impact of alley-cropping on soil faunal biodiversity presented in Section 3.4.1. Reduced models excluded soil physicochemical variables which were significantly influenced by agricultural system, transect position, or their interaction (Table 3.B.1), as their inclusion would have resulted in an underestimation of the indirect influence of alley-cropping on biodiversity via modification of soil properties by tree rows. Modelling was undertaken using the *lm* function of the ‘stats’ package (R Core Team, 2025) and the *lmer* function of the *lme4* package (v. 1.1-35.2, Bates et al., 2015). Model details can be found in Table 3.A.3.

Final models were created following a process of backward stepwise selection. Full linear mixed-effects models (LMMs) were created which included (i) agricultural system, transect position, and their interaction (retained in all final models), (ii) farm-level variables and soil physicochemical properties, and (iii) nested random effects (farm/transect). LMMs were selected as they can account for the dependencies and correlations present between

observations within the same group in data with a nested, hierarchical structure (Harrison et al., 2018). In this case, it was predicted that samples would be more similar within, rather than across, farms (Figures 3.B.1–4) and transects due to localised soil heterogeneity and the unique pedo-climatic contexts management histories of farms. However, where farm-level variables were able to capture the variation explained by farm, they were included as fixed effects and farm was removed as a random effect if this resulted in an improvement in model fit. The random effect ‘transect’ was also removed where its inclusion led to a singular fit, resulting in a linear model.

Fixed effects retained in final models were selected based on their impact on model fit, which was assessed using the corrected Akaike Information Criterion (AICc) via the *AICc* function of the ‘MuMIn’ package (v. 1.47.5, Barton, 2023). AICc was used as it penalises model overfitting and corrects for a small sample size (Hurvich and Tsai, 1993). Each fixed effect was removed independently from the model and the change in AICc recorded. The variable which yielded the greatest improvement in model fit when removed was excluded from the model, and the process repeated until only those variables which reduced model AICc by < 2 when removed were left. This value was selected as models with an AICc of within two of each other each have strong support (Burnham and Anderson, 2002). When autocorrelation occurred, the retained variable was also selected based on which yielded the lowest model AICc.

Goodness of fit of final models was assessed visually from diagnostic plots (i.e., normality of residuals, normality of random effects, heteroscedasticity, homogeneity of variance, and multicollinearity) generated by the *check_model* function of the ‘performance’ package (v. 0.13.0, Lüdtke et al., 2021). Leave-one-group-out cross validation (LOGO-CV) was applied to final models to ensure they were not overfitted (Roberts et al., 2017; Yates et al., 2023). For LOGO-CV, the model was trained on all transects except one and then tested on the withheld transect. Although no standard guideline exists, an increase in the average per-fold root mean square error of $< 20\%$ between training and test data was considered acceptable, as small reductions in performance were expected on unseen data (Hastie et al., 2009; Yates et al., 2023).

The significance of fixed effects retained in final model as predictors of faunal biodiversity was determined by partial F-tests (linear models) or likelihood ratio tests (LMMs) using the *anova* function of the ‘stats’ package (R Core Team, 2025). Pairwise *post hoc* comparisons of estimated marginal means between transect positions in alley-cropping and sole-cropping were made using the *emmeans* function of the ‘emmeans’ package (v. 1.11.0, Lenth, 2025) with a Benjamini-Hochberg false discovery rate correction for multiple comparisons (Benjamini and

Hochberg, 1995; Pike, 2011). A significance threshold of $\alpha = 0.05$ was used for all tests. For LMMs, the proportion of the variance explained by fixed effects (R^2_m) and the combined fixed and random effects (R^2_c) was determined via the *r2* function of the ‘performance’ package (Lüdecke et al., 2021).

Linear and linear or generalised linear mixed-effects models were also applied to investigate the influence of alley-cropping on soil physicochemical properties, the abundance of individual faunal taxa, the taxonomic richness of EMI scores, and the number of taxa used to calculate QBS-ar scores (Model G). However, these models did not include soil physicochemical properties as fixed effects, as the interest was primarily in understanding the partitioning of these properties between agricultural systems and transect positions to explain observed differences in biodiversity, SBQ, and composition. As for models for faunal biodiversity, the random effect ‘farm’ was replaced by farm-level variables where model fit improved sufficiently.

As the QBS-ar score integrates a measure of taxonomic richness – albeit slightly less precisely than the taxonomic resolution applied here – the relationship between soil faunal taxonomic richness and QBS-ar score was investigated via a Pearson’s correlation using the *cor.test* function of the ‘stats’ package (R Core Team, 2025) to address hypothesis (iv).

To investigate how the observed impact of alley-cropping on soil fauna varied in response to the biodiversity metric selected, biodiversity profiles were generated using the *Diversity* function of the ‘SpadeR’ package (v. 0.1.1, Chao et al., 2016) (Figure 3.2C). Hill numbers, or the effective number of species, were calculated for a gradient of *q* (order of diversity) values ranging from 0 to 3, with an interval of 0.25. The smaller the *q* value, the higher the sensitivity to rare species (e.g., 0 = species richness, 1 = Shannon diversity, 2 = Simpson’s diversity, 3 = greatest emphasis on dominant species) (Chao and Chiu, 2016). Thus, it was possible to determine whether the relative diversity of alley-cropping and sole-cropping transect positions changed depending on the weight allocated to dominant versus rare species. These findings partially informed the selection of community dissimilarity indices to assess faunal community composition.

3.3.6.2 Composition

To address hypothesis (iii), the composition of soil faunal taxa and EMI scores were compared between transect positions across both systems, alley- and sole-cropping. Using the *vegdist* function of the ‘vegan’ package (v. 2.7-1, Oksanen et al., 2025), Jaccard or Bray-Curtis dissimilarity matrices were calculated from community matrices containing (i) abundance data

for faunal taxa, (ii) presence-absence data for faunal taxa, (iii) richness data for EMI scores, and (v) presence-absence data for faunal taxa with specific EMI scores (e.g., Collembola were split into seven groups according to the scores that specimens were attributed in the QBS-ar Index protocol). A $\log_{1p}(x)$ transformation was applied to abundance data to reduce the contribution of dominant species to observed dissimilarities (Legendre and Borcard, 2018). Model selection involved the same process as described in Section 3.6.1.1, but model fit was assessed using the *AICc_permanova2* function of the ‘AICcPermanova’ package v. 0.0.2 (Corcoran, 2023). Homogeneity of multivariate group dispersions was confirmed using the *betadisper* function of the ‘vegan’ package.

The influence of agricultural system and transect position, as well as selected farm-level characteristics and soil properties, was determined via PERMANOVA using the *adonis2* function of ‘vegan’. Pairwise differences between transect positions across agricultural systems were calculated using the *pairwise.adonis2* function of the ‘pairwiseAdonis’ package (v. 0.4, Martinez Arbizu, 2020). The contribution (%) of taxa or EMI scores to observed dissimilarities was determined via SIMPER analysis using the *simper* function of ‘vegan’. Faunal and EMI compositions were ordinated in two-dimensional space using principal coordinate analysis (PCoA) via the *cmdscale* function of the ‘stats’ package. A “Lingoes” constant was added to non-diagonal dissimilarities to make all eigenvalues non-negative (Legendre and Andersson, 1999). To visualise the relationship between faunal composition and explanatory variables, distance-based redundancy analysis (db-RDA) was undertaken on the Jaccard dissimilarity matrix using the *capscale* function of the ‘vegan’ package (Legendre and Anderson, 1999). Ellipses for all ordinations were generated using the *veganCovEllipse* function of the ‘vegan’ package.

Research data is available at figshare: 29930429.

3.4 Results

A total of 30 844 soil fauna belonging to 29 taxonomic groups (Table 3.B.2) and 33 QBS-ar Index groups (Table 3.B.3) were identified. Acari (mites) and Collembola (springtails) were the dominant taxa, comprising 60.6 % and 26.7 % of identified soil fauna, respectively. Annelida (earthworms and Enchytraeids) made up a further 5.1 %, with the remaining 7.6 % of fauna belonging to 20 different taxa. Of the fauna collected, 60.1 %, belonging to 29 taxa, were from alley-cropping systems, whereas 39.9 %, belonging to 27 taxa, were from sole-cropping systems. All 27 taxa observed in sole-cropping were shared with alley-cropping.

QBS-ar values were on average 121.8 ($\pm 30.3_{SD}$, range = 62–177) in alley-cropping and 99.8 ($\pm 24.8_{SD}$, range = 50–158) in sole-cropping.

3.4.1 *Abundance, taxonomic richness, and SBQ*

Alley-cropping increased all three biodiversity metrics compared to sole-cropping (Table 3.2). Agricultural system significantly influenced soil faunal abundance ($F_{(1)} = 12.21$, $p < 0.001$), taxonomic richness ($\chi^2_{(1)} = 12.13$, $p < 0.001$), and SBQ ($F_{(1)} = 17.69$, $p < 0.001$). Transect position influenced both taxonomic richness ($\chi^2_{(2)} = 6.96$, $p = 0.031$) and SBQ ($F_{(2)} = 6.19$, $p = 0.003$), whereas the interaction between agricultural system and transect position influenced only taxonomic richness ($\chi^2_{(2)} = 15.33$, $p < 0.001$). Increases were highest in tree rows but extended partially into crop alleys for some biodiversity metrics (Figures 3.2A–B and 3.3A).

Soil faunal abundance, taxonomic richness, and SBQ were all significantly higher at AC0 compared to the sole-cropping average (Table 3.2). However, alley-cropping had no influence on faunal abundance in crop alleys. In contrast, relative to sole-cropping, both taxonomic richness and SBQ were higher at AC3, but this finding was near-significant for SBQ (Table 3.2). Taxonomic richness was also significantly reduced at both sampling locations in crop alleys relative to AC0, whereas this was only true for SBQ at AC13 (Table 3.2). No improvements in soil biodiversity relative to sole-cropping were observed at AC13 (Table 3.2).

The observed influence of alley-cropping on soil faunal diversity differed depending on the metric considered. At low orders of diversity where there is a higher sensitivity to rare taxa, diversity (as expressed by Hill numbers) in alley-cropping was higher than in sole-cropping. In contrast, at higher orders of diversity reflecting a higher sensitivity to common or dominant taxa, the trend was reversed (Figure 3.2C).

Table 3.2. Comparisons of estimated marginal means generated for linear and linear-mixed effects models investigating differences in soil faunal abundance, taxonomic richness, and biological quality ('SBQ') between (i) alley-cropping ('AC') and sole-cropping ('SC') systems, (ii) sole-cropping systems and alley-cropping sampling points positioned in tree rows ('AC0'), 1.5 m intro crop alleys ('AC3'), and the centre of crop alleys ('AC13'), and (iii) alley-cropping tree rows and crop alleys. 'est' = the pairwise difference in estimated marginal means.

	Fixed effect	Model ¹	est	se	df	t	p ²
Abundance							
SC	AC	1	107.0	30.6	79.0	3.48	< 0.001
	AC0		174.9	62.1	51.0	2.81	0.034
	AC3	4	62.9	57.1	51.0	1.10	0.690
	AC13		84.3	57.9	51.0	1.46	0.471
AC0	AC3	1	-111.2	55.7	79.0	1.20	0.148
	AC13		-89.7	56.4	79.0	1.59	0.217
Taxonomic richness							
SC	AC	2	2.0	0.46	56.0	4.32	< 0.001
	AC0		3.9	0.71	51.0	5.52	< 0.001
	AC3	5	1.8	0.71	51.0	2.50	0.024
	AC13		0.36	0.71	51.0	0.51	0.610
AC0	AC3	2	-2.1	0.72	56.0	2.95	0.014
	AC13		-3.5	0.72	56.0	4.88	< 0.001
SBQ							
SC	AC	3	21.4	5.2	78.0	4.11	< 0.001
	AC0		42.4	8.2	53.0	5.16	< 0.001
	AC3	6	17.8	8.2	53.0	2.16	0.053
	AC13		6.0	8.2	53.0	0.73	0.471
AC0	AC3	3	-19.04	9.2	78.0	2.07	0.099
	AC13		-31.02	9.0	78.0	3.44	0.004

¹ Model details can be found in Table 3.A.3.

² A Benjamini-Hochberg false discovery rate correction for multiple comparisons was applied to p-values.

Taxonomic richness and SBQ were strongly correlated ($r = 0.86$, $t_{88} = 15.75$, $p < 0.001$) (Figure 3.B.7) because increases in QBS-ar scores were driven by the presence of a greater richness of QBS-ar groups (i.e. arthropod taxa).

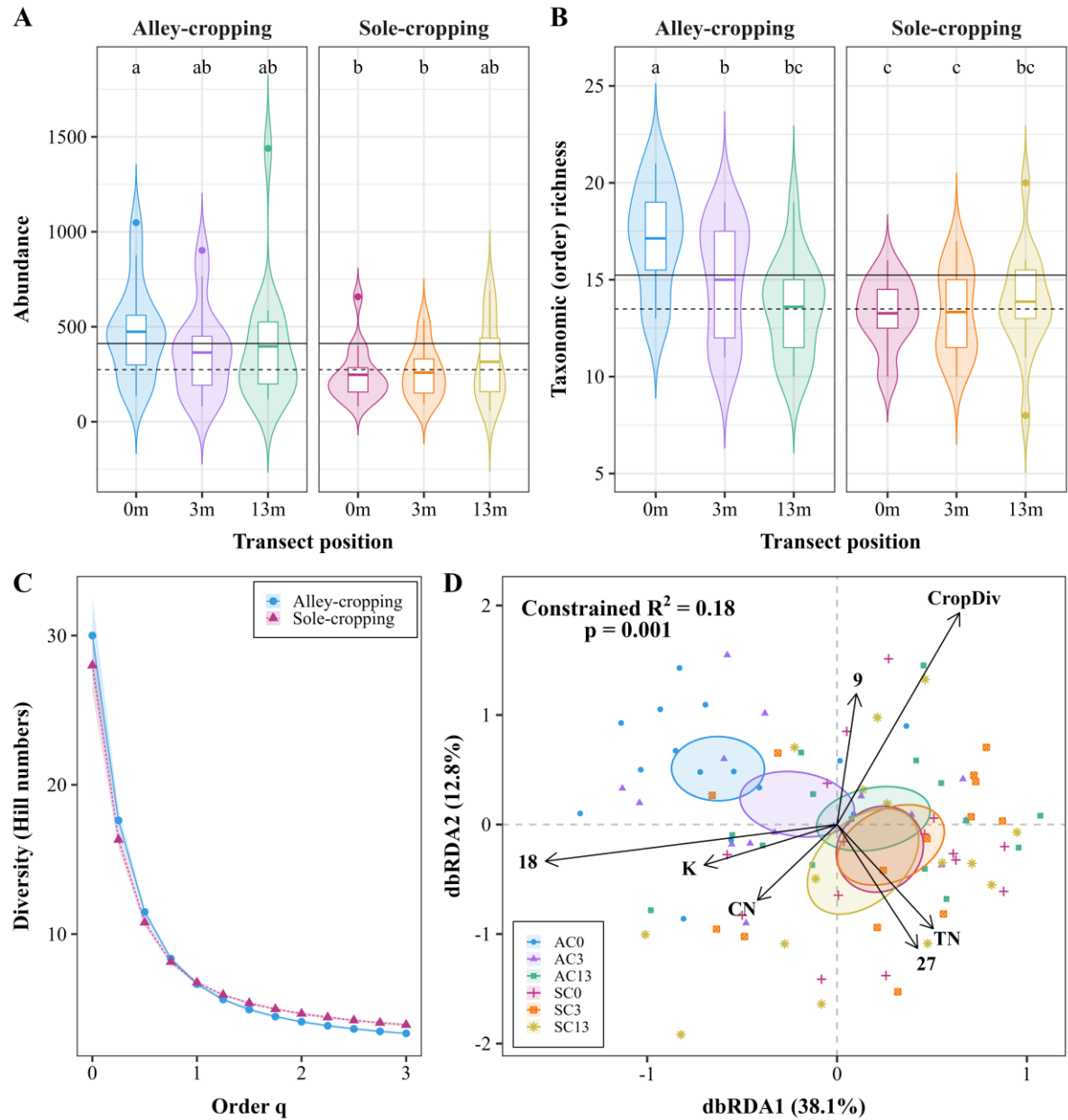


Figure 3.2. Soil faunal biodiversity in alley-cropping and sole-cropping systems. The (A) abundance, (B) taxonomic (order) richness, (C) diversity (Hill numbers) profiles, and (D) community composition of soil meso- and macro-fauna collected from 90 sampling points in alley-cropping and sole-cropping systems at five farms in England, United Kingdom. In Figures 3.2A and 3.2B, boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. Solid and dashed horizontal lines indicate the mean for alley-cropping and sole-cropping, respectively. In Figure 3.2C, shaded errors show 95 % confidence intervals. In Figure 3.2D, points represent the constrained ordination scores of individual sampling points as determined from the presence-absence of soil faunal taxa, determined by distance-based redundancy analysis (db-RDA). Ellipses display two standard errors of the centroid for each transect position in alley-cropping and sole-cropping. Percentages in brackets indicate the proportion of constrained variation explained by each axis. Arrows show the strength and direction of correlations between explanatory variables and constrained ordination axes. Only explanatory variables which demonstrated a significant relationship with faunal composition are displayed: ‘CN’ = soil C:N ratio, ‘CropDiv’ = crop diversity or the number of crops grown from 2021–2024, ‘K’ = soil exchangeable potassium concentration (mg kg^{-1}), ‘TN’ = soil total nitrogen content (g kg^{-1}), numbers 9–27 refer to soil types according to Soilscales, with Soilscale 8 as the reference type (Cranfield Soil and Agrifood Institute, 2025).

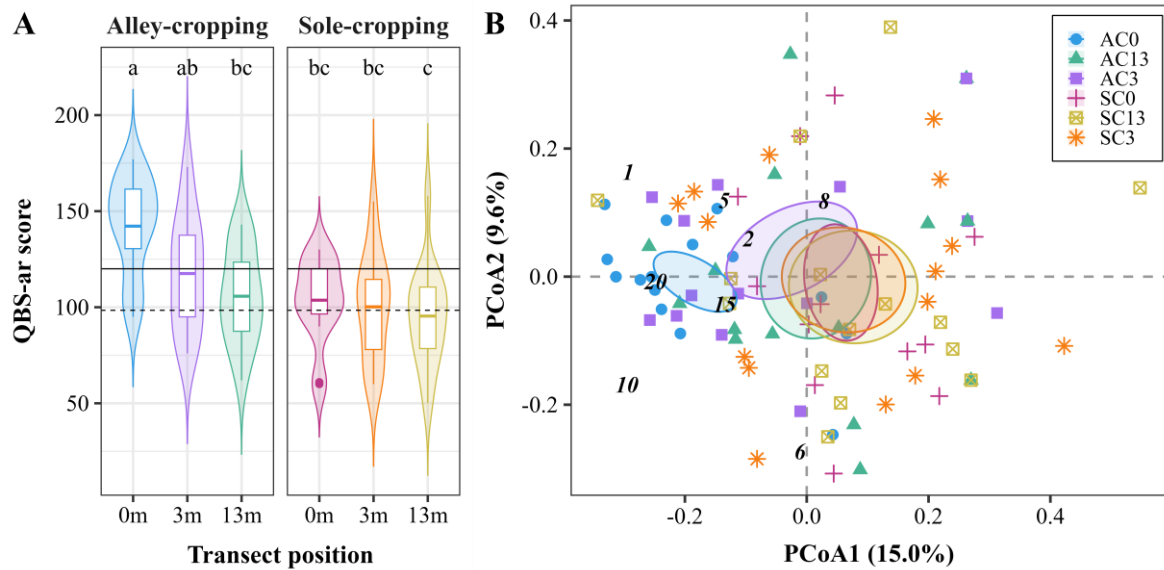


Figure 3.3. SBQ in alley-cropping and sole-cropping systems. (A) QBS-ar score of 90 sampling points in alley-cropping and sole-cropping systems at five farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. Solid and dashed horizontal lines indicate the mean for alley-cropping and sole-cropping, respectively. (B) Composition of EMI scores used to generate QBS-ar scores. Points represent the composition of individual sampling points, based on Bray-Curtis dissimilarities using the taxonomic richness of each score. Ellipses display two standard errors of the centroid. Proportions in brackets describe the total amount of variation in composition explained by each axis. EMI scores (in bold) are positioned according to their Pearson correlation with the ordination axes (site scores). AC = alley cropping; SC = sole-cropping and the respective distance in m along the transect.

3.4.2 Community composition

Alley-cropping influenced the presence and abundance of several faunal taxa (Table 3.B.2), as well as the overall composition of faunal communities. When considering only the presence but not abundance of faunal taxa, composition of soil meso- and macro-fauna differed significantly between transect positions in alley-cropping and sole-cropping (Model H; $F_{(5,84)} = 2.50$, $p = 0.001$, $R^2 = 0.11$) (Figure 3.2D). Changes in faunal composition were predominantly restricted to tree rows, which differed significantly from all sole-cropping transect positions ($p = 0.005$), as well as from AC3 ($F_{(1,21)} = 2.97$, $R^2 = 0.07$, $p = 0.026$) and AC13 ($F_{(1,21)} = 4.69$, $R^2 = 0.12$, $p = 0.008$). Faunal composition at AC3 was also significantly different to SC3 ($F_{(1,21)} = 3.12$, $R^2 = 0.08$, $p = 0.0183$) and SC13 ($F_{(1,21)} = 2.90$, $R^2 = 0.07$, $p = 0.012$). Observed differences in composition were driven by 14 taxonomic groups which contributed fairly evenly to dissimilarities (Figure 3.B.4; Table 3.B.4). Two taxonomic groups, Pseudoscorpiones and Siphonaptera, were recorded only in tree rows. No significant differences in faunal composition were identified between transect positions in the crop alley or between AC13 and sole-cropping ($p > 0.05$). Similar findings were observed for abundance-based faunal composition (Model I; Figure 3.B.5).

Compositional analysis of QBS-ar groups revealed similar findings to those for faunal taxa (see Appendix B, Section 3.9.4.2). Observed dissimilarities were driven by increased incidences of a number of taxa with EMI scores ranging from 1–20 (Figure 3.B.6; Table 3.B.4), indicating that tree rows benefitted organisms with a broad spectrum of life strategies and levels of sensitivity to disturbance. Further supporting this, AC0 exhibited a different composition of EMI scores compared to all other transect positions in alley-cropping and sole-cropping ($p < 0.05$) (Figure 3.3B; Table 3.B.4), driven by a higher richness of QBS-ar groups with EMI scores of 10, 1, 20, and 5 (in order of their contribution to observed dissimilarities) (Model G; Table 3.B.5).

3.4.3 Soil physicochemical properties

Treatment, transect position, and/or their interaction significantly altered multiple soil physicochemical properties, including bulk density, moisture content, soil temperature, pH, SOM, TC, TN, and concentrations of K^+ and Na^+ (Table 3.B.1). Soil type, temporal crop diversity, soil C:N ratio, K^+ concentration, and TN were significant predictors of soil faunal abundance, taxonomic richness, and SBQ (Table 3.3).

Table 3.3. The significance of soil physicochemical properties and system-level variables (fixed effects) as predictors of soil faunal biodiversity metrics. Changes in faunal abundance, taxonomic richness, and soil biological quality (SBQ) to a one unit increase in soil physicochemical properties or crop diversity (est) and standard errors (se) were estimated using linear mixed-effects models. χ^2/F and p-values for fixed effects were determined via ANOVA. ‘-’ indicates that a fixed effect was not included in the model for a given biodiversity metric.

Fixed ¹ effect	Abundance				Taxonomic richness				SBQ			
	est	se	χ^2/F	p	est	se	χ^2/F	p	est	se	χ^2/F	p
Soil type	NA	NA	28.39	< 0.001	NA	NA	17.94	< 0.001	NA	NA	5.49	0.002
Crop _{div}	78.1	33.0	6.19	0.015	-1.0	0.5	5.76	0.016	-	-	-	-
CEC	-0.9	0.7	1.37	0.245	-	-	-	-	-	-	-	-
CN	19.5	11.8	2.76	0.101	-	-	-	-	4.7	2.1	5.27	0.024
K	9.5	3.6	7.35	0.008	-	-	-	-	-	-	-	-
pH	97.4	83.3	1.55	0.218	0.4	1.2	0.06	0.810	-	-	-	-
Temp _{avg}	-46.3	32.5	1.81	0.182	-0.3	0.6	0.40	0.530	-7.0	6.2	1.27	0.263
TN	9.5	6.5	2.13	0.149	-	-	-	-	2.9	1.2	5.98	0.017
BD	-	-	-	-	0.7	1.9	0.07	0.800	-	-	-	-

¹ Fixed effects: ‘Soil type’ = Soil type according to the Soilscales Viewer online soil reporting tool (Cranfield Soil and Agrifood Institute, 2025), ‘Crop_{div}’ = the number of crops grown between 2021–2024, ‘CEC’ = soil cation exchange capacity (meq 100g⁻¹), ‘CN’ = soil C:N ratio, ‘K’ = soil exchangeable potassium concentration (mg kg⁻¹), ‘Temp_{avg}’ = average soil temperature (°C) at 10 cm depth across three sampling events, ‘TN’ = soil total N concentration (g kg⁻¹), ‘BD’ = soil bulk density (g cm⁻³).

Soil type explained all farm-level variation in abundance and SBQ and part of the farm-level variation in taxonomic richness. Soil faunal abundance, taxonomic richness, and SBQ were reduced in Soilscape 8 relative to the remaining soil types (Figure 3.4). Soil faunal abundance was also lower in Soilscape 18 compared to Soilscape 9 (Figure 3.4A).

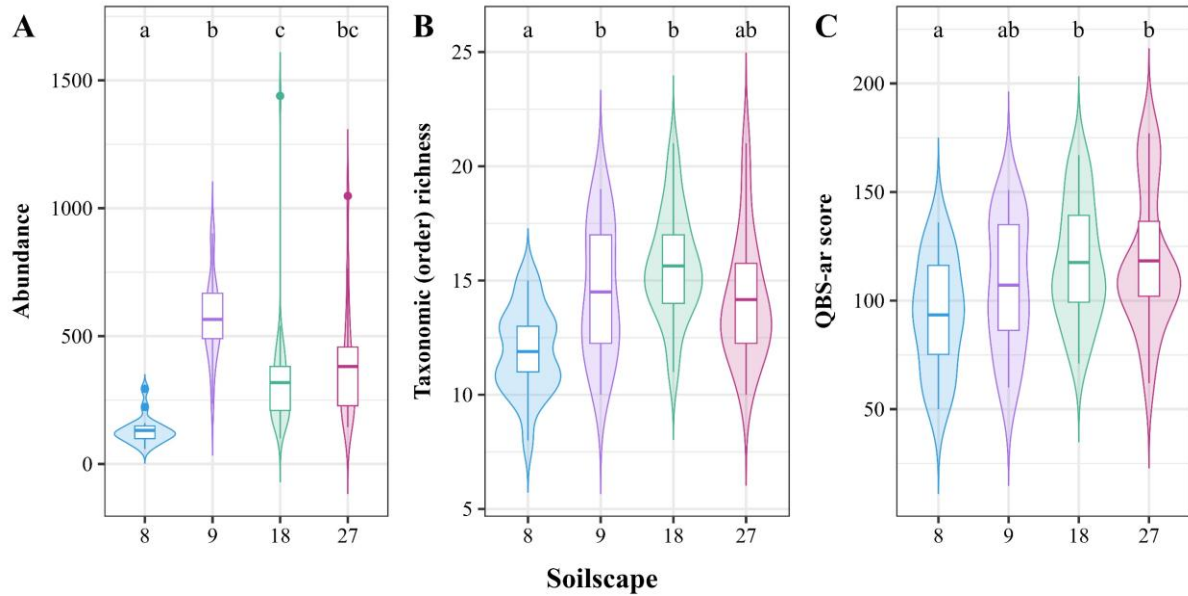


Figure 3.4. Soil faunal (A) abundance, (B) taxonomic (order) richness, and (C) QBS-ar score (SBQ) according to soil type. Soil types were classified according to the Soilsclapes Viewer online soil reporting tool hosted by Cranfield University (Cranfield Soil and Agrifood Institute, 2025): ‘8’ = “slightly acid loamy and clayey soils with impeded drainage”, ‘9’ = “lime-rich loamy and clayey soils with impeded drainage”, ‘18’ = “slowly permeable seasonally wet slightly acid but base-rich loamy and clayey soils”, and ‘27’ = “fen peat soils”. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. No shared letter indicates a significant pairwise difference between soil types for a given biodiversity metric.

As for faunal α -diversity, soil type ($F_{(3)} = 7.31$, $p = 0.001$, $R^2 = 0.15$), crop diversity ($F_{(1)} = 2.86$, $p = 0.008$, $R^2 = 0.02$), C:N ratio ($F_{(1)} = 2.54$, $p = 0.016$, $R^2 = 0.02$), exchangeable K concentration ($F_{(1)} = 2.30$, $p = 0.009$, $R^2 = 0.02$), and TN ($F_{(1)} = 2.57$, $p = 0.019$, $R^2 = 0.02$) were significant predictors of faunal Jaccard composition (Figure 3.2D). In contrast, only soil type ($F_{(3)} = 2.60$, $p = 0.001$, $R^2 = 0.07$), MC_{high} ($F_{(1)} = 1.95$, $p = 0.026$, $R^2 = 0.02$), and TN ($F_{(1)} = 3.16$, $p = 0.001$, $R^2 = 0.03$) were significant predictors of QBS-ar group Jaccard composition.

3.5 Discussion

This study is the first in Europe to comprehensively assess soil meso- *and* macro-faunal communities within alley-cropping systems. As such, it provides novel insight into how soil biodiversity, particularly of understudied groups such as meso-fauna and endogean arthropods (Kletty et al., 2023), respond to tree rows. It was hypothesised that compared to sole-cropping, alley-cropping would increase soil faunal abundance, taxonomic richness, and soil biological quality (SBQ) and drive a shift in faunal composition towards rare and more disturbance-sensitive taxa. However, it was predicted that these benefits would be restricted to tree rows due to the disturbance of faunal communities in crop alleys by agronomic activity.

3.5.1 The impact of alley-cropping on faunal biodiversity

As hypothesised, alley-cropping enhanced faunal abundance, taxonomic richness, and SBQ relative to sole-cropping. Increases were predominantly restricted to tree rows, but increases in taxonomic richness, and to a lesser extent SBQ, were observed at 1.5 m into crop alleys. These findings demonstrate that tree rows can increase the biodiversity of soil meso- and macro-fauna in arable systems, both in tree rows and arable crop areas close to tree rows. Previous research from temperate alley-cropping systems have reported similar increases in soil faunal taxa in and around tree rows (Beule et al., 2025; Gavinelli et al., 2024; Pardon et al., 2019). However, the inconsistent response of different faunal taxa to tree rows (Kletty et al., 2023) and the focus of previous research on limited subsets of soil fauna (Beule et al., 2025) has made it difficult to determine whether the net effect of alley-cropping on the biodiversity of soil faunal communities is positive. The current research shows that, despite the variable response of faunal taxa to alley-cropping, introducing tree rows to arable land improves the biodiversity of whole meso- and macro-faunal communities, offsetting the detrimental effects of intensive management (Tsiafouli et al., 2015; Turbé et al., 2011).

Higher faunal abundance and taxonomic richness led to a distinct faunal composition in tree rows compared to arable crop areas, as well as compositional shifts at 1.5 m into crop alleys compared to sole-cropping. These patterns align with broader findings that afforestation, even at small spatial scales, can reshape soil meso- and macro-faunal communities (Malica et al., 2022). Compositional shifts were largely driven by increases rather than declines in abundances of dominant taxa (e.g., Acari, Collembola, and Oligochaeta) and the presence of uncommon taxa (e.g., Isopoda, Thysanoptera, Protura, Araneae, and Geophilomorpha), showing that the effect of alley-cropping was broadly positive across faunal taxa. Indeed, contrary to the prediction that alley-cropping would especially benefit disturbance-sensitive taxa, compositional analysis using the QBS-ar Index revealed that tree rows supported more taxa with EMI scores of 1, 5, 10, and 20, representing multiple levels of soil adaptation and resistance. These findings demonstrate that alley-cropping tree rows are an important refuge and resource for soil fauna with diverse life-history strategies and functional roles, potentially resulting to improved ecosystem multifunctionality in and near tree rows (Delgado-Baquerizo et al., 2020; dos Santos Nascimento et al., 2025; Schittko et al., 2022)

Biodiversity gains in tree rows were likely the result of (i) reduced disturbance from agronomic activity (e.g., tillage, weeding, direct application of agrochemicals), (ii) enhanced habitat and resource availability, diversity, and quality associated with diverse understory vegetation and a

developed litter layer (Boinot et al., 2019; Pardon et al., 2019), and (iii) microclimatic improvements (e.g., shade, wind speeds, and soil and air humidity) in the vicinity of trees (Jacobs et al., 2022). In the current research, most farms were under minimum tillage, but crop alley soils experienced physical disturbance during cultivation, weeding, and occasional tillage or ploughing. In contrast, tree rows were left undisturbed and allowed to develop diverse UVS and layers of surface litter and humus.

Higher plant diversity and the presence of litter layers increase soil faunal biodiversity through habitat and resource diversification (Wei et al., 2022; Zhang et al., 2022) and buffering of soil microclimates (Rolo et al., 2023; Xiu-Canché et al., 2025), which reduces the physiological stress on less mobile faunal taxa (Aupic-Samain et al., 2020). Reduced physical disturbance also alters the composition of soil meso- and macro-fauna (Cannon et al., 2025) in favour of disturbance sensitive groups such as Oribatida (Betancur-Corredor et al., 2022). Indeed, faunal taxa that overwinter or spend part of their life cycle in soils, and those seeking refuge from adverse environmental conditions, are more common in tree rows than crop alleys (Boinot et al., 2019b; D'Hervilly et al., 2024).

Biodiversity gains in tree rows were also partially explained by increases in soil K^+ and TN concentrations, which enhanced soil faunal abundance and SBQ, respectively. Soil K^+ and N are essential to the growth of plants and microbial biomass (Leghari et al., 2016; Schwalb et al., 2024), which act as direct resources for soil fauna through their living and dead biomass (Betancur-Corredor et al., 2023; Liu et al., 2023; Potapov et al., 2022). Plant roots and microbial biomass also indirectly support the survival, reproduction, and movement of soil fauna by improving soil structure and the distribution of SOM in soils to form unique, stable microhabitats and enhance pore connectivity (Angers and Caron, 1998; Jensen et al., 2019; Mueller et al., 2024). Alternatively, as the decomposition of litter and organic matter are both major sources of soil nutrients (Yang et al., 2022), as well food sources for soil fauna (Potapov et al., 2022), here K^+ and N concentrations may have been acting as proxies for higher resource availability in tree rows. However, given the role that soil fauna play in decomposition (García-Palacios et al., 2013; Handa et al., 2014), it is possible that the causal relationship between soil nutrients and faunal biodiversity observed in the current research was in reality reversed or even cyclical and should thus be interpreted with caution.

Contrary to the hypothesis that agronomic disturbance would negate any positive influence of tree rows on crop alleys, taxonomic richness and SBQ were increased at 1.5 m into the crop alley relative to sole-cropping. Biodiversity gains at 1.5 m into crop alleys may be the result of

changes to soil conditions and resource availability in proximity to tree rows (Pardon et al., 2017; Guillot et al., 2021; Swieter et al., 2021), although tree rows had no discernible influence on measured soil physicochemical properties in crop alleys in the current research. That both mobile taxa and arthropods with limited mobility (e.g., Pauropoda, Protura, and Diplura) demonstrated higher incidences at 1.5 m into crop alleys suggests both unmeasured soil improvements and spill-over of fauna from tree rows may be contributing mechanisms.

A global review of agroforestry's impacts on soil fauna found no systematic effect of tree rows on crop alleys (Marsden et al., 2020), though some studies have reported small spatial gradients in faunal abundance or density extending short distances into crop alleys (D'Hervilly et al., 2021,2022; Pardon et al., 2020; Park et al., 1994). Findings from the current research thus strengthen the evidence that tree rows can increase faunal biodiversity in crop alleys and show, for the first time, that they significantly influence meso- and macro-faunal community composition beyond the tree-row boundary. This may enhance faunal-mediated soil functions involved in nutrient cycling, soil structure maintenance, and pest regulation (Briones, 2018), potentially benefitting crop productivity and partially offsetting losses associated with tree-crop competition.

3.5.2 Farm- and system-level drivers of faunal biodiversity

In this study, alley-cropping impacts were broadly consistent across farms, but a strong farm-level influence on faunal biodiversity was evident. These differences were explained by a combination of soil type and temporal crop diversity. At the field scale, soil C:N ratio also significantly influenced SBQ. Soil type exerts a strong influence on soil faunal communities because it integrates physical, chemical, biological, and hydrological properties that determine habitat and resource availability and quality (Lavelle et al., 2022; Peng et al., 2022b). Faunal biodiversity was possibly lower in Soilscape 8 relative to the remaining soil types because it is characterised by impeded drainage and periodic waterlogging (Cranfield Soil and Agrifood Institute, 2025). Period waterlogging creates anaerobic soil conditions which result in faunal mortality or migration (Ausden et al., 2001; Kiss et al., 2021) and heightens the risk of soil structural degradation negatively impacting upon faunal taxa (Beylich et al., 2010). Although Soilscape 9 also experiences impeded drainage, the farm located in Soilscape 8 (N1) experiences cooler and wetter conditions compared to the farm in Soilscape 9 (C1) (Met Office, 2025), increasing the risk of waterlogging. Seasonal waterlogging and compaction risk in Soilscape 18 may also explain its lower faunal abundance relative to Soilscape 9.

Temporal crop diversity (between 2021–2024) increased faunal abundance but reduced taxonomic richness. Declines in taxonomic richness in systems with higher rotation diversity are assumed to be the result of more frequent and intensive disturbance (Struijk et al., 2026). This was not the case at farm C2, which grew only one crop (low temporal crop diversity) but cultivated their fields annually (high disturbance). However, the impact of physical disruption on taxonomic richness may have been less evident at this farm due to its more coarse-textured soils (Cooper et al., 2025). Increases in faunal abundance with temporal crop diversity may reflect the population growth of disturbance-resistant taxa where disturbance has enhanced resource availability (e.g., by incorporating residues into soils) or alleviated issues with soil drainage and compaction.

As for soil K^+ and TN, the influence of soil C:N ratio on SBQ was likely indirect, mediated through its effects on plant growth, microbial biomass, and nutrient cycling. The positive impact of soil C:N ratio on SBQ, but not taxonomic richness, suggests that higher soil C:N ratios are particularly beneficial for arthropod taxa with high soil adaptation levels. Higher C:N ratios typically indicate greater plant-derived C inputs, slower fungal-dominated decomposition pathways, and more persistent organic horizons (Castañeda-Gómez et al., 2023; Heděnek et al., 2023). These conditions increase resource heterogeneity and provide more complex and stable microhabitats for arthropod taxa with higher EMI scores (e.g., 10–20).

3.5.3 *Suitability of the QBS-ar Index*

Applications of the QBS-ar Index in the UK remain limited (see Menta et al., 2018), particularly within agricultural settings. This study therefore offers valuable early insight into the index's suitability as a bioindicator in UK agricultural soils. QBS-ar scores across sampled farms ranged from 50–177, consistent with values reported for UK soils and international agricultural lands and woodlands (Menta et al., 2018). All sampling points exceeded the European continent-wide threshold for “good quality” soils (93.7) (Menta et al., 2018).

The QBS-ar Index was a practical option for assessing the impacts of alley-cropping on soil fauna, which yielded similar findings to an assessment of order-level taxonomic richness but required less sample processing time and taxonomic expertise to apply. As predicted in the study's fourth hypothesis, QBS-ar scores were highly correlated with order-level taxonomic richness but provided additional information on the degree of faunal adaptation to soils, supporting a more nuanced interpretation of community composition without requiring detailed knowledge of individual taxa. However, the QBS-ar Index was less sensitive than taxonomic

assessment to fine-scale trends in soil faunal communities in response to physicochemical changes occurring within crop alleys. Consequently, the index may be best applied alongside, rather than instead of, low resolution taxonomic biodiversity measures.

3.5.4 Study limitations

Interpretation of this study's findings should involve consideration of its limitations. First, although earthworms, Enchytraeids, and several epigeal taxa were recorded, the sampling approach was optimised for hemi-edaphic and endogean arthropods. As such, the results complement previous studies focusing on earthworms (Cardinael et al., 2019; D'Hervilly et al., 2021; Vaupel et al., 2023) or epigeal and overwintering fauna sampled via pitfall or emergence traps (Boinot et al., 2019b, 2020; Matevski et al., 2024; Pardon et al., 2019, 2020). Second, Protura were identified to class rather than order, which may have introduced minor bias in biodiversity indices. However, as only two Proturan orders occur in England (Acerentomata and Eosentomata) and the class represented just 0.30 % of recorded fauna, any effect on estimates of faunal biodiversity was expected to be negligible. Third, sampling occurred only in spring and autumn. The absence of winter and late-summer sampling, periods when fauna may use tree rows as refuges from adverse environmental conditions, may have resulted in an underestimation of alley-cropping's positive effects. Finally, although paired alley-cropping and sole-cropping fields were managed identically at three of the five sampled farms, differences in crop rotations (2021–2024), and therefore disturbance regimes, occurred at two farms (S1 and S2).

Crop rotation phase is known to influence soil faunal groups such as Acari, Collembola, and earthworms (Struijk et al., 2026), potentially confounding the effect of tree rows on crop alleys at farms S1 and S2. Differences in crops grown in 2021 (two years before sampling commenced) at farm S2 were accounted for through the inclusion of 'temporal crop diversity' in final models. Crops cultivated in 2023 and 2024 were also evaluated as fixed effects to capture rotation differences at farm S1 but explained less variation in faunal biodiversity than soil type, a variable they both correlated strongly with. Including either crop variable in final models neither changed significance patterns nor meaningfully altered estimates of pairwise differences between alley-cropping and sole-cropping. It was therefore considered unlikely that crop-rotation differences at S1 or S2 materially affected the conclusions regarding tree row influences on crop alleys.

3.6 Conclusions

Several studies have explored whether alley-cropping agroforestry can offset the impacts of intensive agriculture on soil fauna, showing that tree rows can enhance the abundance, density, and richness of various taxa in temperate farmland. However, soil meso-fauna and endogean fauna have been largely overlooked in existing literature and few studies have characterised the biodiversity of faunal communities, rather than a subset of taxa, in temperate alley-cropping systems. As a result, understanding of soil faunal responses to alley-cropping remains incomplete, particularly for faunal groups which are most sensitive to disturbance.

This study found that, across five commercial arable farms in England, United Kingdom, alley-cropping had a strongly positive effect on soil faunal biodiversity. Relative to sole-cropping, alley-cropping increased faunal abundance, taxonomic richness, and soil biological quality (determined by the QBS-ar Index). Community composition in alley-cropping systems also shifted to support both higher abundances of dominant taxa and increased occurrences of rare and uncommon taxa representing a range of life strategies and degrees of dependence on undisturbed soil. Alley-cropping benefits were greatest in tree rows but increases in taxonomic richness and soil biological quality, as well as compositional shifts, were also evident at 1.5 m into the crop alley. Changes to faunal biodiversity in alley-cropping tree rows, but not crop alleys, were partially attributed to increases in soil exchangeable K concentration, total N content, and maximum moisture content.

Higher soil faunal biodiversity in alley-cropping systems could, at least partially, offset the detrimental effects of intensive agriculture on soil biodiversity and function, as well as contribute to biodiversity gains in wider arable landscapes. Nevertheless, further research is needed to substantiate findings from the current research, particularly studies incorporating temporal analyses of faunal communities and investigations into the mechanistic drivers underlying observed faunal patterns. Further validation of the QBS-ar Index in UK agricultural systems is also recommended to overcome practical barriers to widespread, standardised soil faunal assessments or alternatively provide valuable complementary insights into faunal responses to agricultural management.

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3.7 References

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3.8 Appendix A | Additional methodological details

Contents

3.8.1. Alley-cropping tree species

Table 3.A.1

3.8.2. Quality control data for soil nutrient concentrations

Table 3.A.2

3.8.3. Model details

Table 3.A.3

3.8.4. Influence of farm on faunal biodiversity

Table 3.A.4

3.8.1 Alley-cropping tree species

Table 3.A.1: Tree species in alley-cropping systems at five farms in England, United Kingdom.

Farm	Tree species
C1	<i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Alnus cordata</i> , <i>Aronia melanocarpa</i> , <i>Betula pendula</i> , <i>Carpinus betulus</i> , <i>Castanea sativa</i> , <i>Corylus avellana</i> , <i>Corylus maxima</i> , <i>Cydonia oblonga</i> , <i>Ilex aquilifolium</i> , Jostaberry (<i>Ribes x nidigrolaria</i>), <i>Juglans regia</i> , <i>Malus domestica</i> , <i>Mespilus germanica</i> , <i>Prunus avium</i> , <i>Prunus domestica</i> , <i>Prunus dulcis</i> , <i>Pyrus communis</i> , <i>Quercus sp.</i> , <i>Salix caprea</i> , <i>Sambucus canadensis</i> , <i>Sambucus nigra</i> , <i>Tilia cordata</i>
C2	<i>Malus domestica</i>
N1	<i>Castanea sativa</i> , <i>Juglans regia</i> , <i>Malus domestica</i> , <i>Malus sylvestris</i> , <i>Sambucus sp.</i>
S1	<i>Acer pseudoplatanus</i> , <i>Castanea sativa</i> , <i>Fagus sylvatica</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Quercus robur</i>
S2	<i>Juglans regia</i> , <i>Malus domestica</i> , <i>Prunus domestica</i>

3.8.2 Quality control data for soil nutrient concentrations

Table 3.A.2: Quality control information for soil carbon and nutrient concentrations. Values provided represent the mean (and range) across analytical runs, except for precision, which provides the median (and range).

Element ¹	Accuracy ² (%)	DL ³ (mg kg ⁻¹)	Precision ⁴ (%)
Al (mg kg ⁻¹)	114.0 (110.9-116.7)	7.4 (6.1-8.3)	25.2 (20.5-95.9)
Ca (mg kg ⁻¹)	106.3 (104.8-107.5)	154.9 (9.4-443.1)	0.84 (0.79-1.5)
Fe (mg kg ⁻¹)	43.8 (36.9-55.2)	4.5 (3.3-4.1)	32.9 (12.2-41.5)
K (mg kg ⁻¹)	122.1 (117.8-126.8)	79.9 (13.7-153.4)	7.5 (6.2-12.5)
Mg (mg kg ⁻¹)	109.6 (109.3-109.9)	4.2 (0.24-11.5)	0.7 (0.5-1.4)
Mn (mg kg ⁻¹)	111.0 (109.7-112.0)	1.1 (0.68-1.3)	2.1 (1.2-7.6)
Na (mg kg ⁻¹)	116.3 (113.5-118.2)	56.6 (0-126.8)	7.1 (6.2-13.4)
TC (g kg ⁻¹)	104.6 (100.9-110.6)	17.4 (17.4-21.2)	2.85 (0.4-6.0)
TN (g kg ⁻¹)	98.4 (93.2-105.1)	1.5 (1.0-1.7)	4.7 (0.0-8.7)

¹ Element concentrations were determined via ICP-OES, except for TC and TN which were calculated via elemental analysis.

² For ICP-OES, instrumental accuracy was determined through analysis of Merck ICP multi-element standard solution IV at a concentration of 0.25 mg L⁻¹. Accuracy for TC and TN was determined via analysis of 20 mg of a soil reference standard material (0.13 % N, 1.55 % C).

³ Detection limits were determined by ten repeat analyses of a calibration blank (or nine for TC and TN) (Walsh, 1997). Concentrations are provided in mg kg⁻¹ excluding TC and TN which are in g kg⁻¹.

⁴ Precision was determined through duplicate analysis of 10 % of samples on each analytical run (Gill and Ramsey, 1997). Values presented are the median precision (and range).

3.8.3 Model details

Table 3.A.3: Model structures used to estimate the influence of alley-cropping, farm-level characteristics, and soil physicochemical properties on soil faunal biodiversity. Fixed effects in bold were retained in reduced models used to assess the influence of alley-cropping on soil faunal biodiversity.

Model name	Model type ¹	Response variable ²	Random effects ³	Fixed effects ⁴	Error structure
1	LM	sqrt(Abundance)	NA	Agricultural system * Transect position + Soil type + Crop_{div} + CEC + C:N ratio + K + pH + Temp_{avg} + TN	Gaussian
2	LMM	Taxonomic richness	Transect	Agricultural system * Transect position + Soil type + Crop_{div} , BD + pH + Temp_{avg}	Gaussian
3	LM	QBS-ar score	NA	Agricultural system * Transect position + Soil type + Crop_{div} + C:N ratio + Temp_{avg} + TN	Gaussian
4	LM	sqrt(Abundance)	NA	Positions_{Cavg} + Soil type + Crop_{div} + CEC + C:N ratio + K + pH + Temp_{avg} + TN	Gaussian
5	LMM	Taxonomic richness	Transect	Positions_{Cavg} + Soil type + Crop_{div} + BD + pH + Temp_{avg}	Gaussian
6	LM	QBS-ar score	NA	Positions_{Cavg} + Soil type + Crop_{div} + C:N ratio + Temp_{avg} + TN	Gaussian
7	LM	Richness _{EMI} or richness _{QBS}	NA	Agricultural system * Transect position + Soil type + Crop _{div}	Gaussian
8	PERM	Jaccard dissimilarity matrix (taxa)	NA	Agricultural system * Transect position + Soil type + Crop_{div} + BD + CEC + C:N ratio + K + MC_{range} + pH + Temp_{low} + TN	NA
9	PERM	Bray-Curtis dissimilarity matrix (taxa)	NA	Agricultural system * Transect position + Soil type + Crop_{div} + BD + CEC + C:N ratio + K + MC_{range} + pH + Temp_{low} + TN	NA
10	PERM	Jaccard dissimilarity matrix (QBS-ar groups)	NA	Agricultural system * Transect position + Soil type + Crop_{div} + CEC + C:N ratio + MC_{high} + pH + Temp_{low} + TN	NA

¹ Model types: LM = linear model; LMM = linear mixed effects model; PERM = permutational multivariate analysis of variance.

² Response variables: abundance = number of individuals; taxonomic richness = number of taxonomic orders; QBS-ar score, calculated according to the QBS-ar Index; richness_{EMI} = number of faunal taxa attributed a given EMI score (1–20) as their maximum; richness_{QBS} = number of faunal taxa contributing to a given QBS-ar score.

³ Random effects: transect = a 30-level factor indicating the experimental transect; NA = no random effect included in model.

⁴ Fixed effects: agricultural system = a two-level factor indicating the farming system (alley-cropping or sole-cropping); transect position = a three-level factor (0, 3, or 13 m) indicating distance (m) along the experimental transect; positions_{Cavg} = a four-level factor including three transect positions in alley-cropping and the average across transect positions for each transect in sole-cropping; soil type = Soilscape (Cranfield Soil and Agrifood Institute, 2025); crop_{div} = number of crops grown between 2021–2024; BD = bulk density (g cm⁻³); CEC = cation exchange capacity (meq 100 g⁻¹); K = exchangeable potassium concentration (mg kg⁻¹); MC_{high} = highest soil moisture content measured across the sampling events (g H₂O 100g⁻¹); MC_{range} = difference in moisture content between the lowest and highest recorded values at a given sampling point; temp_{low} = lowest soil temperature measured across the sampling events (°C), TN = total nitrogen (mg kg⁻¹), C:N = carbon-to-nitrogen ratio.

3.9 Appendix B | Additional Results

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3.9.1 Soil physicochemical properties in alley-cropping and sole-cropping systems

Table 3.B.1: Mean ($\pm$ standard deviation) of soil physicochemical properties measured at 90 sampling points (0–15 cm soil depth) in paired alley-cropping ('AC') and sole-cropping ('SC') systems at five farms in England, United Kingdom. The influence of agricultural system ('S'; alley-cropping or sole-cropping), transect position ('TP'; 0m, 3m, or 13m), and their interaction ('S*TP') on soil physicochemical properties as determined by linear mixed models are indicated by the following: ns = not significant, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. No shared superscript letter indicates a statistically significant pairwise difference, as determined by post-hoc comparisons of estimated marginal means using a false discovery rate correction for multiple comparisons.

Soil properties ¹	Alley-cropping			Sole-cropping			Fixed effects		
	Row	Edge	Centre	Row	Edge	Centre	S	TP	S*TP
Temp _{avg} (°C)	9.72 ^a ± 0.31	10.24 ^b ± 0.61	10.14 ^{ab} ± 0.53	9.81 ^{ab} ± 0.65	9.93 ^{ab} ± 0.73	9.94 ^{ab} ± 0.72	ns	***	*
Temp _{low} (°C)	7.83 ^a ± 0.83	8.64 ^b ± 0.76	8.63 ^b ± 0.64	8.11 ^{ab} ± 0.79	8.27 ^{ab} ± 0.81	8.35 ^{ab} ± 0.78	ns	**	ns
Temp _{high} (°C)	11.77 ^a ± 1.13	12.63 ^b ± 1.16	12.47 ^b ± 0.90	11.86 ^{ab} ± 1.76	11.98 ^{ab} ± 1.73	11.97 ^{ab} ± 1.87	ns	**	*
Temp _{range} (°C)	3.93 ^{ns} ± 1.88	3.99 ^{ns} ± 1.15	3.83 ^{ns} ± 0.90	3.75 ^{ns} ± 2.11	3.71 ^{ns} ± 1.85	3.62 ^{ns} ± 2.22	ns	ns	ns
MC _{avg} (g 100g ⁻¹)	39.73 ^a ± 12.51	30.89 ^b ± 11.75	30.65 ^b ± 11.33	33.14 ^b ± 9.58	33.13 ^b ± 10.86	33.33 ^b ± 10.83	ns	***	***
MC _{low} (g 100g ⁻¹)	34.58 ^a ± 11.57	26.61 ^b ± 10.95	26.29 ^b ± 11.73	29.59 ^c ± 9.31	29.57 ^c ± 11.24	29.64 ^c ± 11.25	ns	***	***
MC _{high} (g 100g ⁻¹)	46.02 ^a ± 16.23	34.63 ^b ± 12.86	34.42 ^b ± 11.16	36.65 ^b ± 10.37	36.39 ^b ± 10.73	36.44 ^b ± 11.30	ns	***	***
MC _{range} (g)	11.44 ^{ns} ± 12.00	8.02 ^{ns} ± 3.51	8.14 ^{ns} ± 6.54	7.06 ^{ns} ± 4.36	6.82 ^{ns} ± 3.60	6.80 ^{ns} ± 2.95	ns	ns	ns
BD (g cm ⁻³)	0.88 ^a ± 0.21	1.04 ^b ± 0.25	1.05 ^b ± 0.24	0.99 ^{ab} ± 0.21	1.01 ^{ab} ± 0.22	1.01 ^b ± 0.23	ns	**	*
SOM (g 100g ⁻¹)	11.01 ^a ± 10.57	9.34 ^b ± 9.70	9.38 ^b ± 9.65	9.61 ^b ± 9.92	9.63 ^b ± 9.91	9.74 ^b ± 10.18	ns	***	***
TC (g kg ⁻¹)	59.38 ^a ± 53.81	51.17 ^b ± 50.50	51.49 ^b ± 49.66	57.37 ^{ab} ± 55.26	56.69 ^{ab} ± 54.71	55.95 ^{ab} ± 53.76	ns	***	**
TN (g kg ⁻¹)	4.38 ^a ± 3.62	3.76 ^b ± 3.46	3.78 ^b ± 3.31	4.87 ^{ab} ± 5.51	4.79 ^{ab} ± 4.94	4.76 ^{ab} ± 5.00	ns	***	***
CN	13.19 ^{ns} ± 1.49	13.16 ^{ns} ± 1.69	13.03 ^{ns} ± 1.45	12.27 ^{ns} ± 2.49	12.22 ^{ns} ± 2.43	12.27 ^{ns} ± 2.55	ns	ns	ns
pH	7.00 ^a ± 0.76	7.15 ^{ab} ± 0.71	7.23 ^b ± 0.61	7.02 ^{ab} ± 0.59	6.99 ^{ab} ± 0.57	6.93 ^{ab} ± 0.66	ns	ns	*
CEC (meq 100g ⁻¹)	13.11 ^{ns} ± 7.19	13.51 ^{ns} ± 8.07	13.86 ^{ns} ± 8.72	13.32 ^{ns} ± 7.19	23.49 ^{ns} ± 26.62	23.62 ^{ns} ± 38.12	ns	*	ns
Ca (mg kg ⁻¹)	6559.4 ^{ns} ± 4003.6	6455.6 ^{ns} ± 4394.6	6681.3 ^{ns} ± 4776.7	6325.2 ^{ns} ± 4237.5	9209.2 ^{ns} ± 11461	6300.1 ^{ns} ± 3909.3	ns	ns	ns
K (mg kg ⁻¹)	650.4 ^a ± 953.0	344.7 ^b ± 184.8	354.1 ^b ± 193.6	245.4 ^b ± 60.60	258.2 ^b ± 85.39	332.4 ^b ± 304.6	**	ns	*
Mg (mg kg ⁻¹)	447.86 ^{ns} ± 321.56	554.02 ^{ns} ± 1007.6	680.85 ^{ns} ± 806.16	745.04 ^{ns} ± 1004.3	950.51 ^{ns} ± 1299.1	720.64 ^{ns} ± 923.21	ns	ns	ns
Mn (mg kg ⁻¹)	13.50 ^{ns} ± 18.94	10.18 ^{ns} ± 11.79	14.20 ^{ns} ± 19.79	7.67 ^{ns} ± 6.06	8.34 ^{ns} ± 7.13	10.07 ^{ns} ± 8.56	ns	ns	ns
Na (mg kg ⁻¹)	59.61 ^{ns} ± 63.02	64.61 ^{ns} ± 66.76	62.19 ^{ns} ± 64.10	78.25 ^{ns} ± 57.98	77.48 ^{ns} ± 62.11	76.23 ^{ns} ± 57.56	*	ns	ns

¹ Abbreviations: 'BD' = bulk density (g cm⁻³), 'CEC' = cation exchange capacity (meq 100 g⁻¹), 'MC_{avg}' = average moisture content across all sampling periods (g 100 g⁻¹), 'MC_{low/high}' = the lowest/highest soil moisture content measured across the three sampling events, 'SOM' = organic matter content (g 100 g⁻¹), 'Temp_{avg}' = average soil temperature across all sampling periods (°C), 'Temp_{low/high}' = the lowest/highest soil temperature measured across the three sampling events, 'TC' = total carbon (mg kg⁻¹), 'TN' = total nitrogen (mg kg⁻¹), and 'CN' = the ratio of carbon to nitrogen; 'MC_{range}' and 'Temp_{range}' range provide the difference in moisture content and soil temperature between the lowest and highest recorded values at any given sample point, respectively.

3.9.2 Identified soil faunal taxa

Table 3.B.2: The mean ($\pm$ standard deviation) abundance of soil faunal taxa (orders) measured in paired alley-cropping and sole-cropping systems at five farms in England, United Kingdom. Soil fauna were collected from 90 sampling points at three distances along ten linear transects: ‘0m’ = 1.5 m into the tree row, ‘3m’ = 1.5 m into the crop alley, ‘13m’ = the centre of the crop alley; distances were replicated in sole-cropping systems, without the presence of tree rows. Values in brackets next to taxa names indicate the range of ecomorphological index scores individuals were attributed, according to the QBS-ar Index; values in brackets below abundance values indicate the proportion of sampling points for that agricultural system and transect position in which the taxonomic group was observed. Different superscript letters indicate a statistically significant difference in abundance between transect positions, as determined by LMMs and Tukey post-hoc comparisons.

	Alley-cropping			Sole-cropping		
	0m	3m	13m	0m	3m	13m
Annelida						
Crassiclitellata (0)	7.7 $\pm$ 4.9 ^a (100)	3.9 $\pm$ 2.6 ^b (93.3)	4.8 $\pm$ 2.8 ^{ab} (100)	6.5 $\pm$ 3.9 ^{ab} (93.3)	6.7 $\pm$ 4.9 ^{ab} (100)	5.9 $\pm$ 2.6 ^{ab} (100)
Enchytraeidae (0)	11.9 $\pm$ 8.4 ^{ns} (86.7)	14.6 $\pm$ 14.7 ^{ns} (100)	11.9 $\pm$ 8.7 ^{ns} (93.3)	9.6 $\pm$ 9.6 ^{ns} (100)	11.7 $\pm$ 9.5 ^{ns} (100)	10.5 $\pm$ 8.8 ^{ns} (93.3)
Arachnida						
Araneae (1–5)	1.4 $\pm$ 1.45 ^a (60.0)	0.47 $\pm$ 0.83 ^{ab} (26.7)	0.47 $\pm$ 1.1 ^{ab} (20.0)	0.53 $\pm$ 0.83 ^{ab} (33.3)	0.40 $\pm$ 0.63 ^{ab} (33.3)	0.27 $\pm$ 0.59 ^b (20.0)
Pseudoscorpion (20)	0.07 $\pm$ 0.26 (6.7)	-	-	-	-	-
Acari						
Mesostigmata (20)	51.6 $\pm$ 28.9 ^a (100)	44.4 $\pm$ 29.3 ^{ab} (100)	39.9 $\pm$ 23.5 ^{ab} (100)	32.9 $\pm$ 24.9 ^{ab} (100)	28.8 $\pm$ 21.6 ^b (100)	36.7 $\pm$ 31.8 ^{ab} (100)
Sarcoptiformes (20)	205.7 $\pm$ 156.1 ^a (100)	132.5 $\pm$ 100.5 ^{abc} (100)	198.5 $\pm$ 293.2 ^{ab} (100)	76.9 $\pm$ 63.7 ^c (100)	102.3 $\pm$ 81.2 ^{bc} (100)	127.3 $\pm$ 112.7 ^{abc} (100)
Trombidiformes (20)	31.7 $\pm$ 29.1 ^{ns} (100)	35.1 $\pm$ 36.7 ^{ns} (100)	22.3 $\pm$ 18.2 ^{ns} (100)	21.2 $\pm$ 15.7 ^{ns} (100)	30.5 $\pm$ 23.8 ^{ns} (100)	27.6 $\pm$ 18.2 ^{ns} (100)
Entognatha						
Campodeida (20)	0.87 $\pm$ 1.7 ^{ns} (33.3)	0.67 $\pm$ 1.5 ^{ns} (26.7)	0.13 $\pm$ 0.35 ^{ns} (13.3)	0.40 $\pm$ 0.63 ^{ns} (33.3)	0.27 $\pm$ 0.46 ^{ns} (26.7)	0.53 $\pm$ 0.83 ^{ns} (33.3)
Protura (20)	4.0 $\pm$ 9.3 ^a (66.7)	1.0 $\pm$ 1.6 ^{ab} (40.0)	0.80 $\pm$ 1.5 ^{ab} (33.3)	0.20 $\pm$ 0.56 ^b (13.3)	0.07 $\pm$ 0.26 ^b (6.7)	-
Collembola						
Entomobryomorpha (1–6)	39.1 $\pm$ 35.3 ^{ab} (100)	36.0 $\pm$ 28.7 ^{ab} (100)	41.1 $\pm$ 26.1 ^a (100)	25.1 $\pm$ 14.1 ^{ab} (100)	21.5 $\pm$ 13.4 ^b (100)	25.9 $\pm$ 18.8 ^{ab} (100)
Neelipleona (10)	0.47 $\pm$ 0.92 ^{ns} (26.7)	0.87 $\pm$ 2.2 ^{ns} (20.0)	0.40 $\pm$ 0.83 ^{ns} (26.7)	0.40 $\pm$ 0.74 ^{ns} (26.7)	0.53 $\pm$ 0.83 ^{ns} (40.0)	0.93 $\pm$ 0.96 ^{ns} (60.0)
Poduromorpha (6–20)	68.9 $\pm$ 69.7 ^a (100)	61.9 $\pm$ 42.5 ^{ab} (100)	51.9 $\pm$ 43.0 ^{ab} (100)	55.9 $\pm$ 54.6 ^{ab} (100)	33.8 $\pm$ 23.7 ^b (100)	56.6 $\pm$ 35.4 ^{ab} (100)
Symphyleona (4)	8.6 $\pm$ 10.4 ^a (86.7)	5.8 $\pm$ 11.8 ^{ab} (80.0)	3.3 $\pm$ 3.3 ^b (80.0)	2.5 $\pm$ 2.5 ^b (93.3)	3.7 $\pm$ 4.4 ^{ab} (86.7)	4.7 $\pm$ 5.0 ^{ab} (93.3)
Gastropoda						
Pulmonata (0)	0.73 $\pm$ 0.96 ^{ns} (46.7)	0.60 $\pm$ 1.3 ^{ns} (33.3)	0.13 $\pm$ 0.35 ^{ns} (13.3)	0.07 $\pm$ 0.26 ^{ns} (6.7)	0.13 $\pm$ 0.52 ^{ns} (6.7)	0.13 $\pm$ 0.35 ^{ns} (13.3)
Insecta						
Coleoptera (1–15)	10.1 $\pm$ 6.1 ^a (100)	7.9 $\pm$ 5.4 ^{ab} (100)	6.5 $\pm$ 4.0 ^{bd} (93.3)	3.5 $\pm$ 2.1 ^c (100)	4.3 $\pm$ 3.8 ^d (86.7)	3.9 $\pm$ 3.9 ^c (93.3)
Diptera (1–10)	3.9 $\pm$ 3.3 ^{ns} (93.3)	3.8 $\pm$ 3.3 ^{ns} (93.3)	4.2 $\pm$ 3.5 ^{ns} (100)	2.2 $\pm$ 2.3 ^{ns} (80.0)	4.5 $\pm$ 6.0 ^{ns} (100)	2.5 $\pm$ 2.1 ^{ns} (86.7)
Hemiptera (1)	8.5 $\pm$ 27.6 ^a (40.0)	1.5 $\pm$ 2.2 ^{ab} (60.0)	2.5 $\pm$ 6.3 ^{ab} (33.3)	0.27 $\pm$ 0.80 ^b (13.3)	0.27 $\pm$ 0.80 ^b (13.3)	0.47 $\pm$ 0.74 ^b (33.3)
Hymenoptera (1–5)	0.47 $\pm$ 0.92 ^{ns} (20.0)	0.33 $\pm$ 0.62 ^{ns} (20.0)	0.13 $\pm$ 0.35 ^{ns} (13.3)	0.53 $\pm$ 1.3 ^{ns} (20.0)	0.40 $\pm$ 0.83 ^{ns} (26.7)	0.27 $\pm$ 0.46 ^{ns} (26.7)
Lepidoptera (1–10)	0.73 $\pm$ 1.2 ^a (40.0)	0.07 $\pm$ 0.26 ^b (6.7)	-	-	-	0.07 $\pm$ 0.26 ^b (6.7)
Thysanoptera (1)	1.7 $\pm$ 1.5 ^{ns} (73.3)	1.1 $\pm$ 1.7 ^{ns} (46.7)	1.4 $\pm$ 2.5 ^{ns} (33.3)	0.33 $\pm$ 0.62 ^{ns} (26.7)	1.2 $\pm$ 2.4 ^{ns} (33.3)	1.1 $\pm$ 1.7 ^{ns} (46.7)

Table 3.B.2 continued.

	Alley-cropping			Sole-cropping		
	0m	3m	13m	0m	3m	13m
Siphonaptera (1)	0.07 ± 0.26 (6.7)	-	-	-	-	-
Malacostrans						
Isopoda (10)	3.3 ± 2.8 ^a (80.0)	1.0 ± 1.7 ^b (40.0)	0.40 ± 1.1 ^b (13.3)	0.13 ± 0.35 ^b (13.3)	0.13 ± 0.52 ^b (6.7)	0.13 ± 0.35 ^b (13.3)
Myriapoda						
Cephalostigmata (10)	0.80 ± 1.4 ^{ns} (40.0)	0.60 ± 1.8 ^{ns} (20.0)	0.67 ± 1.3 ^{ns} (40.0)	0.47 ± 0.83 ^{ns} (26.7)	0.67 ± 1.2 ^{ns} (33.3)	0.80 ± 1.3 ^{ns} (40.0)
Tetramerocerata (20)	1.4 ± 1.6 ^{ns} (53.3)	1.5 ± 1.5 ^{ns} (66.7)	0.60 ± 0.83 ^{ns} (46.7)	0.53 ± 0.64 ^{ns} (46.7)	0.40 ± 0.74 ^{ns} (26.7)	0.53 ± 0.92 ^{ns} (33.3)
Chilopoda						
Geophilomorpha (20)	2.4 ± 3.3 ^a (66.7)	1.3 ± 1.6 ^{ab} (60.0)	0.87 ± 1.1 ^b (46.7)	0.40 ± 0.63 ^b (33.3)	0.80 ± 1.2 ^b (40.0)	0.53 ± 0.74 ^b (40.0)
Lithobiomorpha (10)	1.5 ± 2.0 ^a (53.3)	0.60 ± 1.1 ^{ab} (33.3)	0.60 ± 1.2 ^{ab} (26.7)	0.27 ± 0.59 ^b (20.0)	0.47 ± 0.92 ^{ab} (26.7)	0.33 ± 0.49 ^b (33.3)
Scolopendromorpha (10)	-	0.07 ± 0.26 ^{ns} (6.7)	-	0.07 ± 0.26 ^{ns} (6.7)	-	-
Diplopoda						
Chordeumatida (20)	-	0.20 ± 0.56 ^{ns} (13.3)	0.27 ± 0.46 ^{ns} (20.0)	0.07 ± 0.26 ^{ns} (6.7)	0.07 ± 0.26 ^{ns} (6.7)	0.07 ± 0.26 ^{ns} (6.7)
Julida (20)	0.07 ± 0.26 ^{ns} (6.7)	0.07 ± 0.26 ^{ns} (6.7)	-	-	0.20 ± 0.41 ^{ns} (20.0)	-
Polydesmida (20)	0.20 ± 0.41 ^{ns} (20.0)	-	0.07 ± 0.26 ^{ns} (6.7)	0.40 ± 0.74 ^{ns} (26.7)	0.13 ± 0.35 ^{ns} (13.3)	0.47 ± 0.99 ^{ns} (20.0)

Table 3.B.3: The mean ($\pm$ standard deviation) abundance of soil faunal taxa in alley-cropping and sole-cropping systems attributed ecomorphological (EMI) scores according to the QBS-ar Index. For sampling details and descriptions please see Table 3.B.2.

	Alley-cropping			Sole-cropping		
	0m	3m	13m	0m	3m	13m
Acari (20)	294.9 $\pm$ 187.2 (100)	218.6 $\pm$ 155.1 (100)	263.2 $\pm$ 298.9 (100)	136.9 $\pm$ 107.1 (100)	166.4 $\pm$ 109.8 (100)	198.9 $\pm$ 156.9 (100)
Araneae						
Araneae (1)	0.27 $\pm$ 0.59 (20.0)	0.20 $\pm$ 0.56 (13.3)	0.47 $\pm$ 1.13 (20.0)	0.13 $\pm$ 0.35 (13.3)	0.07 $\pm$ 0.26 (6.7)	0.07 $\pm$ 0.26 (6.7)
Araneae (5)	1.1 $\pm$ 1.2 (60.0)	0.27 $\pm$ 0.59 (20.0)	-	0.40 $\pm$ 0.74 (26.7)	0.33 $\pm$ 0.62 (26.7)	0.20 $\pm$ 0.56 (13.3)
Chilopoda						
Chilopoda (10)	1.5 $\pm$ 2.0 (53.3)	0.67 $\pm$ 1.1 (40.0)	0.60 $\pm$ 1.2 (26.7)	0.33 $\pm$ 0.62 (26.7)	0.40 $\pm$ 0.91 (20.0)	0.33 $\pm$ 0.49 (33.3)
Chilopoda (20)	2.4 $\pm$ 3.3 (66.7)	1.3 $\pm$ 1.6 (60.0)	0.87 $\pm$ 1.1 (46.7)	0.40 $\pm$ 0.63 (33.3)	0.87 $\pm$ 1.2 (46.7)	0.53 $\pm$ 0.74 (40.0)
Collembola						
Collembola (1)	0.53 $\pm$ 0.83 (33.3)	0.27 $\pm$ 0.46 (26.7)	0.27 $\pm$ 0.46 (26.7)	0.20 $\pm$ 0.56 (13.3)	0.33 $\pm$ 0.49 (33.3)	0.27 $\pm$ 0.70 (13.3)
Collembola (2)	8.3 $\pm$ 9.2 (93.3)	11.5 $\pm$ 12.2 (86.7)	11.1 $\pm$ 14.6 (100)	6.1 $\pm$ 4.8 (86.7)	6.0 $\pm$ 5.1 (93.3)	6.9 $\pm$ 8.4 (73.3)
Collembola (4)	36.3 $\pm$ 35.9 (100)	28.1 $\pm$ 27.4 (100)	28.1 $\pm$ 19.2 (100)	18.3 $\pm$ 11.3 (100)	17.1 $\pm$ 12.5 (100)	20.8 $\pm$ 17.2 (100)
Collembola (6)	2.6 $\pm$ 4.0 (60.0)	1.9 $\pm$ 2.8 (53.3)	4.9 $\pm$ 6.8 (66.7)	2.9 $\pm$ 4.1 (60.0)	1.8 $\pm$ 2.5 (60.0)	2.6 $\pm$ 3.1 (66.7)
Collembola (8)	22.7 $\pm$ 65.9 (93.3)	13.2 $\pm$ 22.0 (93.3)	12.5 $\pm$ 15.2 (93.3)	5.1 $\pm$ 6.5 (66.7)	7.0 $\pm$ 11.1 (73.3)	8.3 $\pm$ 8.2 (86.7)
Collembola (10)	0.47 $\pm$ 0.92 (26.7)	0.87 $\pm$ 2.2 (20.0)	0.93 $\pm$ 2.1 (33.3)	0.40 $\pm$ 0.74 (26.7)	0.53 $\pm$ 0.83 (40.0)	0.93 $\pm$ 0.96 (60.0)
Collembola (20)	46.6 $\pm$ 37.2 (100)	48.9 $\pm$ 38.8 (100)	39.6 $\pm$ 39.6 (100)	51.1 $\pm$ 56.2 (100)	26.9 $\pm$ 20.9 (100)	48.5 $\pm$ 35.7 (100)
Coleoptera						
Coleoptera (1)	0.73 $\pm$ 1.4 (26.7)	-	-	0.07 $\pm$ 0.26 (6.7)	-	0.20 $\pm$ 0.78 (6.7)
Coleoptera (5)	1.1 $\pm$ 1.4 (60.0)	0.47 $\pm$ 0.74 (33.3)	0.33 $\pm$ 0.49 (33.3)	0.20 $\pm$ 0.41 (20.0)	0.60 $\pm$ 0.74 (46.7)	0.27 $\pm$ 0.46 (26.7)
Coleoptera (10)	2.5 $\pm$ 2.0 (86.7)	0.67 $\pm$ 0.82 (53.3)	0.53 $\pm$ 0.92 (33.3)	1.0 $\pm$ 1.3 (66.7)	0.60 $\pm$ 0.91 (40.0)	0.33 $\pm$ 0.62 (26.7)
Coleoptera (15)	0.67 $\pm$ 1.1 (33.3)	0.07 $\pm$ 0.26 (6.7)	0.40 $\pm$ 1.1 (20.0)	0.07 $\pm$ 0.26 (6.7)	-	-
Coleoptera larvae (10)	5.1 $\pm$ 3.2 (100)	6.7 $\pm$ 5.0 (100)	5.3 $\pm$ 3.7 (86.7)	2.1 $\pm$ 1.7 (73.3)	3.1 $\pm$ 3.2 (80.0)	3.1 $\pm$ 3.7 (80.0)
Diplopoda (20)	0.27 $\pm$ 0.59 (20.0)	0.27 $\pm$ 0.59 (20.0)	0.33 $\pm$ 0.49 (33.3)	0.47 $\pm$ 0.74 (33.3)	0.40 $\pm$ 0.51 (40.0)	0.53 $\pm$ 1.2 (20.0)
Diplura (20)	0.87 $\pm$ 1.7 (33.3)	0.67 $\pm$ 1.5 (26.7)	0.13 $\pm$ 0.35 (13.3)	0.40 $\pm$ 0.63 (33.3)	0.27 $\pm$ 0.46 (26.7)	0.53 $\pm$ 0.83 (33.3)
Diptera (1)	0.20 $\pm$ 0.56 (13.3)	0.53 $\pm$ 0.83 (33.3)	0.47 $\pm$ 0.64 (40.0)	0.33 $\pm$ 0.49 (33.3)	0.27 $\pm$ 0.59 (20.0)	0.33 $\pm$ 0.62 (26.7)
Diptera larvae (10)	3.7 $\pm$ 3.1 (86.7)	3.3 $\pm$ 3.1 (80.0)	3.7 $\pm$ 3.6 (93.3)	1.9 $\pm$ 2.1 (80.0)	4.2 $\pm$ 6.1 (93.3)	2.1 $\pm$ 1.9 (80.0)
Hemiptera (1)	8.5 $\pm$ 27.6 (40.0)	1.5 $\pm$ 2.2 (60.0)	2.5 $\pm$ 6.3 (33.3)	0.27 $\pm$ 0.80 (13.3)	0.27 $\pm$ 0.80 (13.3)	0.47 $\pm$ 0.74 (33.3)
Hymenoptera						
Hymenoptera (1)	0.20 $\pm$ 0.56 (13.3)	0.13 $\pm$ 0.35 (13.3)	0.13 $\pm$ 0.35 (13.3)	0.47 $\pm$ 1.3 (20.0)	0.27 $\pm$ 0.59 (20.0)	0.20 $\pm$ 0.41 (20.0)

Table 3.B.3 continued.

	Alley-cropping			Sole-cropping		
	0m	3m	13m	0m	3m	13m
Hymenoptera (5)	0.27 ± 0.80 (13.3)	0.20 ± 0.41 (20.0)	-	0.07 ± 0.26 (6.7)	0.13 ± 0.35 (13.3)	0.07 ± 0.26 (6.7)
Isopoda (1)	3.3 ± 2.8 (80.0)	1.0 ± 1.7 (40.0)	0.40 ± 1.1 (13.3)	0.13 ± 0.35 (13.3)	0.13 ± 0.52 (6.7)	0.13 ± 0.35 (13.3)
Lepidoptera (1)	0.07 ± 0.26 (6.7)	-	-	-	-	-
Lepidoptera larvae (10)	0.66 ± 1.1 (40.0)	0.07 ± 0.26 (6.7)	-	-	-	0.07 ± 0.26 (6.7)
Paupoda (20)	1.4 ± 1.6 (53.3)	1.5 ± 1.5 (66.7)	0.60 ± 0.83 (46.7)	0.53 ± 0.64 (46.7)	0.40 ± 0.74 (26.7)	0.53 ± 0.92 (33.3)
Protura (20)	4.0 ± 9.3 (66.7)	1.0 ± 1.6 (40.0)	0.80 ± 1.5 (33.3)	0.20 ± 0.56 (13.3)	0.07 ± 0.26 (6.7)	-
Pseudoscorpion (20)	0.07 ± 0.26 (6.7)	-	-	-	-	-
Siphonaptera (1)	0.07 ± 0.26 (6.7)	-	-	-	-	-
Thysanoptera (1)	1.7 ± 1.5 (73.3)	1.1 ± 1.7 (46.7)	1.4 ± 2.5 (33.3)	0.33 ± 0.62 (26.7)	1.2 ± 2.4 (33.3)	1.1 ± 1.7 (46.7)
Symphyla (10)	0.80 ± 1.4 (40.0)	0.60 ± 1.8 (20.0)	0.67 ± 1.3 (40.0)	0.47 ± 0.83 ⁿ (26.7)	0.67 ± 1.2 (33.3)	0.80 ± 1.3 (40.0)

3.9.3 Farm-level comparisons of soil faunal biodiversity metrics

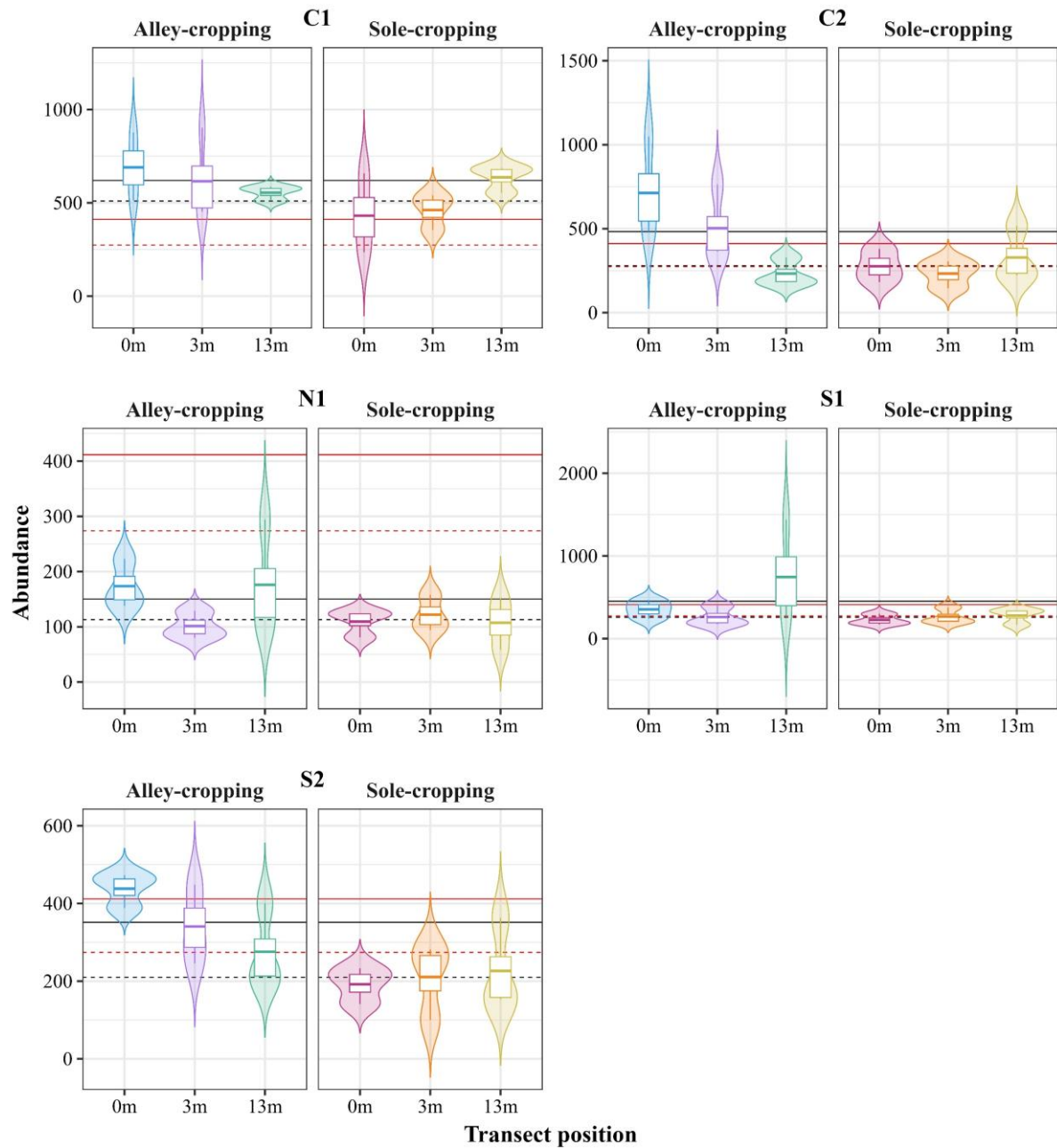


Figure 3.B.1. Abundance of soil fauna in alley-cropping and sole-cropping transect positions at five farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. Distances refer to distance in m along linear experimental transects. In alley-cropping systems, ‘0m’ = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), ‘3m’ = 1.5 m into the crop alley from the edge of the UVS, ‘13m’ = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Solid and dashed lines indicate the average abundance for AC and SC, respectively. Black lines = the average for the entire data set, red lines = the average for the displayed farm.

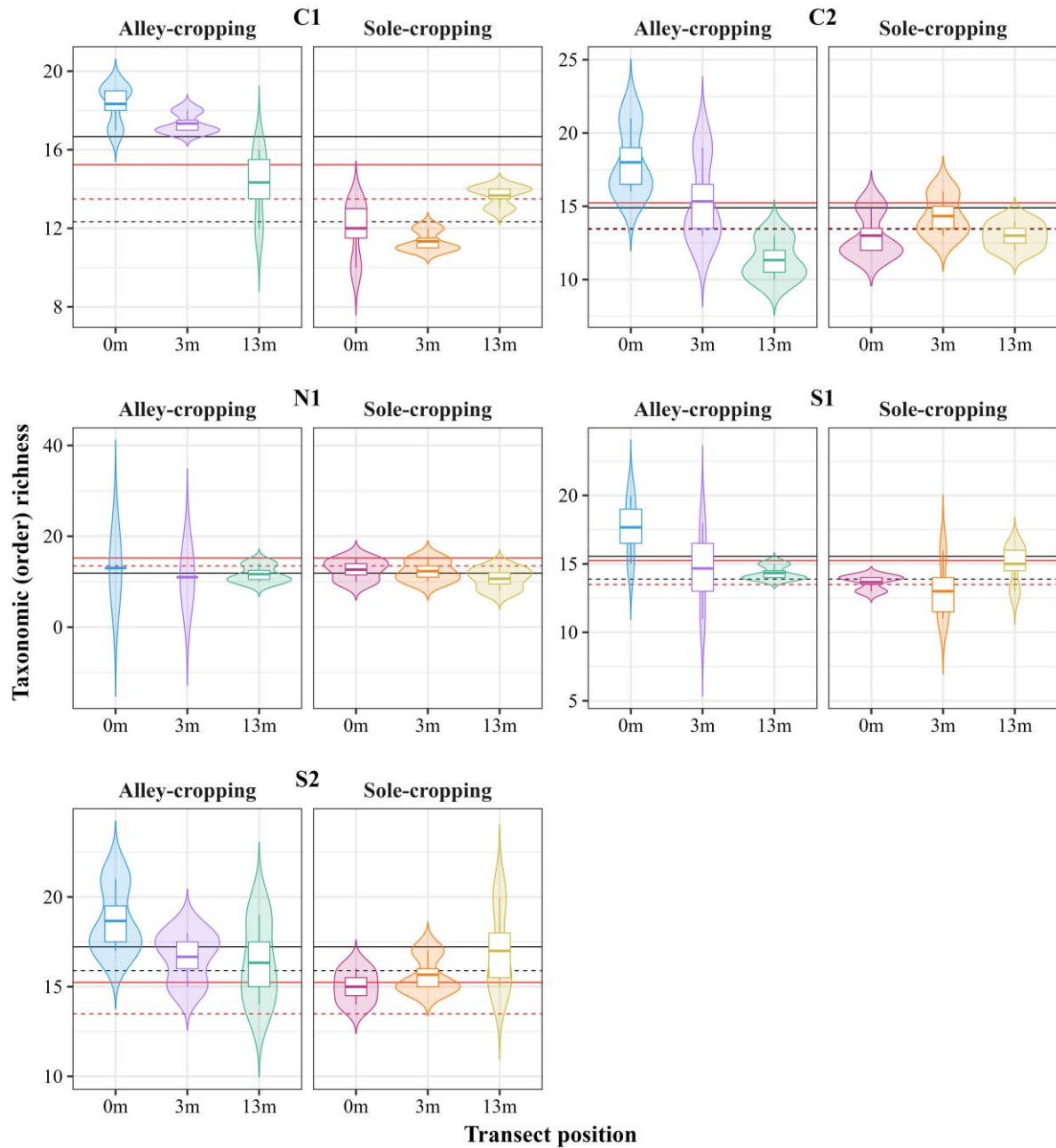


Figure 3.B.2. Taxonomic (order) richness of soil fauna in alley-cropping and sole-cropping transect positions at five commercial farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. Distances refer to distance in m along linear experimental transects. In alley-cropping systems, '0m' = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), '3m' = 1.5 m into the crop alley from the edge of the UVS, '13m' = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Solid and dashed lines indicate the average taxonomic richness for AC and SC, respectively. Black lines = the average for the entire data set, red lines = the average for the displayed farm.

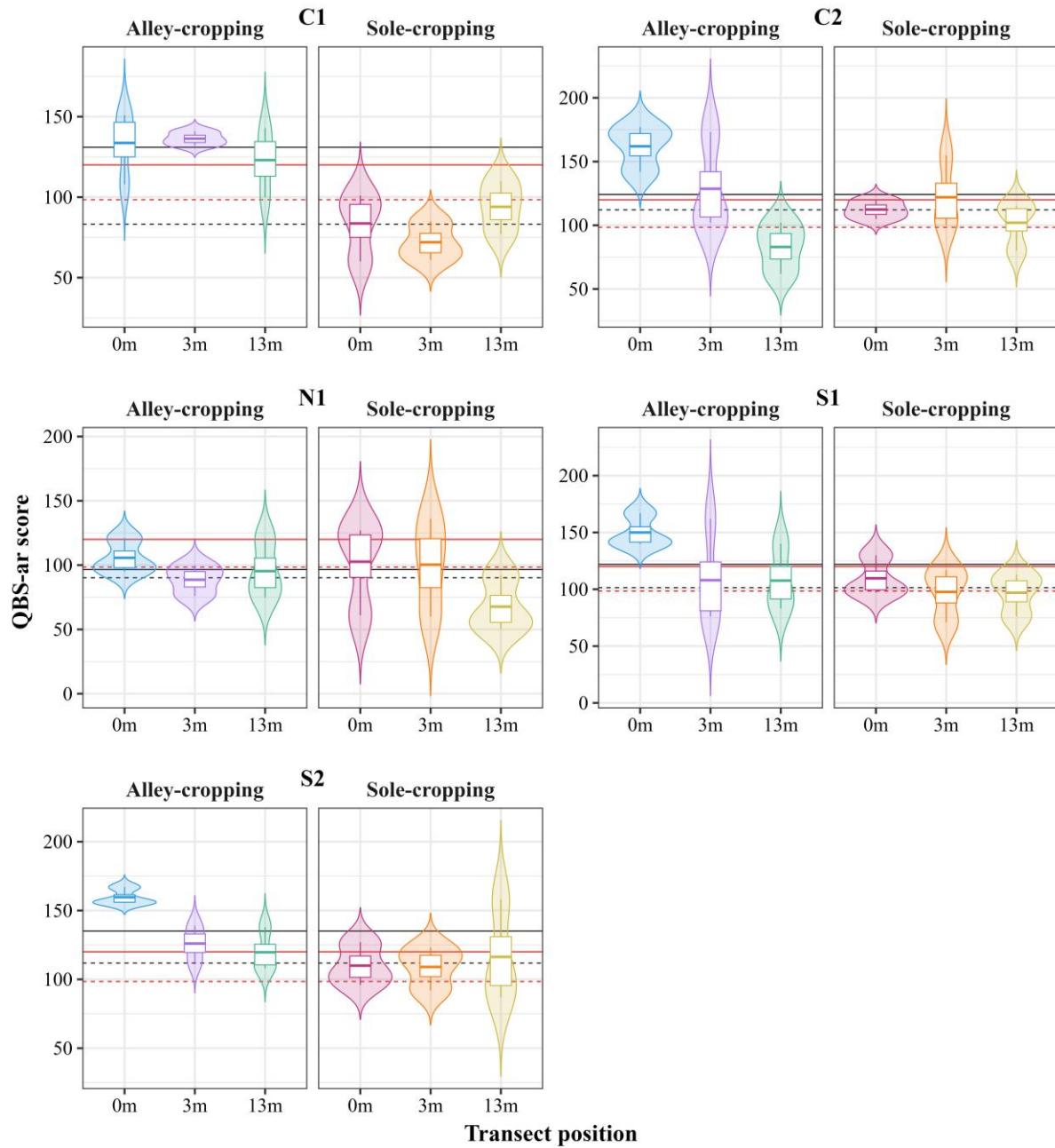


Figure 3.B.3. QBS-ar scores of soil fauna in alley-cropping and sole-cropping transect positions at five commercial farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5). Violin plots display the distribution of the data points and individual points represent outliers. Distances refer to distance in m along linear experimental transects. In alley-cropping systems, ‘0m’ = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), ‘3m’ = 1.5 m into the crop alley from the edge of the UVS, ‘13m’ = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Solid and dashed lines indicate the average QBS-ar score for AC and SC, respectively. Black lines = the average for the entire data set, red lines = the average for the displayed farm.

3.9.4 Compositional analyses

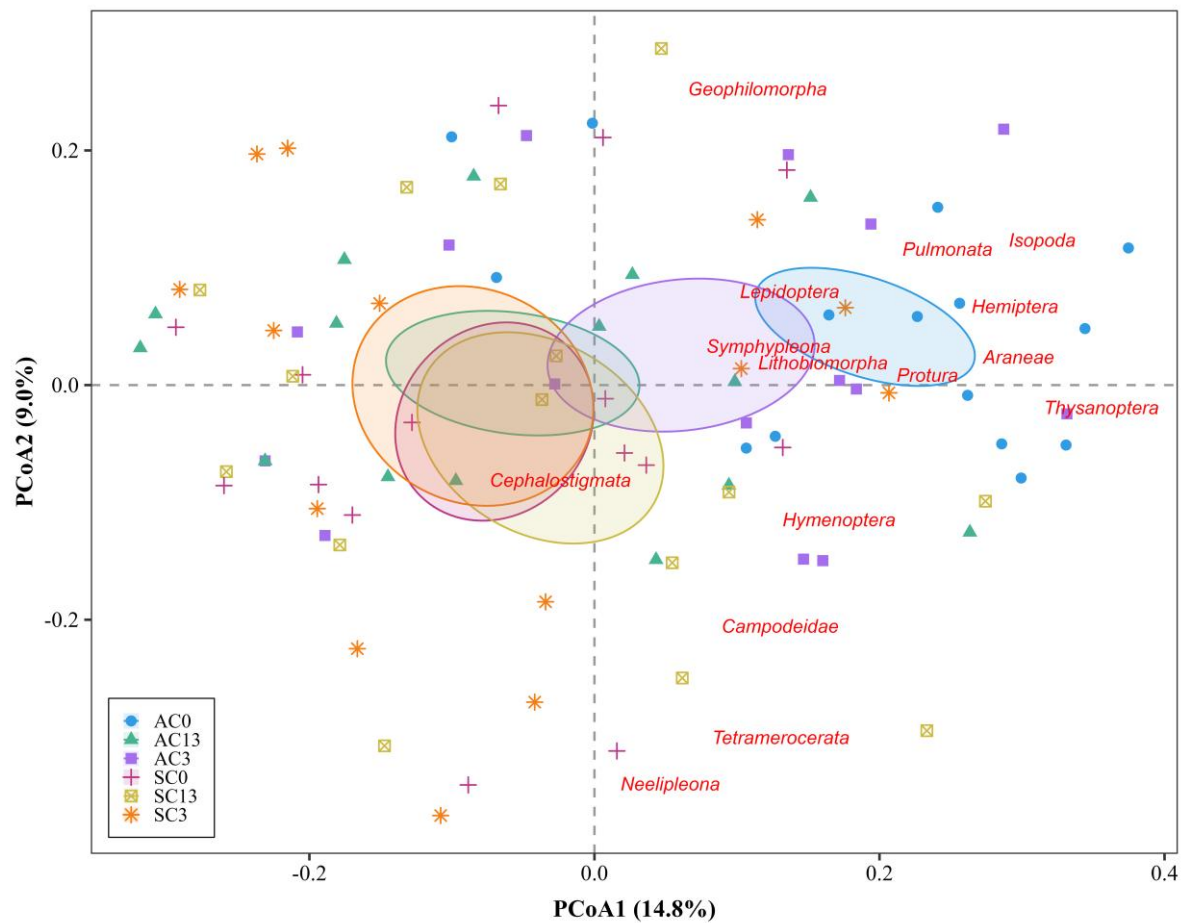


Figure 3.B.4. The Jaccard community composition of soil meso- and macro-fauna collected from 90 sampling points in alley-cropping (AC) and sole-cropping (SC) systems at five farms in England, United Kingdom. Transect positions indicate distance (m) along the experimental transect. In alley-cropping systems, ‘0m’ = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), ‘3m’ = 1.5 m into the crop alley from the edge of the UVS, ‘13m’ = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Ellipses display the standard error of the centroid for each transect position. Proportions in brackets describe the total amount of variation in composition explained by each axis. Soil meso- and macro-fauna taxa (in red) are positioned according to their Pearson correlation with the ordination axes (site scores).

3.9.4.1 Taxonomic composition (Bray-Curtis) results

When considering both the presence and abundance of taxa, faunal composition differed significantly between transect positions in both alley-cropping and sole-cropping ($F_{5,84} = 2.11$, $p = 0.003$, $R^2 = 0.11$). Changes in faunal composition were restricted to the tree row, which differed significantly from all sole-cropping transect positions ($p = 0.005$), as well as from AC3 ($F_{(1,22)} = 3.18$, $p = 0.024$, $R^2 = 0.06$) and AC13 ($F_{(1,22)} = 4.00$, $p = 0.008$, $R^2 = 0.09$). Taxa identified to have the most influence on observed differences in composition between tree rows and sole cropping were: Acari (Sarcoptiformes, Trombidiformes, and Mesostigmata), Isopoda, Collembola (Symphypleona, Poduromorpha, Entomobryomorpha), Oligochaeta (Lumbricina and Tubificina), Protura, Geophilomorpha, Araneae, and insects Coleoptera, Diptera,

Hemiptera, and Thysanoptera. Transect positions in the crop alley did not demonstrate significant differences in composition to each another or sole-cropping ($p > 0.05$).

When considering abundance and richness, soil type ($F_{(3)} = 7.34$, $p = 0.001$, $R^2 = 0.15$), crop diversity ($F_{(1)} = 3.10$, $p = 0.006$, $R^2 = 0.02$), soil C:N ratio ($F_{(1)} = 2.53$, $p = 0.015$, $R^2 = 0.02$), exchangeable K concentration ($F_{(1)} = 3.06$, $p = 0.006$, $R^2 = 0.02$), and TN ($F_{(1)} = 2.49$, $p = 0.016$, $R^2 = 0.02$) significantly influenced faunal composition, whereas BD, CEC, MC_{range} , pH, and temp_{low} did not.

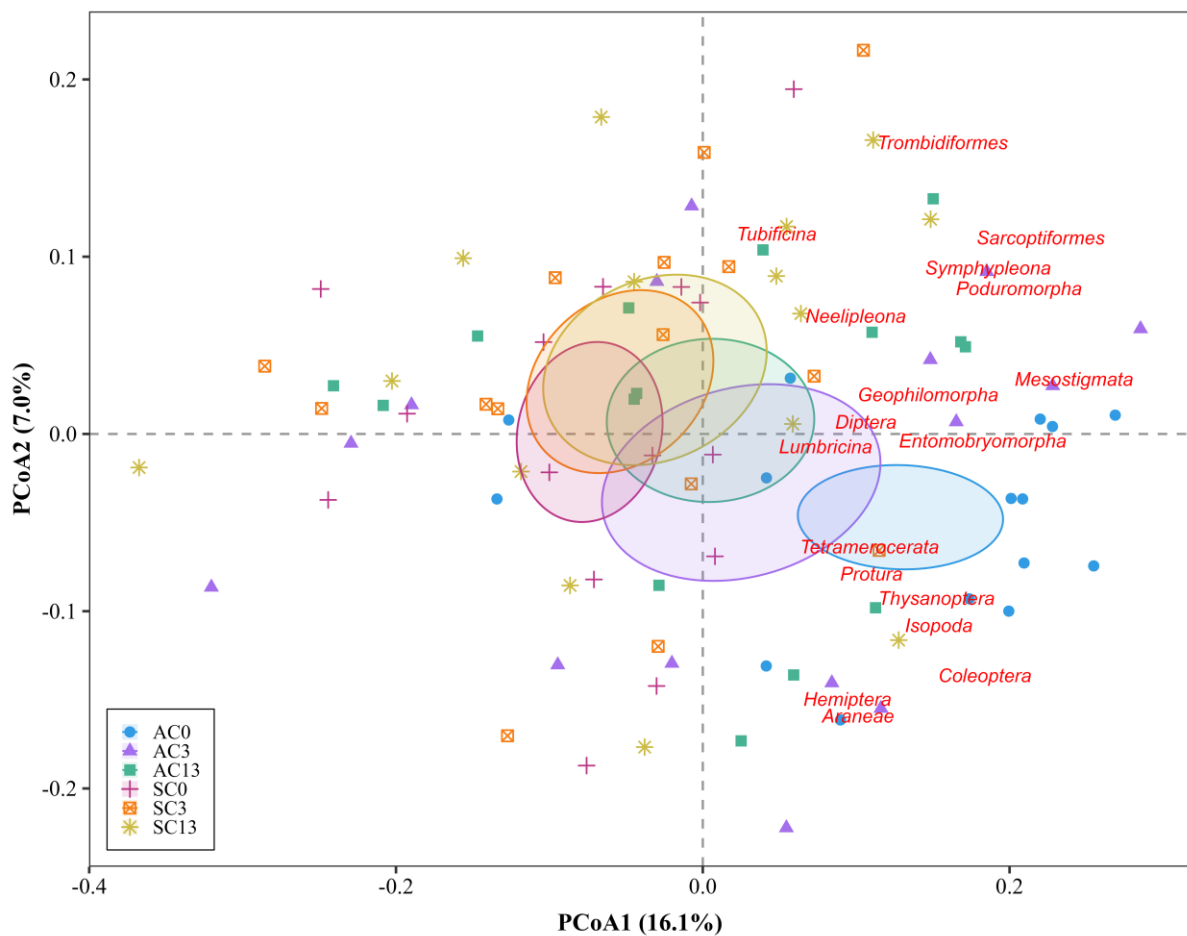


Figure 3.B.5. The Bray-Curtis community composition of soil meso- and macro-fauna collected from 90 sampling points in alley-cropping (AC) and sole-cropping (SC) systems at five farms in England, United Kingdom. Transect positions indicate distance (m) along the experimental transect. In alley-cropping systems, '0m' = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), '3m' = 1.5 m into the crop alley from the edge of the UVS, '13m' = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Ellipses display two standard errors of the centroid for each transect position. Proportions in brackets describe the total amount of variation in composition explained by each axis. Soil meso- and macro-fauna taxa (in red) are positioned according to their Pearson correlation with the ordination axes (site scores).

3.9.4.2 QBS-ar group composition results

Agricultural system and transect position had a small but significant influence on the composition of QBS-ar groups (i.e., faunal taxa classified according to EMI scores) (Model J; $F_{(5,78)} = 1.89$, $p = 0.001$, $R^2 = 0.09$). Compositional changes were restricted to the tree rows of alley-cropping systems, which differed significantly from all positions in sole-cropping ($p < 0.01$), as well as AC3 ($F_{(1,22)} = 2.45$, $R^2 = 0.07$, $p = 0.021$) and AC13 ($F_{(1,22)} = 3.85$, $R^2 = 0.11$, $p = 0.004$) (Figure 3.4B).

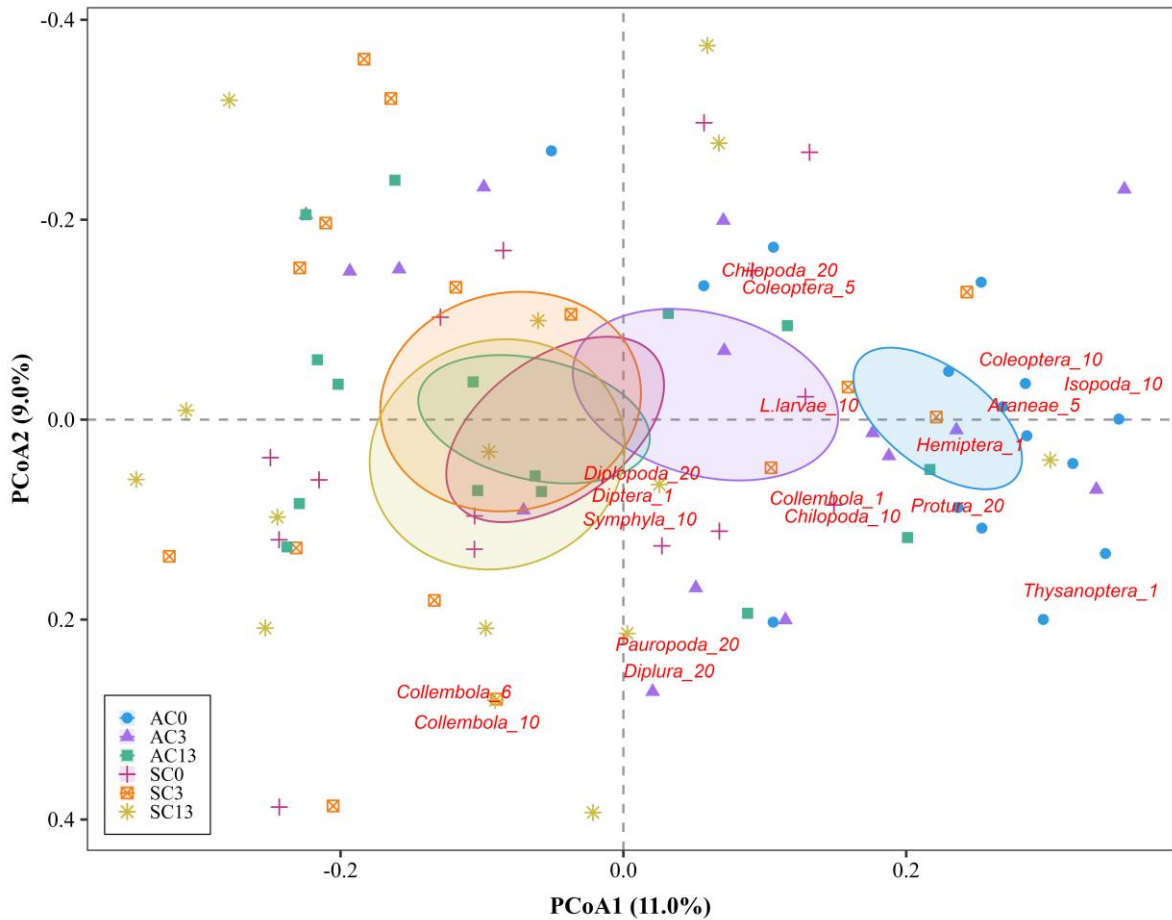


Figure 3.B.6. The Jaccard community composition of soil meso- and macro-fauna QBS-ar groups (class- or order-level taxa attributed specific ecomorphological index scores) collected from 90 sampling points in alley-cropping (AC) and sole-cropping (SC) systems at five farms in England, United Kingdom. Transect positions indicate distance (m) along the experimental transect. In alley-cropping systems, ‘0m’ = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), ‘3m’ = 1.5 m into the crop alley from the edge of the UVS, ‘13m’ = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Ellipses display two standard errors of the centroid for each transect position. Proportions in brackets describe the total amount of variation in composition explained by each axis. Soil meso- and macro-faunal taxa (in red) are positioned according to their Pearson correlation with the ordination axes (site scores). Numbers provided with faunal taxa indicate the associated ecomorphological index score.

Table 3.B.4. Contribution (%) of individual taxonomic groups, ecomorphological index ('EMI') scores, and QBS-ar groups to observed dissimilarities in composition between alley-cropping tree rows and transect positions in the crop alley and sole-cropping. '0m', '3m', and '13m' refer to distances in m along linear experimental transects. 'Avg. dissimilarity' = mean dissimilarity between transect positions, 'Cumulative %' = the total proportion of variation in composition between two transect positions explained by the listed groups. Dissimilarity calculations: taxonomic groups and QBS-ar taxa = Jaccard Index, EMI scores = Bray-Curtis Index. Numbers in parentheses indicate the EMI score attributed to a given taxon.

	AC0 vs:			AC3 vs:			
	AC3	AC13	SC0	SC3	SC13	SC3	SC13
Taxonomic groups							
Avg. dissimilarity	0.39	0.42	0.43	0.43	0.43	0.39	0.40
Cumulative %	74.65	70.25	70.06	70.22	70.51	71.34	71.07
Isopoda	7.24	8.86	8.67	9.15	8.58	5.61	5.63
Araneae	6.90	6.86	6.46	6.46	6.64	5.83	-
Protura	6.75	6.78	7.33	7.55	7.65	5.66	5.25
Hemiptera	6.66	5.64	5.01	5.00	5.42	8.10	7.40
Thysanoptera	6.55	7.12	7.31	6.96	6.24	6.86	6.84
Lithobiomorpha	6.34	6.18	6.11	6.08	5.98	5.89	6.06
Tetramerocerata	6.29	6.16	6.08	6.10	5.99	8.51	7.92
Pulmonata	6.11	5.68	5.53	5.50	5.51	-	-
Geophilomorpha	6.00	6.32	6.73	6.46	6.36	7.49	7.22
Cephalostigmata	5.50	5.85	5.50	5.62	5.69	5.70	6.05
Campodeida	5.17	-	5.32	-	-	-	5.68
Lepidoptera	5.14	4.82	-	-	-	-	-
Neelipleona	-	-	-	5.34	6.44	6.15	7.70
Hymenoptera	-	-	-	-	-	5.54	5.31
EMI scores (taxonomic richness per score)							
Avg. dissimilarity	0.23	0.25	0.25	0.26	0.27	-	-
Cumulative %	83.23	85.29	80.72	70.30	83.03	-	-
10	28.31	29.16	28.04	27.38	27.14	-	-
1	20.54	22.25	20.55	22.52	21.69	-	-
20	19.58	18.29	17.88	20.40	19.70	-	-
5	14.80	15.60	14.26	-	14.50	-	-
QBS-ar taxa							
Avg. dissimilarity	0.51	0.54	0.56	0.56	0.57	-	-
Cumulative %	73.14	70.81	73.22	73.35	72.76	-	-
Isopoda (10)	5.47	6.60	6.31	6.78	6.28	-	-
Araneae (5)	5.21	5.90	4.77	4.84	4.89	-	-
Coleoptera (5)	5.09	4.92	5.00	4.56	4.85	-	-
Thysanoptera (1)	5.05	5.30	5.31	5.18	4.56	-	-
Protura (20)	4.99	5.26	5.28	5.52	5.52	-	-
Hemiptera (1)	4.88	4.16	3.61	3.65	3.95	-	-
Chilopoda (10)	4.72	4.57	4.42	4.49	4.36	-	-
Collembola (6)	4.72	4.31	4.26	4.32	4.11	-	-
Paupoda (20)	4.72	4.56	4.43	4.50	4.36	-	-
Coleoptera (10)	4.68	6.60	3.34	5.25	5.98	-	-
Chilopoda (20)	4.50	4.66	4.90	4.62	4.86	-	-
Symphyla (10)	4.14	4.34	4.01	4.19	4.16	-	-
Diplura (20)	3.86	-	3.88	3.69	3.82	-	-
Lepidoptera larvae (10)	3.85	-	3.47	-	3.54	-	-
Collembola (1)	3.79	3.67	-	3.88	3.03	-	-
Diptera (1)	3.46	3.83	3.33	-	-	-	-
Collembola (10)	-	3.72	3.40	3.96	4.66	-	-
Diplopoda (20)	-	-	3.50	3.91	-	-	-

Table 3.B.5. Mean ($\pm$ standard deviation) number of QBS-ar taxa attributed EMI scores of 1–20 in paired alley-cropping (‘AC’) and sole-cropping (‘SC’) systems and at specific transect positions (0, 3, or 13 m) in AC and SC. ‘Count’ = the number of QBS-ar taxa contributing to QBS-ar score calculations. Superscript letters indicate a significant pairwise difference between systems *or* transect positions¹ ($p < 0.05$), as determined by linear models and post hoc tests with a false discovery rate correction for multiple comparisons.

	AC	SC	AC0	AC3	AC13	SC0	SC3	SC13
1	2.0 $\pm$ 1.4 ^a	1.4 $\pm$ 1.2 ^b	2.3 $\pm$ 1.4 ^a	1.9 $\pm$ 1.3 ^{ab}	1.7 $\pm$ 1.5 ^{ab}	1.3 $\pm$ 1.0 ^b	1.3 $\pm$ 1.3 ^b	1.5 $\pm$ 1.5 ^{ab}
2	0.9 $\pm$ 0.3 ^{ns}	0.8 $\pm$ 0.4 ^{ns}	0.9 $\pm$ 0.3 ^{ns}	0.9 $\pm$ 0.4 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	0.9 $\pm$ 0.4 ^{ns}	0.9 $\pm$ 0.3 ^{ns}	0.7 $\pm$ 0.5 ^{ns}
4	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}	1.0 $\pm$ 0.0 ^{ns}
5	0.8 $\pm$ 0.9 ^{ns}	0.6 $\pm$ 0.7 ^{ns}	1.3 $\pm$ 1.0 ^{ns}	0.7 $\pm$ 0.8 ^{ns}	0.3 $\pm$ 0.5 ^{ns}	0.5 $\pm$ 0.5 ^{ns}	0.9 $\pm$ 0.7 ^{ns}	0.5 $\pm$ 0.6 ^{ns}
6	0.6 $\pm$ 0.5 ^{ns}	0.6 $\pm$ 0.5 ^{ns}	0.6 $\pm$ 0.5 ^{ns}	0.5 $\pm$ 0.5 ^{ns}	0.7 $\pm$ 0.5 ^{ns}	0.6 $\pm$ 0.5 ^{ns}	0.6 $\pm$ 0.5 ^{ns}	0.7 $\pm$ 0.5 ^{ns}
8	0.9 $\pm$ 0.3 ^{ns}	0.8 $\pm$ 0.4 ^{ns}	0.9 $\pm$ 0.6 ^{ns}	0.9 $\pm$ 0.6 ^{ns}	0.9 $\pm$ 0.6 ^{ns}	0.7 $\pm$ 0.5 ^{ns}	0.7 $\pm$ 0.5 ^{ns}	0.9 $\pm$ 0.4 ^{ns}
10	4.0 $\pm$ 1.6 ^a	3.3 $\pm$ 1.1 ^b	5.1 $\pm$ 1.1 ^a	3.7 $\pm$ 1.6 ^b	3.3 $\pm$ 1.6 ^b	3.2 $\pm$ 1.0 ^b	3.2 $\pm$ 1.0 ^b	3.4 $\pm$ 1.4 ^b
15	0.2 $\pm$ 0.4 ^{ns}	0.0 $\pm$ 0.2 ^{ns}	0.3 $\pm$ 0.5 ^{ns}	0.1 $\pm$ 0.3 ^{ns}	0.2 $\pm$ 0.4 ^{ns}	0.1 $\pm$ 0.3 ^{ns}	0.0 $\pm$ 0.0 ^{ns}	0.0 $\pm$ 0.0 ^{ns}
20	4.1 $\pm$ 1.2 ^a	3.4 $\pm$ 1.0 ^b	4.5 $\pm$ 1.1 ^a	4.1 $\pm$ 1.4 ^{ab}	3.7 $\pm$ 1.6 ^{ab}	3.6 $\pm$ 0.9 ^{ab}	3.5 $\pm$ 1.3 ^{ab}	3.3 $\pm$ 0.9 ^b
Count	9.5 $\pm$ 2.7 ^a	7.8 $\pm$ 2.2 ^b	11.3 $\pm$ 2.0 ^a	9.2 $\pm$ 2.7 ^b	8.1 $\pm$ 2.3 ^{bc}	7.9 $\pm$ 1.9 ^{bc}	7.7 $\pm$ 2.3 ^c	7.7 $\pm$ 2.5 ^c

¹ Pairwise comparisons were made between ‘AC’ and ‘SC’ *or* between the six transect positions (‘AC0’ to ‘SC13’).

3.9.5 Correlation between taxonomic richness and QBS-ar scores

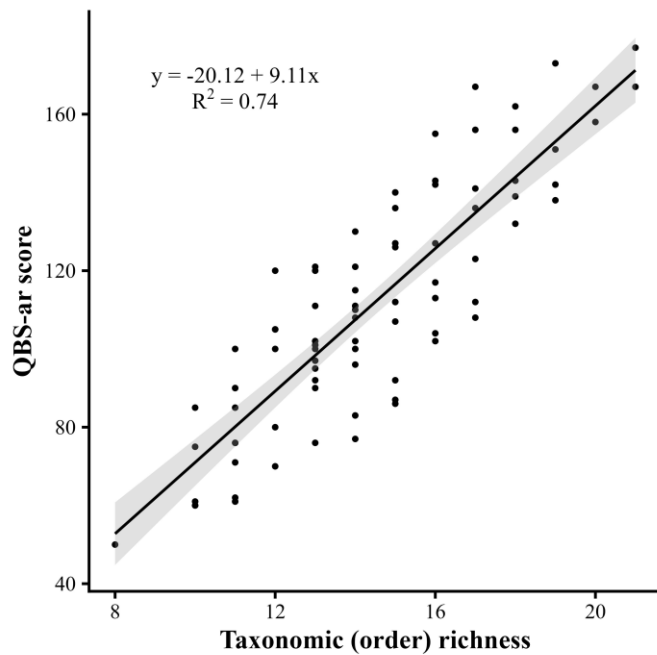


Figure 3.B.7. The relationship between soil faunal QBS-ar score and taxonomic (order) richness. Points represent observed values. The regression line and confidence intervals were estimated from a linear model generated via the R function *stat_smooth* from the ‘ggplot2’ package (Wickham, 2016). Shaded areas provide the 95 % confidence interval of the mean.

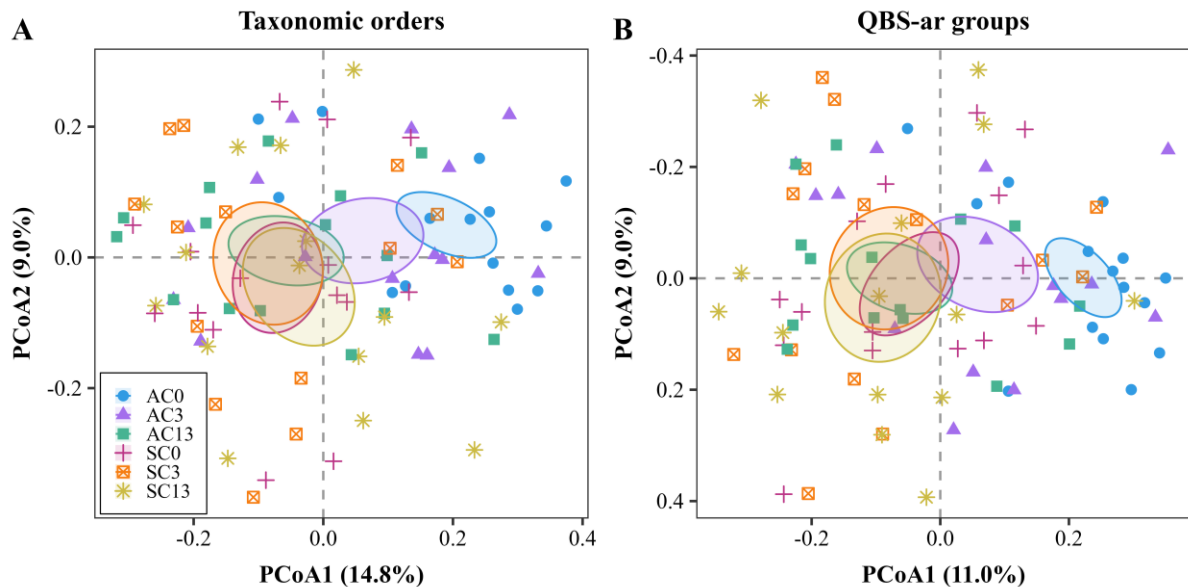


Figure 3.B.8. The Jaccard community composition of soil meso- and macro-fauna (A) taxonomic orders and (B) QBS-ar groups (class- or order-level taxa attributed specific ecomorphological index scores) collected from 90 sampling points in alley-cropping (AC) and sole-cropping (SC) systems at five farms in England, United Kingdom. Transect positions indicate distance (m) along the experimental transect. In alley-cropping systems, ‘0m’ = 1.5 m into the tree row from the edge of the understory vegetation strip (UVS), ‘3m’ = 1.5 m into the crop alley from the edge of the UVS, ‘13m’ = the centre of the crop alley or 11.5 m from the edge of the UVS (7.5 m in the case of S2). Ellipses display two standard errors of the centroid for each transect position. Proportions in brackets describe the total amount of variation in composition explained by each axis.

4 Alley-cropping and endogean soil fauna promote litter decomposition in temperate agroecosystems

4.1 Abstract

Litter decomposition is central to carbon and nutrient cycling within temperate alley-cropping systems. However, alley-cropping's impacts on litter decomposition, and particularly soil faunal contributions to litter decomposition, remain poorly understood. This study evaluated the influence of alley-cropping, soil fauna, and their interactions on *Phleum pratense* decomposition across five arable farms in England, United Kingdom.

Litter decomposition over 16 weeks was 4.1 % (± 1.4) higher in alley-cropping than sole-cropping systems ($p = 0.006$). The effect varied with proximity to tree rows: relative to sole-cropping, increases of 7.2 % (± 1.8 ; $p = 0.001$) in tree rows and by 5.3 % (± 1.8 ; $p = 0.010$), while no significant difference was detected at 11.5 m into crop alleys. Litter decomposition also declined by 4.3 % (± 1.8) at 11.5 m into crop alleys compared to tree rows ($p = 0.041$). Soil fauna increased litter decomposition by 4.8 % (± 1.0) ($p < 0.001$). Faunal contributions to litter decomposition were unaffected by alley-cropping but increased in soils with higher CEC ($p = 0.019$) and declined with increasing pH ($p = 0.025$) and Ca^{2+} concentrations ($p = 0.009$). Farm-level differences in litter decomposition were explained by soil type and temporal crop diversity.

Compared to sole-cropping, alley-cropping enhanced litter decomposition on arable farmland both in tree rows and at 1.5 m into crop alleys. Incorporation of litter-derived C and N into soil organic matter could enhance carbon sequestration and nutrient availability. However, alley-cropping's impacts are context-dependent, with more research needed to inform effective implementation.

4.2 Introduction

The decomposition of plant residues is a fundamental component of terrestrial C and nutrient cycling (Prescott and Vesterdal, 2021; Zhao et al., 2025), transferring $\sim 60 \text{ Pg C yr}^{-1}$ to soils globally (Lal, 2018). Within agroecosystems, litter decomposition is a major pathway for soil organic matter (SOM) formation (Blanco-Canqui and Lal, 2009; Kumar and Goh, 1999), maintaining belowground energy fluxes (Potapov, 2022), storing substantial quantities of C, and supplying plant-available nutrients (Cotrufo et al., 2015). Intensive agricultural practices (e.g., sole-cropping, tillage, agrochemical applications, and mechanisation) threaten these vital pathways by causing widespread soil degradation (Panagos et al., 2022; Prăvălie et al., 2024; Wiesmeier et al., 2018) which reduces litter decomposition rates (Cassani et al., 2021; Castro-Huerta et al., 2015; Domínguez et al., 2014; Martínez-García et al., 2021). Combined with fewer organic inputs to soils (Gattinger et al., 2012), lower rates of litter decomposition in intensive systems present a barrier to both the restoration of depleted soil organic matter and efforts to address the heavy reliance of the agricultural sector on mineral fertilisers (Demay et al., 2023).

Soil biodiversity loss is a central mechanism behind reduced decomposition in intensive agroecosystems (Beaumelle et al., 2023). Decomposition arises from interactions between soil organisms and their environment (Raza et al., 2023). Although soil microorganisms are the primary agents of decomposition (Bardgett and van der Putten, 2014), soil fauna make significant contributions (García-Palacios et al., 2013; Peng et al., 2023) by (i) consuming and translocating plant litter (Heděnc et al., 2022), fragmenting organic material and increasing its accessibility to microorganisms (Briones, 2018), (ii) stimulating microbial activity via grazing, activation in faunal gut passages, and/or creation of hot spots and moments through release or movement of C-rich compounds (e.g., earthworm mucus) (Angst et al., 2024; Frouz, 2018); and (iii) maintaining soil physical conditions conducive to decomposition (Briones, 2018; Frouz, 2018). Soil fauna increase litter decomposition by $\sim 30 \%$ in agroecosystems (García-Palacios et al., 2013) and crucial relationships have been identified between soil faunal biodiversity, litter decomposition, and the cycling of terrestrial C, N and P (Handa et al., 2014; Peng et al., 2023; Hättenschwiler et al., 2005; Kitz et al., 2015). Declines in soil biodiversity (Lavalley et al., 2020; Tsiafouli et al., 2015), particularly of decomposers and detritivores (Beaumelle et al., 2023; Carlesso et al., 2019; Cassani et al., 2021), under intensive agriculture impact their ability to maintain important soil functions, such as carbon transformations (de Graaff et al., 2015; Geisen et al., 2019).

Promotion of litter decomposition processes within agroecosystems is dependent on more organic inputs to soils, reduced soil degradation, and protection and enhancement of soil biodiversity. Alley-cropping, a modern agroforestry practice in which crops or livestock are produced between parallel rows of trees, is a multifunctional land-use system (Quinkenstein et al., 2009; Wolz et al., 2018b) capable of delivering several benefits which may offset the detrimental effects of intensive agriculture on litter decomposition. Alley-cropping can: (i) reduce disturbance underneath tree rows and provide physical protection from erosion (Torralba et al., 2016), (ii) supply regular, high quality organic inputs to soils (Cardinael et al., 2018; Swieter et al., 2022), (iii) support diverse decomposer and detritivore communities (Beule et al., 2022b; D’Hervilly et al., 2021; Pardon et al., 2019, 2020), and (iv) beneficially modify soil microclimates and nutrient availability which regulate decomposition processes (Jacobs et al., 2022; Pardon et al., 2017). Alley-cropping systems have been shown to increase SOM (Ivezić et al., 2022) and nutrient availability (Pardon et al., 2017) relative to arable controls. However, our mechanistic understanding of these increases, including the contribution of litter-derived C and N to accrued SOM, remains limited.

Despite the potential for alley-cropping to enhance litter decomposition, evidence from temperate regions is mixed. Several recent studies reported no consistent effect of alley-cropping on litter decomposition in temperate regions (Moran-Rodas et al., 2025; O’Connor et al., 2025; Sutterlütti et al. 2024). In contrast, studies combining stable isotopes with litter bags found that residue breakdown and accompanied C and N losses were greater in alley-cropping tree rows compared to arable crop alleys (Giray et al., 2025; Wachendorf et al., 2020). Thus, alley-cropping’s impact on litter decomposition remains unclear, with conflicting findings reported even from the same site (Oelbermann et al., 2006; Wotherspoon et al., 2014). Crucially, where a tangible impact of alley-cropping on litter decomposition has been reported, the contributions of soil biota have rarely been quantified (but see Giray et al., 2025), limiting insight into potential drivers and future opportunities for intervention.

Litter bag studies with an exclusion element remain scarce in agroecosystems (Chassain et al., 2021) and, to the best of the authors’ knowledge, none have quantified soil faunal contributions to litter decomposition in temperate alley-cropping systems. The contributions of soil-dwelling (i.e., hemi-edaphic and endogean) fauna to litter decomposition are also poorly understood (Xie, 2020), despite residue incorporation into soils being a common and beneficial practice for fertility and C management in agroecosystems (Dămătîrcă et al., 2023; Lehtinen et al., 2014; Smerald et al., 2023). In contrast to findings for more extensively studied epigeal soil

fauna, Kampichler and Bruckner (2009) reported a negative effect of microarthropods on litter decomposition after correcting for methodological biases, potentially altering the way we interpret below-ground litter decomposition dynamics in alley-cropping systems. Further information on litter decomposition dynamics, especially those of understudied soil fauna, within alley-cropping systems is needed to better understand how this multifunctional practice could contribute to soil fertility management and climate change adaptation.

In the current research, a buried litter bag experiment examined the decomposition of *Phleum pratense* in five arable systems with (alley-cropping) and without (sole-cropping) tree rows in England, United Kingdom. An exclusion component investigated the relative contribution of soil microorganisms and soil meso- and macro-fauna (hereafter referred to as soil fauna) to litter decomposition. Due to the influence of tree rows on the frequency of soil disturbance, biodiversity, and soil physicochemical properties, it was hypothesised that (i) litter decomposition would be promoted on alley-cropping fields relative to sole-cropping. Increases were predicted to be (ii) greatest underneath tree rows but extend partially into crop alleys where soils are influenced by the tree canopy, root system, and litterfall. As soil fauna increase decomposition in agroecosystems, (iii) litter bags which permitted access to soil fauna were predicted to experience higher decomposition compared to those accessible to microorganisms only. Finally, as tree rows can increase detritivore biodiversity, (iv) the relative contribution of soil fauna to litter decomposition was hypothesised to be highest underneath or in the immediate vicinity of tree rows.

4.3 Methods

4.3.1 Field sites

Litter decomposition was measured at five farms located in Cambridgeshire (C1 and C2), Nottinghamshire (N1), and Suffolk (S1 and S2) (Figure 4.1A). At each farm, two fields were selected for inclusion in the litter bag experiment: one with tree rows (alley-cropping) and one without (sole-cropping) (Figure 4.1B). Farms were selected where they had alley-cropping and sole-cropping systems with similar crop rotations, soil management regimes, and soil textures and tree rows were at least five years old. Aside from these commonalities, farms differed in their crop rotation, soil management practices, and alley-cropping system configurations (Table A.1). Detailed site descriptions are provided in Evans et al. (2025b). Crops grown during the litter decomposition experiment are provided in Table 4.A.1.

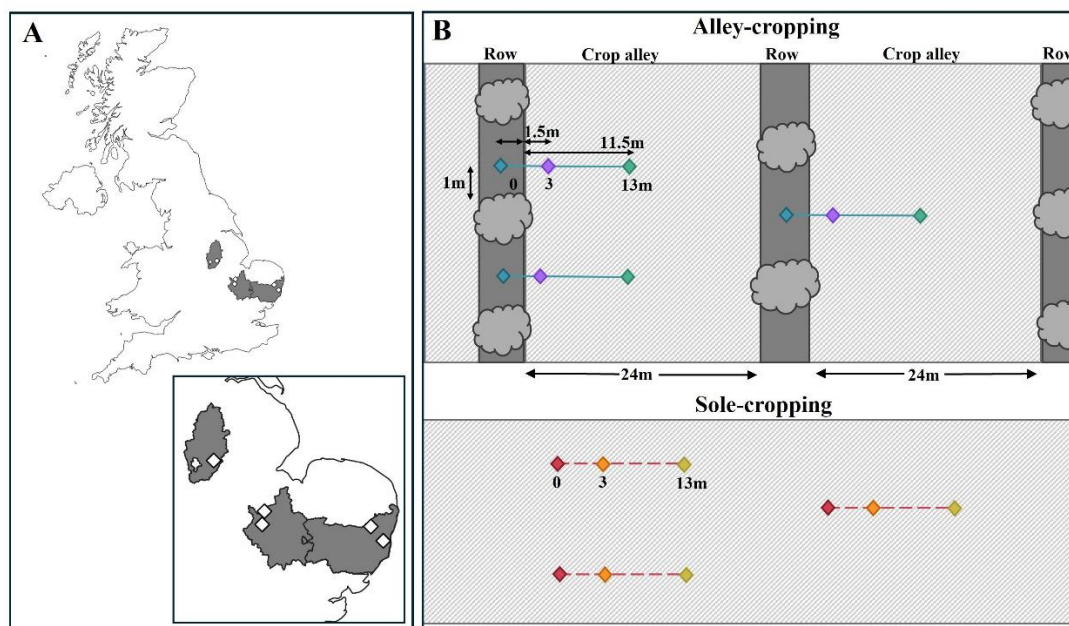


Figure 4.1. Sampling locations and experimental design. (A) Location of five arable farms in England, United Kingdom. English counties of Nottinghamshire (left), Cambridgeshire (centre), and Suffolk (right) are represented by grey polygons. The locations of sampled farms are indicated by white diamonds. (B) Schematic representation of the experimental design on paired alley-cropping and sole-cropping fields at each farm. Transects are denoted by black lines, with individual sampling points represented by diamonds positioned at three distances (m) along the transect. In alley-cropping systems, transect positions were located as follows: ‘0m’ = within the tree row, 1.5 m in from the edge of the understory vegetation strip or UVS,); ‘3m’ = 1.5 m into the crop alley from the edge of UVS; ‘13m’ = in the crop alley centre, which was 7.5 m or 11.5 m from the edge of the UVS depending on alley width. Each experimental system contained three transects. UK map created using QGIS software (QGIS Development Team, 2025).

At the time of the litter decomposition experiment, none of the studied farms applied chemical fertilisers or crop protection products to their crops or tree rows. All utilised a combination of herbal leys and crop residue retention to manage their soil fertility. In addition, farm C1 maintained soil fertility via the application of a chopped red and white clover mulch and farm S1 had grazing sheep on fields when under a herbal ley mixture. Farm N1 transitioned to organic farming in September 2023, prior to which both their alley-cropping and sole-cropping systems were treated with liquid nitrogen, mineral fertiliser, and Glyphosate as required. All farms employed a form of tillage or ploughing. No soil management occurred between placement and collection of litter bags at any farm.

4.3.2 Litter bag design

A total of 180 litter bags (90 μ m nylon mesh, internal dimensions of 8 cm x 7 cm) were filled with 4 g ($\pm 0.4_{SD}$) of air-dried pesticide-free *P. pratense* shoots (approximately 10 cm in length) and closed by heat-sealing. *P. pratense* was selected because it was a novel substrate to studied farms, thus avoiding potentially confounding home-field advantage effects (Tian et al., 2018).

However, *P. pratense* is a common constituent of multi-species seed mixtures used for leys or more permanent grasslands in the UK and its decomposition dynamics are thus relevant to various alley-cropping systems (e.g., arable, mixed, or grassland). A mesh size of 90 μm was selected to exclude all soil meso- and macro-fauna, except for potentially the smallest juveniles (Barrios, 2007; Jurburg et al., 2021). To permit entry of soil meso- and macrofauna, half of the litter bags had three equally spaced circular holes ($\varnothing$ 1 cm) arranged in a straight line down the centre of their upper side to limit litter loss via dislodgement or leaching.

4.3.3 Experimental design

Sampling followed the design outlined in Evans et al. (2025b). Briefly, litter bags were buried in paired alley-cropping and sole-cropping systems at three distances along linear transects (0, 3, and 13 m). In alley-cropping systems, distances equated to 1.5 m into the tree row from the edge of the understory vegetation strip (UVS) (0 m, AC0), 1.5 m into the crop alley from the edge of the UVS (3 m, AC3), and the centre of the crop alley (13 m, AC13). The crop alley centre was 11.5 m from the edge of the UVS at all farms excluding S2, where it was 7.5 m into the crop alley (Table 4.A.1). Distances (SC0, SC3, and SC13) and orientation of transects was replicated in sole-cropping systems.

In November 2023, two litter bags, with and without holes, were buried at each sampling point at a soil depth of 10 cm. Sample incubation at 5–10 cm depth is a common method to quantify litter decomposition by soil decomposer communities, including hemi-edaphic and endogean soil fauna (Carlesso et al., 2019; Giray et al., 2025; Xie, 2020). A depth of 10 cm was therefore selected to capture the contribution of soil microorganisms and hemi-edaphic and endogean soil fauna (hereafter referred to as soil fauna) to the decomposition of incorporated residues. Soil holes for litter bags were excavated using a corer ($\varnothing$ 10 cm), with the intact core, including any surface litter, re-established in its original position on top of the bag. A 2 cm layer of soil from the bottom of the core was removed to ensure the re-established core was level with the ground surface and, where necessary, this soil was used to fill any gaps between the core and surrounding soil.

Litter bags were established in late autumn after soils had been prepared for the next crop and would not be disturbed again until the following year, allowing for the longest possible incubation time. At the point of burial, the previous year's crop residues and tree litter had just been incorporated into soils via cultivation, representing an ideal time to measure litter

decomposition in arable topsoils. Litter bags were not buried in tramlines to avoid disturbance by farm machinery. Litter bags were collected after 16 weeks of incubation.

Originally, the described litter decomposition experiment involved incubation of 960 litter bags with four sampling events at 4, 8, 16, and 32 weeks. This experimental design was intended to provide insights into the impacts of alley-cropping and endogean soil fauna on litter in various stages of decomposition. Unfortunately, the final replicate set of litter bags was disturbed by agronomic activity, and the first two replicate sets were damaged in a laboratory flood. Consequently, data from the 16-week collection was presented in the current research.

4.3.4 Litter analysis

To avoid loss of material during collection, litter bags were sealed in labelled paper bags in the field and paper bags were placed immediately into a convection oven at 60 °C upon arrival at the laboratory. Samples were considered dried when their weight was stable to 0.01 g (International Organization for Standardization, 1993). Oven-dried samples were weighed inside their litter bags before removal and re-weighing without litter bags.

Litter calculations were conducted on ash-free sample weights (determined by Equation i) to account for the contamination of remaining litter by mineral soil (Harmon et al., 1999; Potthoff and Loftfield, 1998).

$$(i) \quad Mass_{AF} = Mass_{total} - Mass_i$$

Where ‘mass’ = oven-dried weight of *P. pratense* litter (g), ‘ $_{AF}$ ’ = ash-free (organic), ‘ $_{total}$ ’ = all litter (organic + inorganic), ‘ $_i$ ’ = inorganic.

Initial oven-dried ash-free mass of samples was calculated by applying a correction to sample weights which removed the average *P. pratense* moisture (3.9 ± 0.2 %) and ash (6.3 ± 0.3 %) content as determined from 10 samples (Potthoff and Loftfield, 1998). After collection, litter samples (still inside their bags) were oven-dried at 60 °C until the weight was stable to 0.01 g. Contamination of litter samples with mineral soil was measured via loss-on-ignition (Sluiter et al., 2005). Briefly, litter samples were ground to 2 mm using a Turimon electric grinder (UPC 791564856300). Samples were ground for intervals of 60 seconds at 30 000 rpm, with short breaks every 12 seconds to allow the instrument to cool. Sample material was passed through a 2 mm sieve at the end of each interval, until no material remained in the grinder. A maximum of 4 g of each sieved sample was heated for four hours at 550 °C in a Carbolite CWF 12/5 Chamber Furnace. The remaining weight, a combination of litter ash and the mineral

component of contaminant soil, was removed from sample weights to generate a final ash-free mass (Potthoff and Loftfield, 1998).

Although commonly applied to address the contamination of litter samples with mineral soil in traditional litter bag experiments (e.g., Berenstecher et al., 2021; Bethe et al., 2025; Röder et al., 2024), comparisons of ash-free mass do not account for contamination with organic material such as soil organic matter, faunal biomass, or invertebrate frass (Idol et al., 2002). Consequently, the potential influence of soil organic matter contamination on observed trends in litter decomposition were investigated via the method outlined in Appendix A and deemed negligible prior to data analysis (Table 4.A.2).

4.3.5 Litter decomposition – calculation methods

Litter decomposition was calculated as the proportion (%) of ash-free mass lost over the incubation period (Equation ii).

$$(ii) \quad Mass\ loss_{AF} = ((Mass_{AF-pre} - Mass_{AF-post}) / Mass_{AF-pre}) \times 100$$

Where ‘mass’ = oven-dried weight of *P. pratense* litter (g), ‘_{AF}’ = ash-free, ‘_{pre}’ = before incubation, ‘_{post}’ = after incubation.

Litter decomposition attributed to soil microorganisms was considered equal to the proportion of ash-free mass lost in bags without holes (i.e., no access for soil meso- and macro-fauna). Litter decomposition mediated by soil fauna was calculated as the difference in ash-free mass between bags with and without holes (i.e., permitting or excluding soil fauna, respectively) (Equation iii). The relative contribution of soil fauna to total litter decomposition was calculated as the litter decomposition attributed to soil fauna as a proportion of total litter decomposition in bags with holes (Equation iv).

$$(iii) \quad Mass\ loss_{fauna} = (Mass_{AF-with} - Mass_{AF-without})$$

$$(iv) \quad Contribution_{fauna} = (Mass\ loss_{fauna} / Mass\ loss_{AF-with}) \times 100$$

Where ‘mass’ = oven-dried weight of *P. pratense* litter (g), ‘_{AF}’ = ash-free (organic), ‘_{without}’ = bag without holes, ‘_{with}’ = bag with holes, ‘_{fauna}’ = faunal-mediated, and ‘*contribution*’ = relative contribution to mass loss in bags with holes.

4.3.6 Soil physicochemical analysis

Soil temperature (Temp, °C) was measured at a depth of 10 cm using a Hanna Instruments EN-13485 Checktemp® Pocket digital thermometer. Soil moisture content (MC, g H₂O 100 g⁻¹) was determined following the method of ISO 11465 (International Organization for

Standardization, 1993). As soil temperature and moisture content were expected to vary over time, they were measured at the time of litter bag burial in November 2023 and during collections in December 2023, January 2024, and March 2024. The average, minimum, and maximum temperature ($Temp_{avg/low/high}$) and MC ($MC_{avg/low/high}$) for each sampling point were calculated. The difference in temperature ($Temp_{range}$) and MC (MC_{range}) between the minimum and maximum recorded values was also calculated as a measure of variability. All other soil physicochemical properties, described below, were measured from a soil core ($\varnothing$ 10 cm x 15 cm depth) extracted in November 2023 from 10 cm to the left of each sampling point. Analyses were conducted on thoroughly mixed, air-dried, 2 mm-sieved samples, except where stated otherwise.

Soil bulk density (BD, $g\ cm^{-3}$) was calculated according to the ISO 11272 volumetric cylinder method (International Organization for Standardization, 2017). Soil texture was determined by feel (Thien, 1979). Organic matter content (SOM, $g\ 100\ g^{-1}$) was calculated by loss-on-ignition at 350 °C overnight in a Carbolite CWF 12/5 Chamber Furnace (Ayub and Boyd, 1994). For pH analysis, 10 g soil was mixed with 25 mL of deionised water and shaken for one hour on an end-over-end shaker at 25 rpm for 15 minutes. The pH of the supernatant was measured using a Thermo Orion Star A111 pH meter calibrated to pH 4.0, 7.0 and 10.0 buffers after leaving the sample to settle for 15 mins (Ministry of Agriculture, Fisheries and Food, 1986).

Cation exchange capacity was calculated using the $BaCl_2$ method of Hendershot and Duquette (1986). Exchangeable Ca, Mg, K, Na, Al, Fe, and Mn in the 0.1 M $BaCl_2$ extract were measured via inductively coupled plasma-optical emission spectroscopy (ICP-OES) using a Thermo iCAP 7000. Instrumental accuracy, determined through analysis of the Merck ICP multi-element standard solution IV at a concentration of $0.25\ mg\ L^{-1}$, was 106-122 %. Precision was within the range of 0.8-25.0 % as determined by duplicate analysis of 10 % of samples (Gill and Ramsey, 1997). Procedural blanks were below the detection limit of the ICP-OES, which were determined by ten repeat analyses of a calibration blank (Walsh, 1997). Concentrations below the detection limit were set to a consistent value (i.e., detection limit / square root of two) for statistical analysis (Croghan and Egeghy, 2003). Fe and Al were excluded from statistical analysis (including calculation of CEC) due to low instrumental accuracy (44 %) and sample concentrations ($< 7\ %$ of samples above detection limit), respectively.

Elemental analysis (Elementar Vario EL Cube) of soil, oven-dried at 40 °C for 48 h and ground to $< 200\ \mu m$ using a Retsch MM200 ball mill, was used to measure total carbon (TC) and nitrogen (TN). Accuracy of the elemental analyser, calculated using 20 mg of a soil reference

standard material (0.13 % N, 1.55 % C), was 104.6 % and 98.4 % for TC and TN, respectively. Concentrations were above detection limits calculated from nine repeat analyses of a calibration blank. Precision, determined through duplicate analysis of 10 % of samples, was 2.9 % for TC and 4.7 % for TN. Full quality control information can be found in Table 4.A.3.

4.3.7 Statistical analysis

Linear and linear mixed-effects (LMM) models were used to investigate litter decomposition dynamics in alley-cropping and sole-cropping systems. As the data had a nested hierarchical structure, LMMs were selected to account for the dependencies and correlations present between observations within the same transects and farms (Harrison et al., 2018), with the assumption being that within-group variation would be smaller than between groups. Model details are available in Table 4.A.4. Statistical analyses were undertaken in R version 4.5.2 (R Core Team, 2025). Modelling was performed using the *lmer* function of the ‘lme4’ package (v. 1.1-35.2, Bates et al., 2015) and *lm* function of the ‘stats’ package (R Core Team, 2025).

4.3.7.1 Model structures

The influence of agricultural system (alley-cropping vs sole-cropping), transect position (0 m, 3 m, or 13 m), their interaction, and the presence of soil fauna (bags with vs without holes) was investigated (hypotheses i–iii; Model A). As high spatial variation was observed in sole-cropping systems, hypothesis (ii) was further addressed by comparing litter decomposition at each of the three transect positions in alley-cropping with the average litter decomposition across the three positions sole-cropping. To elucidate the role of soil microorganisms and fauna to litter decomposition, the effect of agricultural system and transect position on litter mass loss in bags with and without holes, as well as the relative contribution of soil fauna to litter decomposition, was also explored (hypotheses iii–iv; Models B–D). Furthermore, as farm explained a large proportion of the variation in litter decomposition (Section 4.4.1), farm-specific responses to alley-cropping were investigated (Model E).

4.3.7.2 Model selection

Final models presented in Table A.3 were created following a process of backward stepwise selection. First, full LMMs were generated which included (i) agricultural system, transect position, and their interaction (retained in all final models), (ii) soil physicochemical properties (Table B.1) and farm- and system-level variables (Table A.1) which could have influenced litter decomposition, and (iii) nested random effects (farm/transect). Retained fixed effects were then selected based on their impact on model fit, assessed via the *AICc* function of the ‘MuMIn’ package (v. 1.47.5, Bartoń, 2023). The Akaike Information Criterion (*AICc*) was selected as it

corrects for small sample sizes and penalises model overfitting (Hurvich and Tsai, 1993). Fixed effects were removed sequentially from the full model (keeping all others the same) and the one which had the worst impact on model fit was excluded. This process was repeated until removal of individual fixed effects reduced AICc by < 2 , at which point models with and without a given variable were both deemed to have strong support (Burnham and Anderson, 2002). Exclusion of fixed effects causing autocorrelation was also determined based on AICc. Where farm- and system-level variables captured the variation explained by farm and/or transect, they were included as fixed effects and the random effect(s) removed if this improved model fit.

4.3.7.3 Model evaluation

Diagnostic plots (i.e., normality of residuals, normality of random effects, heteroscedasticity, homogeneity of variance, and multicollinearity) were used to assess goodness of fit of final models. Plots were generated by the *check_model* function of the ‘performance’ package (v. 0.13.0, Lüdtke et al., 2021). Assessment of model overfitting was assessed using leave-one-group-out cross validation (LOGO-CV) (Roberts et al., 2017; Yates et al., 2023). This involved training models on all but one transects and then testing it on the withheld transect. With some reductions in performance expected on unseen data, increases in the average per-fold root mean square error (RMSE) of $< 25\%$ between training and test data were accepted (Hastie et al., 2009; Yates et al., 2023).

4.3.7.4 Litter decomposition analyses

The significance of fixed effects retained in final model as predictors of litter decomposition was determined by partial F-tests (linear models) or likelihood ratio tests (LMMs) using the *anova* function of the ‘stats’ package (R Core Team, 2025). Pairwise *post hoc* comparisons of estimated marginal means between transect positions in alley-cropping and sole-cropping were made using the *emmeans* function of the ‘emmeans’ package (v. 1.11.0, Lenth, 2025) with a Benjamini-Hochberg false discovery rate (FDR) correction for multiple comparisons (Benjamini and Hochberg, 1995; Pike, 2011). A significance threshold of $\alpha = 0.05$ was used for all tests. For LMMs, the proportion of the variance explained by fixed effects (R^2_m) and the combined fixed and random effects (R^2_c) was determined via the *r2* function of the ‘performance’ package (Lüdtke et al., 2021). Correlations between microorganism-mediated litter decomposition and faunal contributions to litter decomposition were determined using the *cor.test* function of the ‘stats’ package (R Core Team, 2025).

Research data is available from Figshare: 29940068.

4.4 Results

4.4.1 *The influence of alley-cropping on litter decomposition*

Litter decomposition (measured as % ash-free mass loss) ranged from 22.2–94.7 % after 16 weeks, with an average of 61.9 ($\pm 11.1_{SD}$) %. Litter decomposition was significantly influenced by agricultural system ($\chi^2_{(1)} = 11.63$, $p < 0.001$), transect position ($\chi^2_{(2)} = 15.80$, $p < 0.001$), and their interaction ($\chi^2_{(2)} = 20.25$, $p < 0.001$) (Model A; $\chi^2_{(12)} = 99.88$, $p < 0.001$; $R^2_c = 0.64$, $R^2_m = 0.61$). Alley-cropping increased litter decomposition by 4.1 ($\pm 1.4_{SE}$) % compared to sole-cropping ($t_{(27.1)} = 2.96$, $p = 0.006$). The extent of the increase was dependent on proximity to the tree row; compared to the sole-cropping average, litter decomposition increased by 7.2 % ($\pm 1.8_{SE}$) at AC0 ($t_{(88.2)} = 3.91$, $p = 0.001$) and 5.3 % ($\pm 1.8_{SE}$) at AC3 ($t_{(88.4)} = 2.90$, $p = 0.010$). No significant difference in litter decomposition was observed between sole-cropping and AC13 ($t_{(88.5)} = 1.58$, $p = 0.142$). Comparing transect positions in alley-cropping, litter decomposition at AC0 was 4.3 ($\pm 1.8_{SE}$) % higher than at AC13 ($t_{(156.0)} = 2.43$, $p = 0.041$) (Figure 4.2). No significant differences were identified between AC0 and AC3 or AC3 and AC13 ($p > 0.05$) (Figure 4.2). Litter decomposition rates varied among sole-cropping transect positions, which differed in their relationship to alley-cropping (Figure 4.2).

Farm-level variations in litter decomposition dynamics were observed (Figure 4.B.1). Litter decomposition was significantly influenced by farm ($F_{(4)} = 46.16$, $p < 0.001$) and the interaction between farm and agricultural system ($F_{(20)} = 2.52$, $p < 0.001$) (Model F; $F_{(32,147)} = 11.09$, $p < 0.001$; $R^2_{adj} = 0.64$). Farm-level variation was explained by a combination of soil type and crop diversity.

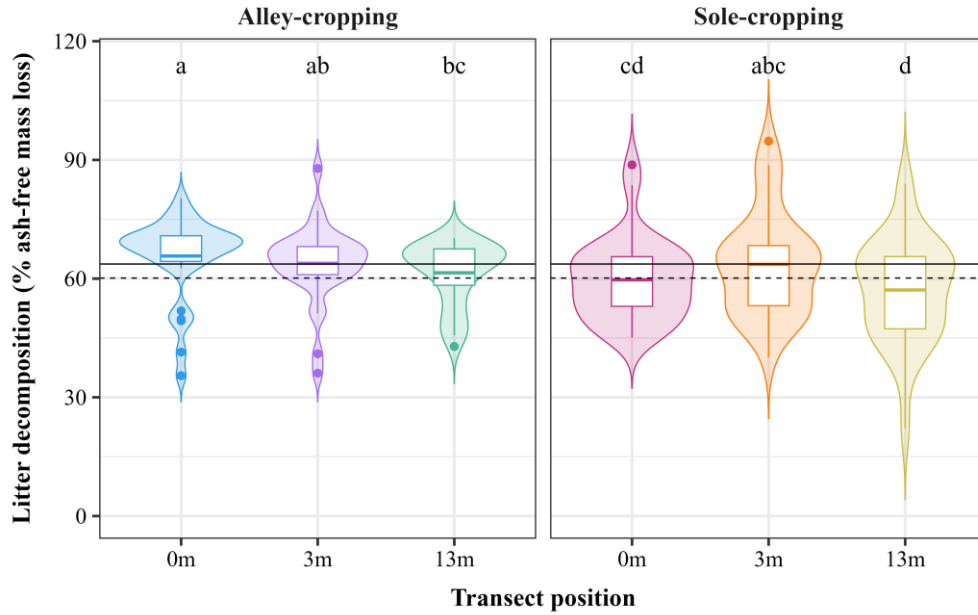


Figure 4.2. Litter decomposition (% ash-free mass loss) in litter bags ($n = 180$) buried at 10 cm depth for 16 weeks in paired alley-cropping and sole-cropping systems at five arable farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5) of ash-free mass loss (%) for each distance along linear experimental transects (or transect positions): 0 m (1.5 m into the tree row from the edge of the understory vegetation strip or UVS), 3 m (1.5 m into the crop alley from the UVS), and 13 m (7.5 m or 11.5 m into the crop alley from the UVS) for sole-cropping (and alley-cropping), respectively. Violin plots display the distribution of the data points for each transect position. Individual points represent outliers. Horizontal lines indicate the average ash-free mass loss (%) for agricultural systems: solid = alley-cropping, dashed = sole-cropping. Letters positioned above violin plots highlight significant pairwise differences in ash-free mass loss (%) between transect positions nested within treatments, as determined by linear mixed-effects modelling and *post hoc* comparisons of estimated marginal means with a false discovery rate correction for multiple comparisons. No shared letter indicates a significant difference at $\alpha = 0.05$.

4.4.2 The contribution of soil fauna to litter decomposition

Soil microorganisms were the dominant decomposers of plant litter. Mean litter decomposition in bags without holes was 59.5 % ($\pm 10.7_{SD}$), representing 92.5 % of litter decomposition in bags with holes. Soil meso- and macro-fauna increased litter decomposition by 4.8 % ($\pm 1.0_{SE}$) ($t_{(143.88)} = 4.66$, $p < 0.001$) (Figure 4.3A), with the presence of holes in litter bags a significant predictor of mass loss ($\chi^2_{(1)} = 21.00$, $p < 0.001$). However, both faunal-mediated litter decomposition (-26.98–35.89 %) and faunal contributions to litter decomposition (-45.79–47.65 %) were highly variable. Furthermore, every increase in microorganism-mediated litter decomposition (proportion of applied litter decomposed by microorganisms) of 1 % reduced the faunal contribution to litter decomposition (as a proportion of decomposed litter) by 1.1 % ($\pm 0.19_{SE}$) ($F_{(1)} = 36.21$, $t = 6.02$, $p < 0.001$).

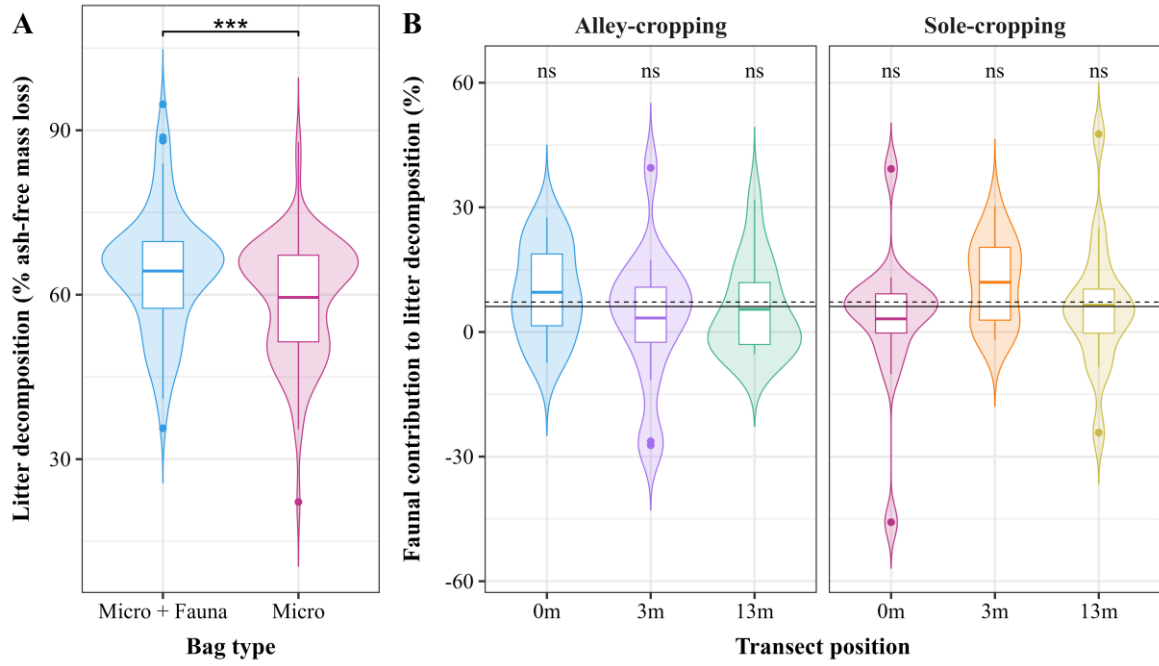


Figure 4.3. The contribution of soil meso- and macro-fauna to litter decomposition. (A) Litter decomposition (% ash-free mass loss) within litter bags ($n = 180$) which permitted soil meso- and macro-fauna and microorganisms ('Micro + Fauna') or microorganisms only ('Micro'); and (B) faunal contribution to litter decomposition (%) as a function of agricultural system (alley-cropping vs. sole-cropping) and transect position. Transect positions refer to distance in m along linear experimental transects: 0 m (1.5 m into the tree row from the edge of the UVS), 3 m (1.5 m into the crop alley from the UVS), and 13 m (7.5 m or 11.5 m into the crop alley from the UVS) for sole-cropping (and alley-cropping). Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (interquartile range $\times 1.5$) of ash-free mass loss (%). Violin plots display the distribution of the data points and individual points represent outliers. Horizontal lines on Figure 4.3B indicate the average proportion of observed ash-free mass loss (%) contributed by soil meso- and macrofauna for each agricultural system: solid = alley-cropping, dashed = sole-cropping. Significant pairwise differences in litter decomposition, as determined by linear mixed models or Tukey post-hoc comparisons, are indicated by the following: *** $p < 0.001$, ns = not significant. No shared letter indicates a significant difference at $\alpha = 0.05$.

4.4.3 The influence of alley-cropping on faunal-mediated litter decomposition

Faunal contribution to litter decomposition was marginally higher in sole-cropping ($7.2 \pm 15.0_{SD} \%$) compared to alley-cropping ($6.1 \pm 13.2_{SD} \%$). However, agricultural system, transect position, and their interaction had no influence on faunal litter decomposition ($p > 0.05$) (Model C; $F_{(11,78)} = 2.36$; $p = 0.014$; $R^2_{adj} = 0.14$) (Figure 4.3B) or the relative contribution of fauna to litter decomposition ($p > 0.05$) (Model D; $F_{(11,78)} = 1.90$; $p = 0.052$; $R^2_{adj} = 0.10$). In contrast, agricultural system was a significant predictor of litter decomposition driven by microorganisms ($\chi^2_{(1)} = 13.99$, $p < 0.001$) (Model B; $F_{(11,78)} = 16.74$; $p < 0.001$; $R^2_{adj} = 0.66$). Microbially driven litter decomposition increased by 5.3 % ($\pm 1.4_{SE}$) in alley-cropping relative to sole-cropping ($t_{(78.0)} = 3.70$, $p < 0.001$). Compared to SC13, microbially driven litter decomposition increased by 8.9 % ($\pm 2.4_{SE}$) at AC0 ($t_{(78.0)} = 3.73$, $p = 0.003$) and 9.0 % ($\pm 2.4_{SE}$) at AC3 ($t_{(78.0)} = 3.78$, $p = 0.003$).

4.4.4 Soil physicochemical properties

Litter decomposition was influenced by crop diversity and soil CEC, and soil Ca^{2+} concentration was a marginally significant predictor (Table 4.1). Consideration of decomposition by soil microorganisms and fauna separately revealed that crop diversity reduced microbially driven litter decomposition but had no effect on litter decomposition by fauna. Faunal litter decomposition, on the other hand, increased with soil CEC and decreased with soil pH and exchangeable Ca concentration (Table 4.1).

Table 4.1. The significance of soil physicochemical properties, farm- and system-level variables (fixed effects) as predictors of litter decomposition by soil microorganisms ('Micro'), fauna, or microorganisms and fauna combined ('Micro + Fauna'). Changes in litter decomposition (%) (est) and standard errors (se) were estimated using linear or linear mixed-effects models. χ^2/F and p-values for fixed effects were determined via comparing models with and without the fixed effect using ANOVA. '-' indicates that a fixed effect was not included in the model for a given litter decomposition metric.

Fixed ¹ effect	Micro + Fauna				Micro				Fauna			
	Est ²	se	χ^2	p	est	se	F	p	est	se	F	p
Soil type	NA	NA	36.03	< 0.001	NA	NA	17.46	< 0.001	NA	NA	4.23	0.008
Crop _{div}	-2.9	1.3	4.80	0.029	-4.1	1.4	8.70	0.004	-	-	-	-
CEC	0.13	0.04	12.13	< 0.001	0.06	0.04	2.74	0.102	0.15	0.06	5.73	0.019
Ca	-0.27	0.14	3.84	0.050	-	-	-	-	-0.62	0.23	7.17	0.009
TN	-	-	-	-	0.41	0.32	1.65	0.204	-0.43	0.31	1.91	0.171
Mn	-	-	-	-	0.08	0.08	1.09	0.300	-	-	-	-
C:N	-	-	-	-	0.59	0.57	1.10	0.298	-	-	-	-
Mg	-	-	-	-	-	-	-	-	1.4	1.1	1.63	0.205
pH	-	-	-	-	-	-	-	-	-10.9	4.8	5.22	0.025
Temp _{avg}	-	-	-	-	-	-	-	-	-5.2	4.0	1.72	0.194

¹ Fixed effects: 'Soil type' = Soil type according to the Soilscales Viewer online soil reporting tool (Cranfield Soil and Agrifood Institute, 2025), 'Crop_{div}' = the number of crops grown between 2021–2024, 'CEC' = soil cation exchange capacity (meq 100 g⁻¹), 'Ca' or 'Mn' = soil exchangeable calcium or magnesium concentration (g kg⁻¹), 'C:N' = soil carbon-to-nitrogen ratio, 'Mn' = soil exchangeable manganese concentration (mg kg⁻¹), pH = concentration of H⁺ ions (μmol), 'TN' = soil total N content (g kg⁻¹).

² Estimates indicate the change in litter decomposition (%) with a one unit increase in the fixed effect.

Soil type was a significant predictor of litter decomposition by soil microorganisms, fauna, and both size classes combined (Table 4.1). However, the impact of soil type on litter decomposition by soil microorganisms or fauna differed (Figure 4.4).

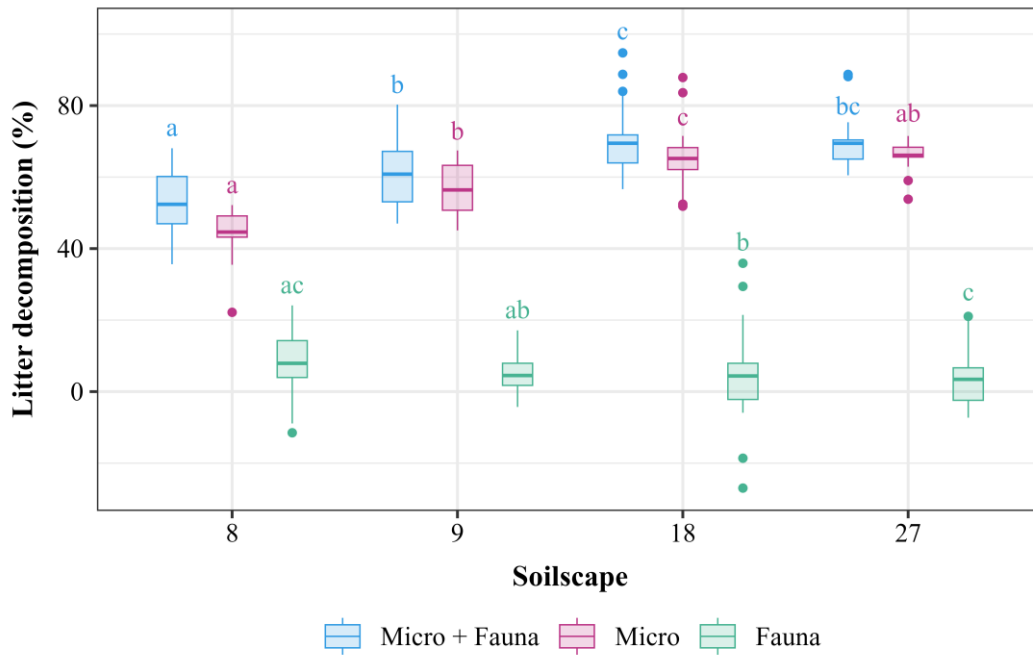


Figure 4.4. Litter decomposition (%) according to soil type and size class of soil organisms. ‘Micro + Fauna’ = soil microorganisms and soil fauna together (blue), ‘Micro’ = microorganisms (red), and ‘Fauna’ = meso- and macro-fauna (green). Soil types were classified into Soilscales according to Cranfield Soil and Agrifood Institute (2025). Litter decomposition is expressed as ash-free mass loss. No shared letter indicates a significant pairwise difference at $\alpha = 0.05$, determined from *post hoc* tests of final linear and linear mixed-effects models with a false discovery rate correction for multiple comparisons.

4.5 Discussion

4.5.1 The influence of alley-cropping on litter decomposition

Relative to sole-cropping, alley-cropping significantly increased below-ground litter decomposition in arable systems, both in tree rows and at 1.5 m into crop alleys. Increases did not extend to the centre of crop alleys, either because they were beyond the influence of alley-cropping trees or this study, with a modest sample size, could not detect the significance of small increases observed at this point in the crop alley. These findings contrast with previous research from temperate alley-cropping systems which reported a negligible impact of tree rows on litter decomposition (Moran-Rodas et al., 2025; Mungai and Motavalli, 2006; O’Connor et al., 2025, Oelbermann et al., 2006; Sutterlütli et al., 2023) or increases in litter decomposition only in tree rows (Giray et al., 2025; Wachendorf et al., 2020). Consequently, they highlight the potential for alley-cropping to enhance soil nutrient cycling functions in arable fields in central and eastern England, as well as the importance of context-specific evidence (e.g., evidence generated within a relevant pedo-climatic context) to inform farmer decision-making and policy development around alley-cropping.

As a biotically-mediated process (Raza et al., 2023), observed increases in litter decomposition were likely associated with an increase in the functional diversity and/or activity of soil organisms, which are often enhanced in the presence of tree rows (Beule et al., 2022b; Marsden et al., 2020). Indeed, at the study farms, the biodiversity of soil-dwelling fauna—organisms which play a central role in litter decomposition (García-Palacios et al., 2013; Handa et al., 2014)—was reported to be higher in alley-cropping tree rows and at 1.5 m into crop alleys than in their sole-cropping counterparts (Evans et al., 2025). Despite this, alley-cropping had no effect on faunal-mediated litter decomposition in the current research, with increases in litter decomposition in tree rows and at 1.5 m into crop alleys instead attributable to microorganisms.

Although this study is the first to investigate the dynamics of faunal-mediated litter decomposition in temperate alley-cropping systems, Mettauer et al. (2022) previously reported that tree rows had no effect on faunal feeding activity as measured by bait lamina. A possible explanation is that any potential increases in detritivore-mediated decomposition driven by biodiversity gains in response to alley-cropping were offset by a higher predator activity-density and complementarity (Boinot et al., 2020; Martin-Chave et al., 2019; Matevski et al., 2024), which ultimately suppressed feeding activity. Alternatively, whilst increases in faunal biodiversity were reported from ambient soil communities (Evans et al., 2025), detritivore communities within litterbags themselves, which more accurately predict litter decomposition (Peng et al., 2023), may have remained unaffected by alley-cropping. Considering the positive response of microorganism-mediated decomposition to alley-cropping in this study, it is likely that tree rows simply created favourable conditions for microbial decomposition, which is known to reduce the relative contribution of soil fauna to litter decomposition (Frouz, 2018; Peguero et al., 2019).

Tree rows create favourable conditions for the diversification and population growth of soil microorganisms through reduced soil disturbance and improved soil structure, moderation of soil microclimates, and the diversification of soil micro-habitats and resource inputs (Beule et al., 2022b, 2025). These benefits can extend beyond the tree row where crop alleys interact with tree root systems, canopy structures, and spillover biodiversity. Consequently, microbial biomass, abundance, and diversity (taxonomic *and* functional) are often enhanced in alley-cropping systems relative to their sole-cropping counterparts, both in tree rows as well as in adjacent areas of crop alleys (Beule et al., 2022b; Mettauer et al., 2022; Vaupel et al., 2023). These changes in microbial diversity, and particularly functional diversity, can increase microbial catabolic potential in tree rows relative to arable crop areas (Beule et al., 2022b; Liu

et al., 2023c). Tree rows have previously been associated with greater potential enzyme activities and substrate-induced respiration than crop alleys (Beule et al., 2022b, 2025), which may have resulted in higher litter decomposition rates in and near tree rows in the current research.

Rhizodeposition and litter from trees and UVS, which predominantly falls within 2 m of tree rows (Swieter et al., 2022), may also have had a priming effect on soil microbial communities (Liu et al., 2020; Luo et al., 2015), resulting in greater decomposition of applied litter. Furthermore, tree species present at the studied farms, such as *Malus domestica*, form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), which can enhance litter decomposition (Gui et al., 2017; Mei et al., 2022). AMF abundances have been found to increase significantly in alley-cropping tree rows and at 1–2 m into crop alleys compared to crop alley centres or sole-cropping systems (Guillot et al., 2021), demonstrating a similar pattern to litter decomposition rates in the current research. However, as microbial communities at the studied farms were not examined, and no relationships were identified between microorganism-mediated litter decomposition and the soil physicochemical variables influenced by tree rows, the mechanisms underlying observed increases in microorganism-mediated decomposition remain unclear.

Regardless of the mechanisms underpinning them, increases in litter decomposition in response to tree rows demonstrate the potential for alley-cropping to enhance soil fertility and organic matter stocks – not just by increasing the amount of litter inputs to soils (Swieter et al., 2022), but also by increasing the rate at which existing litter, such as buried crop residues, is incorporated into SOM. As a result, the efficacy of promising agronomic practices aimed at enhancing soil C sequestration, such as residue incorporation (Taghizadeh-Toosi et al., 2026), may increase. Studies using stable isotopes to trace the fate of litter-derived C and N in temperate alley-cropping systems have reported a higher recovery in soils below litter bags (0–5 cm) in tree rows compared to crop alleys (Giray et al., 2025; Wachendorf et al., 2020), indicating greater SOM accumulation from incorporated litter. Litter decomposition has also been provided as an explanation for improved soil nutrient status in tree rows and crop alleys of alley-cropping systems (Moran-Rodas et al., 2025; Pardon et al., 2017). However, the additional supply of organic matter and nutrients from a 4.1 % increase in litter decomposition, or even lower in crop alleys, would form only a fraction of the nutrients currently applied to cereals as fertilisers in England (Department for Environment, Food, and Rural Affairs, 2025). Consequently, soil C and nutrient gains are dependent on sufficient organic inputs to soils,

decomposition pathways which favour SOM accumulation (rather than C and nutrient losses), and agronomic management which supports SOM persistence, particularly in crop alleys.

4.5.2 *The contribution of soil fauna to litter decomposition*

Soil meso- and macro-fauna increased *P. pratense* decomposition by an average of 4.8 %, consistent with previous findings from temperate agroecosystems (Cassani et al., 2021; Castro-Huerta et al., 2015; Chassain et al., 2021). The observed range of faunal-mediated litter decomposition (-27.0–35.9 %) demonstrates that hemi-edaphic and endogean fauna can substantially enhance or inhibit below-ground litter decomposition. Negative effects have been previously documented: soil fauna reduced decomposition of litter mixtures in temperate forests (Njoroge et al., 2022) and findings from a meta-analysis of litter bag studies indicated that after correcting for methodological biases, microarthropods have a negative impact on litter mass loss (Kampichler and Bruckner, 2009). Such reductions may arise from microbial suppression or delayed microbial colonisation of litter due to faunal grazing, abiotic disturbance, or disruption of microbial networks (e.g., fungal hyphae) (Bradford et al., 2002; Kampichler and Bruckner, 2009). Whether soil fauna enhanced or inhibited litter decomposition was highly idiosyncratic, demonstrating the sensitivity of soil fauna to changes in their abiotic environment even at small spatial scales (Burtis et al., 2024).

An average faunal-mediated increase in litter decomposition of 4.8 % is slightly low relative to typical estimates from temperate regions, which fall in the range of 10–30 % (García-Palacios et al., 2013; Li et al., 2024b; Lin et al., 2019). As faunal contributions to litter decomposition are strongly context-dependent, this may due to the unique context within which the experiment was set (e.g., pedo-climate, management history, local biodiversity) (Birkhofer et al., 2011; Fujii et al., 2018; Li et al., 2024b; Peng et al., 2022b; Wall et al., 2008) and the substrate used (Li et al., 2024b; Sauvadet et al., 2017; Smith and Bradford, 2003), or instead the litter bag design.

Faunal-mediated litter decomposition is typically quantified through comparisons of litter bags with differential mesh sizes (Kampichler and Bruckner, 2009; Zan et al., 2022). This approach can lead to overestimates of up to 25 % (± 9.9) (Bradford et al., 2002; Kampichler and Bruckner, 2009; Siedentop, 1995) due to mesh-induced differences in within-bag microclimates, leaching, litter loss, contamination, and microbial colonisation (Bradford et al., 2002; Cates et al., 2021; Kampichler and Bruckner, 2009; Xie, 2020). Here, a consistent mesh size was used, potentially providing a more accurate estimate of faunal contributions to litter

decomposition. However, the design may have instead restricted faunal translocation of larger *P. pratense* particles (Bokhorst and Wardle, 2013). Furthermore, use of 90 µm mesh may have permitted juvenile detritivores into microorganism-only bags (Cates et al., 2021), potentially elevating estimated microbial decomposition.

4.5.3 *Field- and farm-scale drivers of litter decomposition*

In this study, litter decomposition varied between farms, with differences driven by soil type and agronomic management. Litter decomposition was reduced in Soilscape 8 and 9, both characterised by impeded drainage (Cranfield Soil and Agrifood Institute, 2025). Consequent waterlogging may have created anaerobic conditions and soil structural changes that altered microbial communities and slowed litter decomposition (Carlesso et al., 2019; Liu et al., 2023a). These effects were likely more pronounced at farm N1 (Soilscape 8) than at C1 (Soilscape 9) because fields at N1 were more recently cultivated and experience cooler, wetter conditions (Met Office, 2025). Microorganism-mediated decomposition also declined in systems with higher temporal crop diversity, perhaps due to the consequences of more frequent soil disturbance on decomposer communities and their interactions with detritivores (Domnariu et al., 2025; Yu et al., 2025). However, it should be noted that crop diversity was not a reliable indicator of disturbance at all farms; farm C2 had the lowest crop diversity but, due to a lack of ley years, experienced the most frequent soil disturbance.

CEC positively influenced litter decomposition by soil fauna, whereas Ca^{2+} concentration and pH had negative effects. Soils with higher CEC typically have a higher clay content, more SOM (Helling et al., 1964; van Erp et al., 2001), greater moisture and nutrient retention (Khorshidi et al., 2016; Kim and Park, 2024), and support more microbial biomass (Ge et al., 2013a; Gonzalez-Quñones et al., 2011) than those with lower CEC. These conditions are beneficial for soil fauna, particularly hemi-edaphic and endogean groups sensitive to soil structure, microclimate, and the availability of microbial substrates or microbially conditioned organic residues (Briones et al., 2018; Geisen et al., 2019). Here, CEC may have functioned as a composite soil quality indicator of habitat and resource availability for soil-dwelling fauna.

Higher pH typically enhances microbial decomposition (Malik et al., 2018; Zhang et al., 2020) and changes microbial community structure (Zhalnina et al., 2015; Zhang et al., 2020), which may alter faunal-microbial interactions and weaken indirect faunal effects. Moreover, in this study, soil pH varied among soil types and was reduced in tree rows compared to arable production zones, potentially acting as proxy for the impacts of local geology, vegetation cover

(Mamabolo et al., 2024a), and soil disturbance (Domínguez et al., 2010) on faunal-mediated decomposition. The negative effect of soil Ca^{2+} contrasts with studies showing that litter decomposition, particularly by soil microorganisms such as fungi, increases with the Ca^{2+} concentration of substrates (Zhou et al., 2020) and soils (Lovett et al., 2016; Shabtai et al., 2023). Here, Ca^{2+} may have indirectly reduced faunal-mediated litter decomposition by increasing soil alkalinity (Enesi et al., 2023), although relationships between Ca^{2+} and pH were weak. Alternatively, higher Ca^{2+} may have enhanced the microbial conversion of litter into mineral-associated organic matter (Rowley et al., 2025; Shabtai et al., 2023), thereby limiting faunal contributions to decomposition of microbially processed residues.

As litter decomposition also alters soil CEC, pH, and Ca^{2+} concentrations, it is necessary to consider the reversible or possibly even cyclical nature of the relationships identified between litter decomposition and the aforementioned physicochemical properties. For example, the significant relationship between these soil physicochemical properties and faunal-mediated litter decomposition, specifically, could be the result of soil fauna's often low organic matter assimilation efficiency and release of litter-derived organic acids and nutrients to soils (Frouz, 2018).

4.5.4 Opportunities and limitations

For litter decomposition experiments, an incubation period of 16 weeks (109–115 days) is relatively short (Xie, 2020) and was therefore expected to capture early- to mid-stage decomposition dynamics rather than the breakdown of recalcitrant litter fractions. As soil-dwelling fauna typically consume and process litter which has already been conditioned by microorganisms (Frouz, 2018; Hauer et al., 2025), it was also possible that a 16-week experiment would not capture their contribution to litter decomposition if occurring later in the decomposition process. Nevertheless, after 16 weeks, nearly one quarter (24.4 %) of litter bags accessible to both soil microorganisms and fauna had lost more than 70 % of their initial mass. These values are comparable to those reported from longer-term litter decomposition experiments in alley-cropping systems (Moran-Rodas et al., 2025; Wachendorf et al., 2020), capturing a substantial portion of the overall decomposition process. In some samples, faunal-mediated litter decomposition accounted for up to 35.9 %, demonstrating that their contribution could indeed be measured within the 16-week period. Furthermore, although short relative to many litter decomposition experiments, the incubation period in this study is perhaps more relevant to commercial arable systems, where litter decomposition is frequently interrupted by routine agricultural operations.

The single sampling event in this study inevitably limited insights into the temporal dynamics of litter decomposition in alley-cropping systems. Multiple sampling points would have enabled a more detailed examination of when microorganism versus faunal contributions are most important and at what stage soil-dwelling fauna begin to influence decomposition, a pattern likely to differ markedly from that of the more extensively studied epigeal fauna. Even so, the results presented here provide evidence that, by the mid to late stages: (i) alley-cropping can enhance litter decomposition, particularly through its effects on soil microorganisms, and (ii) hemi-edaphic and endogean soil fauna exert a strong but variable influence on decomposition in both alley-cropping and sole-cropping systems.

4.6 Conclusions

Despite substantial interest in the carbon dynamics of temperate alley-cropping systems, few studies have quantified how tree rows influence litter decomposition. As litter decomposition is central to C and N cycling, this limits our understanding of alley-cropping's potential contributions to soil organic matter enhancements, climate change adaptation, and sustainable nutrient management. In this study, litter decomposition was 4.1 % higher in alley-cropping than in sole-cropping systems, with significant increases in tree rows and at 1.5 m into crop alleys. Litter decomposition in tree rows was also significantly greater than at 11.5 m into crop alleys.

Soil-dwelling meso- and macro-fauna increased litter decomposition by 4.8 %, substantiating their role in carbon and nutrient cycling in temperate agroecosystems. However, their contribution to litter decomposition was varied and relatively low compared to previous reports, potentially highlighting an overestimation bias introduced by the mesh-size effect in many litter bag studies. Soil faunal contributions to litter decomposition were unaffected by alley-cropping but increased in soils with higher CEC and declined with increasing pH and Ca^{2+} concentration.

These findings indicate that alley-cropping can enhance litter decomposition by microorganisms in temperate arable systems, particularly in and adjacent to tree rows. However, the mechanistic underpinnings of these increases remain unclear. Regardless, increases in litter decomposition may result in greater soil carbon sequestration or improved fertility where they are accompanied by sufficient organic inputs and conditions which facilitate soil organic matter retention.

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4.8 Appendix A | Additional methodological details

Contents

4.8.1. Farm and alley-cropping system characteristics

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Table 4.A.4

4.8.1 Farm and alley-cropping system characteristics

Table 4.A.1: Characteristics of alley-cropping ('AC') and sole-cropping ('SC') systems at five farms in England, United Kingdom. This table has been adapted from Evans et al. (2025b); crop rotations in bold have been changed to reflect the crops grown at the time of the litter bag experiment.

	C1	C2	N1	S1	S2
County	Cambridgeshire	Cambridgeshire	Nottinghamshire	Suffolk	Suffolk
Crop rotation ¹ (2021–2024)	ww-ao-ly- ly	ao-ao-ao- ao	lg-ww-sw- sc	AC: sc-wb-ly- ly SC: ly-ly-sw- wb	AC: sw-lg-ly- ly SC: lg-ly-ly- ly
Soil type ²	9	27	8	18	18
Soil texture ³	Silty clay	Sandy clay loam	Sandy clay	Clay/sandy clay	Clay/sandy clay
Year AC established	2015	2008	2015	2014	2000
Tree row orientation ⁴	N-S	N-S	N-S	N-S	N-S
Tree diversity ⁵	25 species	1 species	5 species	6 species	3 species
Tree density (ha ⁻¹)	58	85	75	138	64
Tree row width (m)	4	3	4	6 (double row)	5
Intra-row (m)	4	3	3	3	6
Alley width (m)	24	24	24	24	15

¹ Four most recent crops in the rotation provided. Crops: 'ao' = autumn oats, 'lg' = legumes, 'ly' = fertility-building ley, 'sc' = secondary cereal (e.g., spelt or rye grass), 'sw' = spring wheat, 'ww' = winter wheat, 'wb' = wheat + beans. Bold letters indicate the crop grown at the time of the litter bag experiment.

² Soil type according to the Soilscales Viewer online soil reporting tool hosted by Cranfield University (Cranfield Soil and Agrifood Institute, 2025): '8' = "slightly acid loamy and clayey soils with impeded drainage", '9' = "lime-rich loamy and clayey soils with impeded drainage", '18' = "slowly permeable seasonally wet slightly acid but base-rich loamy and clayey soils", and '27' = "fen peat soils".

³ Soil texture determined by feel (Thien, 1979).

⁴ Orientations: 'N' = North, 'S' = South.

⁵ Tree species information can be found in Table 3.A.1 in Evans et al. (2025b).

4.8.2 Analysis of litter contamination

Contamination of litter samples with (i) soil and (ii) soil organic matter (SOM) after incubation was estimated using the following equations:

$$(i) \quad Con_{soil} = Mass_{total} - Mass_{AF}$$

$$(ii) \quad Con_{SOM} = (Con_{soil} \times SOM\%) / Mass_{AF} \times 100$$

Where Con_{soil} = contamination with soil (g), $Mass_{total}$ = total weight (g) of litter (organic and inorganic components combined), $Mass_{AF}$ = ash-free weight (g) of litter (organic component only), Con_{SOM} = contamination with soil organic matter, $SOM\%$ = the contribution (%) of organic matter to soil weight at a given sample point.

Differences in estimated litter contamination with SOM between (i) alley-cropping and sole-cropping, (ii) alley-cropping transect positions, and (iii) bags with and without holes were determined using linear mixed models and Tukey post-hoc pairwise comparisons (Model H, Table 4.A.2). See Section 4.3.7 for details of R functions and packages.

Litter contamination with SOM was significantly influenced by agricultural system ($\chi^2_{(1)} = 13.75$, $p < 0.001$) and transect position ($\chi^2_{(2)} = 13.09$, $p = 0.001$), but not their interaction ($\chi^2_{(2)} = 0.56$, $p = 0.76$) (Model H; $R^2_c = 0.78$, $R^2_m = 0.13$). Contamination increased by an average of 0.54 % (± 0.03) in sole-cropping compared to AC0 ($p < 0.01$). Compared to AC3, contamination increased by 0.26 % (± 0.03) and 0.27 % (± 0.03) at SC3 ($p = 0.024$) and SC13 ($p = 0.021$), respectively. A marginally significant increase in contamination of 0.12 % (± 0.02) at AC13 compared to AC0 was observed ($p = 0.051$). Based on the small size of differences in estimated litter SOM contamination between agricultural systems, transect positions, and bag types, the impact of litter contamination is expected to be negligible.

Table 4.A.2: Average ($\pm$ standard deviation) contamination of litter samples with soil and soil organic matter (SOM) in paired alley-cropping ('AC') and sole-cropping ('SC') systems and at three distances (m) along linear experimental transects ('0m', '3m', and '13m').

		Soil contamination (g)	SOM contamination (g)	SOM contamination (%) ¹
AC	0m	0.79 $\pm$ 0.61	0.056 $\pm$ 0.028	5.17 $\pm$ 2.72
	3m	1.32 $\pm$ 1.67	0.083 $\pm$ 0.052	6.37 $\pm$ 3.80
	13m	1.30 $\pm$ 1.06	0.089 $\pm$ 0.060	6.62 $\pm$ 4.77
SC	0m	2.05 $\pm$ 2.04	0.12 $\pm$ 0.095	8.19 $\pm$ 5.47
	3m	1.93 $\pm$ 1.97	0.12 $\pm$ 0.11	9.60 $\pm$ 6.28
	13m	2.23 $\pm$ 1.76	0.15 $\pm$ 0.11	9.48 $\pm$ 6.29

¹ SOM contamination (%) refers to litter contamination with SOM as a proportion of the ash-free dry weight at the end of the incubation period.

4.8.3 Quality control data for soil nutrient concentrations

Table 4.A.3: Quality control information for soil carbon and nutrient concentrations. Values provided represent the mean (and range) across analytical runs, except for precision, which provides the median (and range). Table taken from Evans et al. (2025b).

Element ¹	Accuracy ² (%)	DL ³ (mg kg ⁻¹)	Precision ⁴ (%)
Al (mg kg ⁻¹)	114.0 (110.9-116.7)	7.4 (6.1-8.3)	25.2 (20.5-95.9)
Ca (mg kg ⁻¹)	106.3 (104.8-107.5)	154.9 (9.4-443.1)	0.84 (0.79-1.5)
Fe (mg kg ⁻¹)	43.8 (36.9-55.2)	4.5 (3.3-4.1)	32.9 (12.2-41.5)
K (mg kg ⁻¹)	122.1 (117.8-126.8)	79.9 (13.7-153.4)	7.5 (6.2-12.5)
Mg (mg kg ⁻¹)	109.6 (109.3-109.9)	4.2 (0.24-11.5)	0.7 (0.5-1.4)
Mn (mg kg ⁻¹)	111.0 (109.7-112.0)	1.1 (0.68-1.3)	2.1 (1.2-7.6)
Na (mg kg ⁻¹)	116.3 (113.5-118.2)	56.6 (0-126.8)	7.1 (6.2-13.4)
TC (g kg ⁻¹)	104.6 (100.9-110.6)	17.4 (17.4-21.2)	2.85 (0.4-6.0)
TN (g kg ⁻¹)	98.4 (93.2-105.1)	1.5 (1.0-1.7)	4.7 (0.0-8.7)

¹ Element concentrations were determined via ICP-OES, except for TC and TN which were calculated via elemental analysis.

² For ICP-OES, instrumental accuracy was determined through analysis of Merck ICP multi-element standard solution IV at a concentration of 0.25 mg L⁻¹. Accuracy for TC and TN was determined via analysis of 20 mg of a soil reference standard material (0.13 % N, 1.55 % C).

³ Detection limits were determined by ten repeat analyses of a calibration blank (or nine for TC and TN) (Walsh, 1997). Concentrations are provided in mg kg⁻¹ excluding TC and TN which are in g kg⁻¹.

⁴ Precision was determined through duplicate analysis of 10 % of samples on each analytical run (Gill and Ramsey, 1997). Values presented are the median precision (and range).

4.8.4 Model details

Table 4.A.4: Model structures used to investigate litter decomposition dynamics in alley-cropping and sole-cropping systems. All models had a Gaussian error structure. Fixed effects in bold were retained in reduced models used to assess the influence of alley-cropping on litter decomposition.

Name	Type ¹	Response variable	Random effects ²	Fixed effects ^{3,4}
A	LMM	Ash-free mass loss (%)	Transect	Agricultural system * Transect position + Holes + Soil type + Crop_{div} + Ca + CEC
B	LM	Microorganism-mediated ash-free mass loss (%)	NA	Agricultural system * Transect position + Soil type + Crop_{div} + CEC + CN + Mn + TN
C	LM	Faunal-mediated ash-free mass loss (%)	NA	Agricultural system * Transect position + Soil type + Ca + CEC + Mg + pH + Temp_{avg} + TN
D	LM	Faunal contribution to ash-free mass loss (%)	NA	Agricultural system * Transect position + Soil type + Ca + CEC + Mg + pH + TN
E	LM	Ash-free mass loss (%)	NA	Farm * Agricultural system * Location + Holes
F	LMM	SOM contamination	Farm/Transect	Agricultural system * Transect position + Holes

¹ Model types: ‘LM’ = linear model; ‘LMM’ = linear mixed effects model.

² Random effects: ‘transect’ = a 30-level factor indicating the experimental transect; ‘farm’ = a 5-level factor indicating the experimental farm; ‘NA’ = no random effect included in model.

³ Fixed effects: ‘agricultural system’ = a two-level factor indicating the farming system (alley-cropping or sole-cropping); ‘transect position’ = a three-level factor (0, 3, or 13 m) indicating distance (m) along the experimental transect; ‘holes’ = a two-level factor indicating whether litter bags had holes permitting access to soil fauna or not; ‘soil type’ = Soilscape (Cranfield Soil and Agrifood Institute, 2025); ‘crop_{div}’ = number of crops grown between 2021–2024; ‘Ca’ = exchangeable calcium concentration (g kg⁻¹); ‘CEC’ = cation exchange capacity (meq 100 g⁻¹); ‘CN’ = soil carbon-nitrogen ratio; ‘Mg’ = exchangeable magnesium concentration (g kg⁻¹); ‘Mn’ = exchangeable manganese concentration (mg kg⁻¹); ‘temp_{avg}’ = average soil temperature measured across the sampling events (°C); ‘TN’ = total nitrogen (mg kg⁻¹).

⁴ Models A–C were also used to compare alley-cropping transect positions with the sole-cropping average. ‘Agricultural system * transect position’ was replaced by ‘positions_{Scavg}’, a four-level factor including three transect positions in alley-cropping and the average across transect positions for each transect in sole-cropping.

4.9 Appendix B | Additional Results

Contents

4.9.1. Soil physicochemical properties in alley-cropping and sole-cropping systems

Table 4.B.1

4.9.2. Farm-level comparisons of litter decomposition

Figure 4.B.1

4.9.3. Soil physicochemical and system-level drivers of litter decomposition

Figure 4.B.2

4.9.1 Alley-cropping effect on soil physicochemical properties

Table 4.B.1: Mean ($\pm$ standard deviation) of soil physicochemical properties measured at 90 sampling points (0–15 cm soil depth) in paired alley-cropping and sole-cropping systems at five farms in England, United Kingdom. The influence of agricultural system ('S'; alley-cropping or sole-cropping), transect position ('TP'; 0m, 3m, or 13m), and their interaction ('S*TP') on soil physicochemical properties as determined by linear mixed models are indicated by the following: ns = not significant, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. No shared superscript letter indicates a statistically significant pairwise difference, as determined by *post hoc* comparisons of estimated marginal means using a Tukey correction for multiple comparisons. Table adapted from Evans et al. (2025b).

Soil properties ¹	Alley-cropping			Sole-cropping			Fixed effects		
	Row	Edge	Centre	Row	Edge	Centre	S	TP	S*TP
Temp _{avg} (°C)	7.39 ^a ± 0.42	7.06 ^b ± 0.44	7.02 ^b ± 0.38	7.02 ^b ± 0.54	7.05 ^b ± 0.51	6.99 ^b ± 0.54	ns	***	***
Temp _{low} (°C)	2.69 ^a ± 0.64	1.90 ^b ± 0.75	1.93 ^b ± 0.73	2.05 ^b ± 0.95	2.03 ^b ± 0.93	1.99 ^b ± 0.77	ns	***	***
Temp _{high} (°C)	9.91 ^a ± 0.37	9.59 ^b ± 0.60	9.55 ^b ± 0.56	9.55 ^b ± 0.72	9.61 ^b ± 0.65	9.45 ^b ± 0.73	**	**	*
Temp _{range} (°C)	7.22 ^a ± 0.78	7.69 ^b ± 0.90	7.63 ^{ab} ± 0.78	7.50 ^{ab} ± 1.17	7.58 ^{ab} ± 1.04	7.46 ^{ab} ± 0.97	ns	*	*
MC _{avg} (g 100g ⁻¹)	42.03 ^a ± 14.11	37.28 ^b ± 14.78	36.06 ^b ± 15.86	38.40 ^{ab} ± 12.52	37.65 ^{ab} ± 12.41	38.26 ^{ab} ± 12.15	ns	**	***
MC _{low} (g 100g ⁻¹)	36.81 ^{ns} ± 12.93	32.26 ^{ns} ± 12.75	28.41 ^{ns} ± 22.39	33.83 ^{ns} ± 11.76	33.06 ^{ns} ± 12.26	33.40 ^{ns} ± 10.80	ns	ns	ns
MC _{high} (g 100g ⁻¹)	47.31 ^a ± 15.47	42.90 ^{ab} ± 16.50	42.15 ^{ab} ± 14.54	41.97 ^{ab} ± 13.66	41.91 ^{ab} ± 13.57	41.73 ^b ± 13.12	*	ns	ns
MC _{range} (g)	10.50 ^{ns} ± 4.78	10.64 ^{ns} ± 8.02	13.75 ^{ns} ± 15.36	8.15 ^{ns} ± 6.36	8.85 ^{ns} ± 5.85	8.33 ^{ns} ± 5.15	ns	ns	ns
BD (g cm ⁻³)	0.88 ^a ± 0.21	1.04 ^b ± 0.25	1.05 ^b ± 0.24	0.99 ^{ab} ± 0.21	1.01 ^{ab} ± 0.22	1.01 ^b ± 0.23	ns	**	*
SOM (g 100g ⁻¹)	11.01 ^a ± 10.57	9.34 ^b ± 9.70	9.38 ^b ± 9.65	9.61 ^b ± 9.92	9.63 ^b ± 9.91	9.74 ^b ± 10.18	ns	***	***
TC (g kg ⁻¹)	59.38 ^a ± 53.81	51.17 ^b ± 50.50	51.49 ^b ± 49.66	57.37 ^{ab} ± 55.26	56.69 ^{ab} ± 54.71	55.95 ^{ab} ± 53.76	ns	***	**
TN (g kg ⁻¹)	4.38 ^a ± 3.62	3.76 ^b ± 3.46	3.78 ^b ± 3.31	4.87 ^{ab} ± 5.51	4.79 ^{ab} ± 4.94	4.76 ^{ab} ± 5.00	ns	***	***
CN	13.19 ^{ns} ± 1.49	13.16 ^{ns} ± 1.69	13.03 ^{ns} ± 1.45	12.27 ^{ns} ± 2.49	12.22 ^{ns} ± 2.43	12.27 ^{ns} ± 2.55	ns	ns	ns
pH	7.00 ^a ± 0.76	7.15 ^{ab} ± 0.71	7.23 ^b ± 0.61	7.02 ^{ab} ± 0.59	6.99 ^{ab} ± 0.57	6.93 ^{ab} ± 0.66	ns	ns	*
CEC (meq 100g ⁻¹)	13.11 ^{ns} ± 7.19	13.51 ^{ns} ± 8.07	13.86 ^{ns} ± 8.72	13.32 ^{ns} ± 7.19	23.49 ^{ns} ± 26.62	23.62 ^{ns} ± 38.12	ns	*	ns
Ca (mg kg ⁻¹)	6559.4 ^{ns} ± 4003.6	6455.6 ^{ns} ± 4394.6	6681.3 ^{ns} ± 4776.7	6325.2 ^{ns} ± 4237.5	9209.2 ^{ns} ± 11461	6300.1 ^{ns} ± 3909.3	ns	ns	ns
K (mg kg ⁻¹)	650.4 ^a ± 953.0	344.7 ^b ± 184.8	354.1 ^b ± 193.6	245.4 ^b ± 60.60	258.2 ^b ± 85.39	332.4 ^b ± 304.6	**	ns	*
Mg (mg kg ⁻¹)	447.86 ^{ns} ± 321.56	554.02 ^{ns} ± 1007.6	680.85 ^{ns} ± 806.16	745.04 ^{ns} ± 1004.3	950.51 ^{ns} ± 1299.1	720.64 ^{ns} ± 923.21	ns	ns	ns
Mn (mg kg ⁻¹)	13.50 ^{ns} ± 18.94	10.18 ^{ns} ± 11.79	14.20 ^{ns} ± 19.79	7.67 ^{ns} ± 6.06	8.34 ^{ns} ± 7.13	10.07 ^{ns} ± 8.56	ns	ns	ns
Na (mg kg ⁻¹)	59.61 ^{ns} ± 63.02	64.61 ^{ns} ± 66.76	62.19 ^{ns} ± 64.10	78.25 ^{ns} ± 57.98	77.48 ^{ns} ± 62.11	76.23 ^{ns} ± 57.56	*	ns	ns

¹ Abbreviations: 'BD' = bulk density (g cm⁻³), 'CEC' = cation exchange capacity (meq 100 g⁻¹), 'MC_{avg}' = average moisture content across all sampling periods (g 100 g⁻¹), 'MC_{low/high}' = the lowest/highest soil moisture content measured across the three sampling events, 'SOM' = organic matter content (g 100 g⁻¹), 'Temp_{avg}' = average soil temperature across all sampling periods (°C), 'Temp_{low/high}' = the lowest/highest soil temperature measured across the three sampling events, 'TC' = total carbon (mg kg⁻¹), 'TN' = total nitrogen (mg kg⁻¹), and 'CN' = soil carbon-to-nitrogen ratio; 'MC_{range}' and 'Temp_{range}' provide the difference in moisture content and soil temperature between the lowest and highest recorded values at any given sample point, respectively.

4.9.2 Farm-level comparisons of litter decomposition

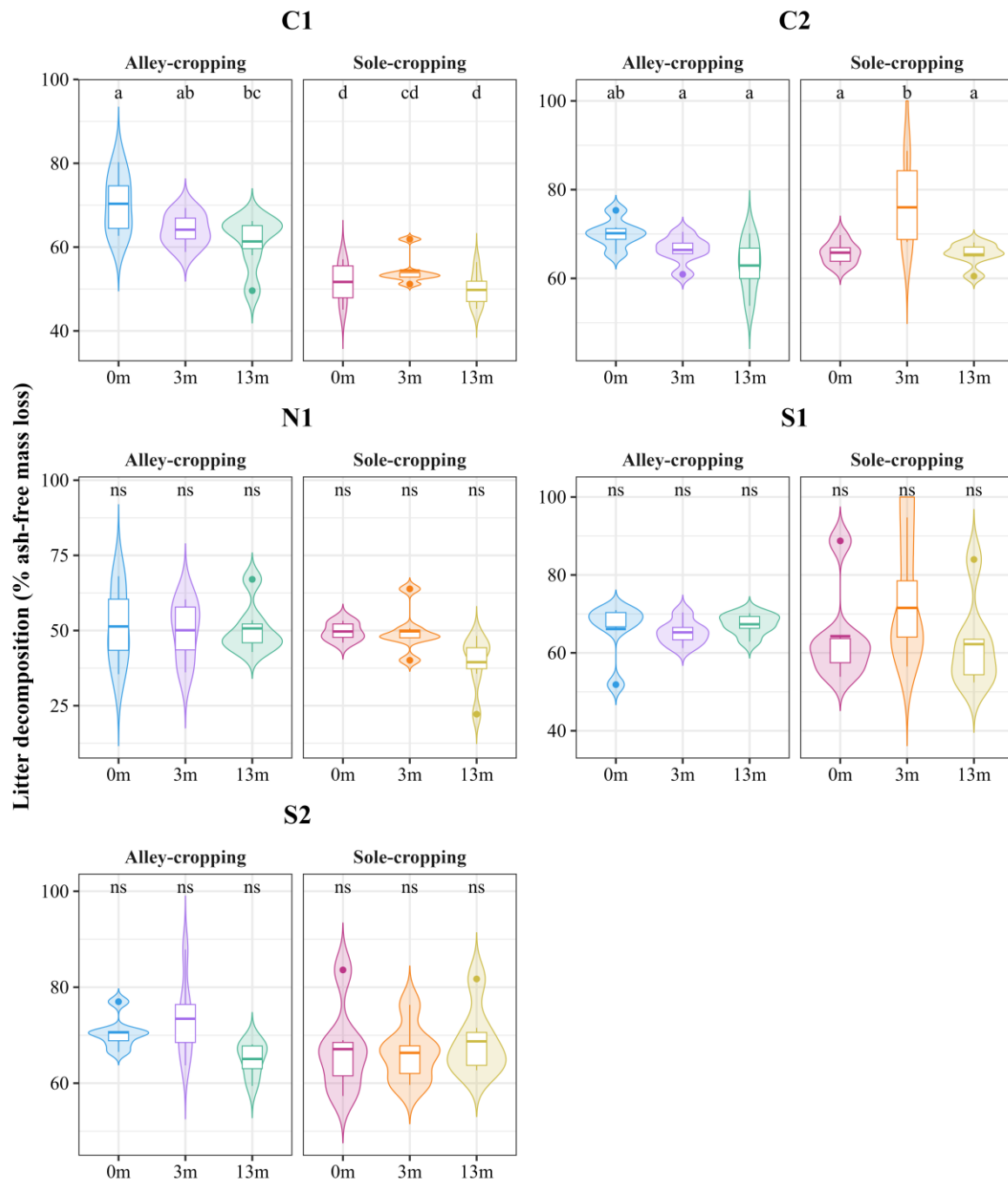


Figure 4.B.1. Litter decomposition (% ash-free mass loss) in litter bags (n = 180) buried at 10 cm depth for 16 weeks on paired alley-cropping and sole-cropping fields at five arable farms in England, United Kingdom. Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (IQR $\times$ 1.5) of ash-free mass loss (%) for each transect position: 0 m (1.5 m into the tree row), 3 m (1.5 m from the understory vegetation strip), and 13 m (11.5 m from the understory vegetation strip) for sole-cropping and alley-cropping, respectively. Violin plots display the distribution of the data points for each transect position. Individual points represent outliers. Letters above the violin plots highlight significant pairwise differences in ash-free mass loss (%) between transect positions nested within agricultural systems, as determined by linear mixed models with varying intercepts. No shared letter indicates a significant difference at $\alpha = 0.05$, ns = not significant.

4.9.3 Soil physicochemical and system-level drivers of litter decomposition

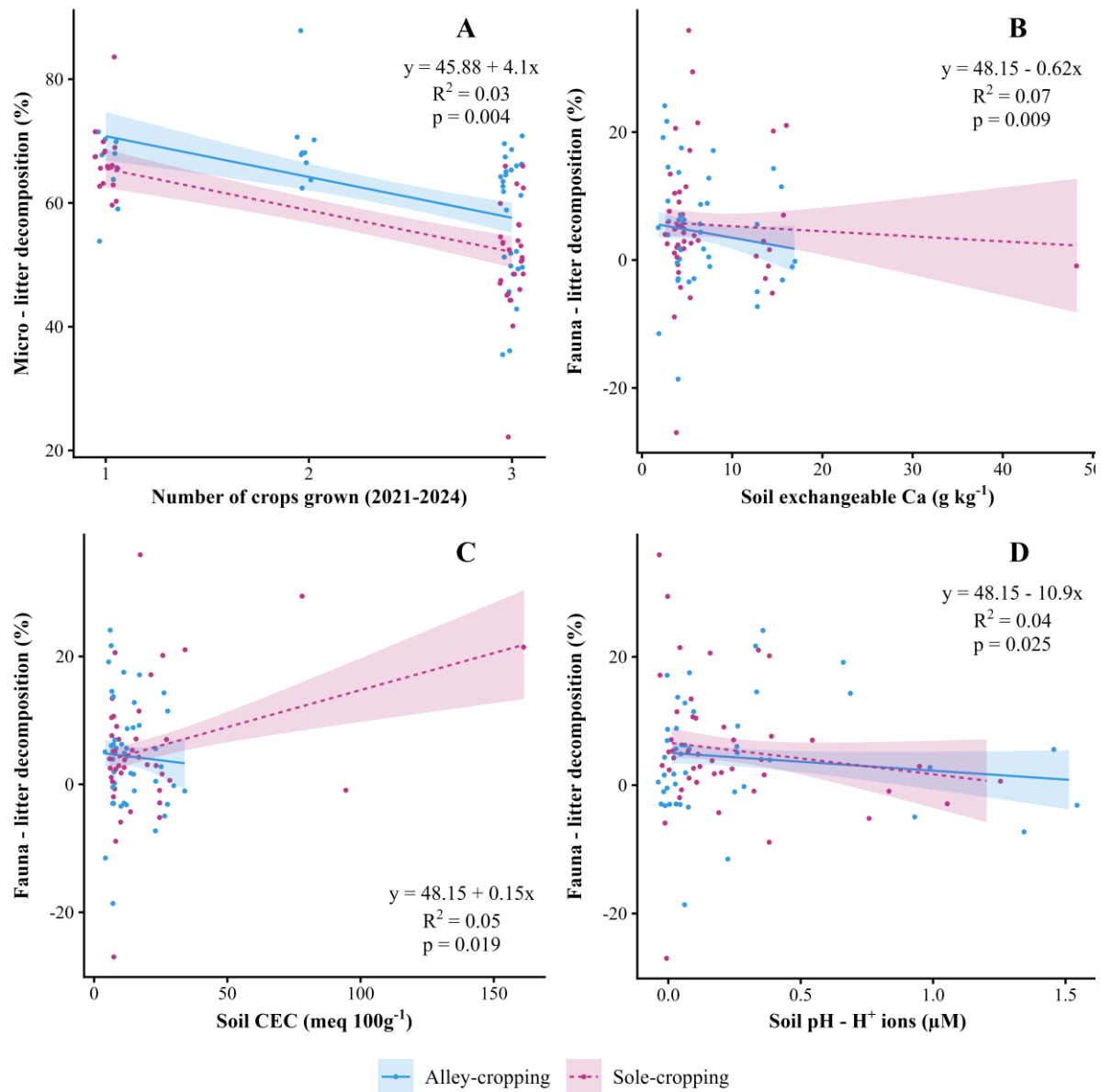


Figure 4.B.2. Litter decomposition (%) by soil microorganisms (‘micro’) and fauna (‘fauna’) as a function of (A) the number of major crops grown between 2021–2024, (B) soil exchangeable calcium concentration (g kg^{-1}), (C) soil cation exchange capacity ($\text{meq } 100\text{g}^{-1}$), and (D) soil pH expressed as H^+ ion concentration (μM) in alley-cropping and sole-cropping systems. Points represent observed ash-free mass loss values. Regression lines were estimated from full models B and C and generated in-plot using the *predict* function of the ‘car’ package (Fox and Weisberg, 2018). Solid blue line = alley-cropping, dashed red line = sole-cropping. Shaded areas provide the 95 % confidence intervals of the mean. Equations provide the intercept and estimate for a given fixed effects across both agricultural systems. R^2 and p-values were calculated as the change in R^2 and the significance of the change in model fit between linear models with and without a given fixed effect, respectively.

4.10 Supplementary material | Relationships between litter decomposition and faunal biodiversity

4.10.1 Background

Litter decomposition is responsive to soil faunal biodiversity (de Graaff et al., 2015; Handa et al., 2014; Mamabolo et al., 2024b), presumably due to complementary activity of diverse organisms in the decomposition of substrates with differing levels of complexity and solubility (Paul et al., 2016). However, the effect of soil fauna on litter decomposition has been previously shown to be better predicted by within-bag rather than ambient soil faunal communities (Peng et al., 2023). This section therefore aimed to determine whether ambient soil faunal biodiversity was a significant predictor of litter decomposition in alley-cropping and sole-cropping systems.

4.10.2 Materials and methods

Spearman correlations were calculated between faunal biodiversity metrics calculated in Section 3.3 (abundance, taxonomic richness, and SBQ) and litter decomposition by soil microorganisms, fauna, and microorganisms and fauna combined using the *cor.test* function of the ‘stats’ package in R (R Core Team, 2025). To determine the significance of faunal biodiversity metrics as predictors of litter decomposition, abundance, taxonomic richness, and SBQ were added independently to models A–C (Table 4.A.4) as fixed effects. Model fit with and without a given biodiversity metric was compared using the *anova* function of the ‘stats’ package.

4.10.3 Results and interpretation

Soil faunal abundance, taxonomic richness, and SBQ correlated significantly with litter decomposition by soil microorganisms, fauna, and microorganisms and fauna combined (Figure 4.S.1). However, when incorporated into models predicting litter decomposition, soil biodiversity metrics were not identified as significant predictors (Table 4.S.1). This suggests that in the current research, soil biodiversity and litter decomposition are responding to the same major drivers (e.g., soil type, agronomic management) but soil biodiversity does not significantly influence litter decomposition.

Table 4.S.1: The significance of soil faunal abundance, taxonomic (order) richness ('richness'), and soil biological quality ('SBQ') as predictors of litter decomposition by soil microorganisms ('Micro'), fauna, or microorganisms and fauna combined ('Micro + Fauna'). Changes in litter decomposition (%) (est) and standard errors (se) were estimated using linear or linear mixed-effects models. χ^2/F and p-values for biodiversity metrics were determined via comparing models with and without the fixed effect using ANOVA.

Fixed ¹ effect	Micro + Fauna				Micro				Fauna			
	Est ²	se	χ^2	p	est	se	F	p	est	se	F	p
Abundance	0.01	0.00	0.09	0.763	0.01	0.00	2.79	0.099	-0.01	0.01	3.30	0.073
Richness	0.38	0.27	1.83	0.176	0.21	0.37	0.34	0.563	0.48	0.48	0.98	0.326
SBQ	0.03	0.02	1.11	0.293	0.01	0.03	0.15	0.705	0.04	0.04	1.72	0.194

¹ Faunal biodiversity metrics were calculated in Section 3.3 using the same sampling points as the litter bag assay described in Section 4.

² Estimates indicate the change in litter decomposition (%) with a one unit increase in faunal biodiversity metrics.

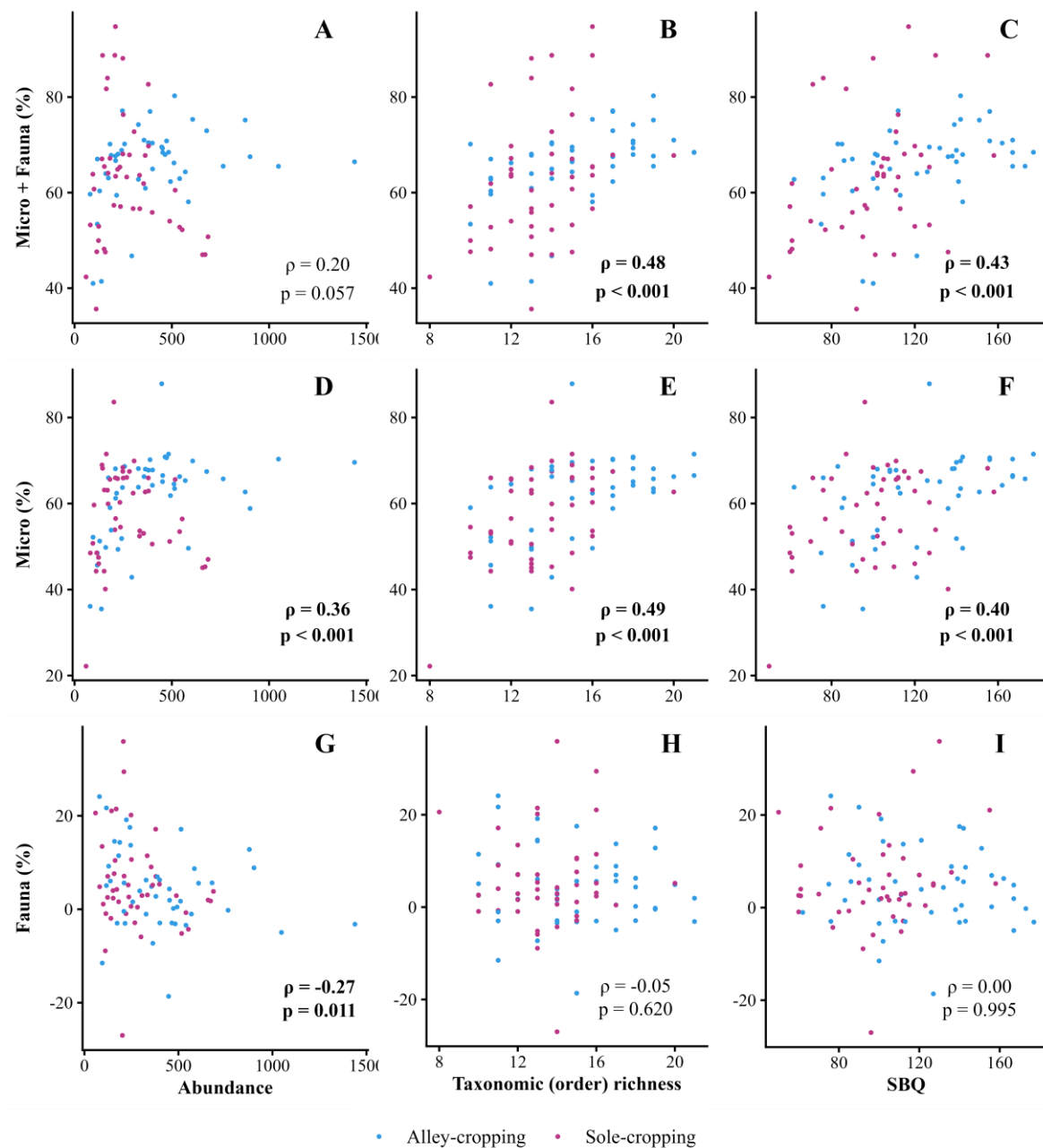


Figure 4.S.1. Spearman correlations between soil meso- and macro-faunal biodiversity metrics and litter decomposition. Litter decomposition by soil microorganisms and fauna ('Micro + Fauna'; A–C), microorganisms ('Micro'; D–F), and fauna ('Fauna'; G–I) is plotted against soil faunal abundance (A, D, G), taxonomic (order) richness (B, E, H), and soil biological quality according to the QBS-ar Index ('SBQ') (C, F, I). Spearman's rank correlation test ρ and p-values are provided, with significant correlations in bold. Data point colours: blue = alley-cropping, red = sole-cropping.

5 Tree rows reduce mineral-associated organic matter formation from applied litter in temperate alley-cropping systems

5.1 Abstract

Background and aims

Temperate alley-cropping can increase soil organic matter, but the effects of tree rows on the formation and persistence of SOM fractions with contrasting residence remains uncertain. This study assessed whether alley-cropping enhances the persistence of particulate organic matter (POM) and the formation of mineral-associated organic matter (MAOM) relative to sole-cropping.

Methods

Dual-labelled *Lolium perenne* was incubated for 28 days in soils collected in June 2024 from paired alley-cropping and sole-cropping systems at five commercial farms in England, United Kingdom. Samples were taken along transects at three distances (0, 3, and 13 m), representing tree rows, 1.5 m into crop alleys, and the centre of crop alleys, respectively. Recovery of litter-derived ^{13}C and ^{15}N in POM and MAOM was compared between agricultural systems and transect positions.

Results

Alley cropping had no effect on POM persistence and MAOM formation was similar between agricultural systems. However, recovery of litter-derived ^{13}C and ^{15}N was lower in tree row soils than in soils from crop alleys and sole-cropping systems. Recovery of litter-derived ^{13}C and ^{15}N in MAOM increased under organic management and with higher soil Mn^{2+} concentration, while higher soil N concentrations increased litter-derived ^{13}C losses.

Conclusions

Alley-cropping had no detectable influence on POM persistence, but tree rows reduced MAOM formation relative to arable crop areas. In established systems, tree rows may have limited capacity to form new MAOM, instead experiencing greater C and N losses from litter inputs. Further field-based research across more farms is required to confirm these patterns.

5.2 Introduction

European cropland soils are a dynamic reservoir of C and N, storing ~21 % of Europe's soil C (Andrés et al., 2022) and substantial N stocks (Almaraz et al., 2025). They therefore play a central role in climate change adaptation strategies (Bellassen et al., 2022; Panagos et al., 2022) and efforts to curb nutrient pollution (Liu et al., 2024a; Luna Juncal et al., 2023). However, widespread soil degradation is driving major losses of soil organic matter (SOM) (Panagos et al., 2024), contributing to C declines of 0.04–0.4 t ha⁻¹ yr⁻¹ (Bellassen et al., 2022; De Rosa et al., 2024) and exacerbating N surpluses (Batoool et al., 2022; Eastman et al., 2023). Intensively managed soils are particularly vulnerable because they receive limited organic inputs and experience frequent disturbance which disrupts aggregates (Edlinger et al., 2023; Li et al., 2023), increases aeration and decomposition (Erickson, 1982), and reduces soil biodiversity involved in C and N cycling (de Graaff et al., 2019; de Vries et al., 2013; Tsiafouli et al., 2015). These processes lower SOM accumulation and diminish C and N storage (Fließbach et al., 2007; Grandy and Robertson, 2007). Transition to agricultural systems that protect and enhance SOM is therefore essential to maintain soil multifunctionality (van Rijssel et al., 2025), achieve C neutrality, and stay within critical environmental thresholds (Fontaine et al., 2024; Schulte-Uebbing et al., 2022).

Alley-cropping, an agroforestry practice where crops are grown between parallel tree rows, is a multifunctional land-use system (Quinkenstein et al., 2009; Wolz et al., 2018b) that can increase SOM (Ivezić et al., 2022) and improve soil nutrient retention (Pardon et al., 2017; Schmidt et al., 2021). Temperate alley-cropping soils sequester an estimated 0–2.6 t C ha⁻¹ year⁻¹ (Cardinael et al., 2018; Kim et al., 2016; Oelbermann and Voroney, 2007; Peichl et al., 2006) and mature tree rows can increase soil N stocks by 556 kg ha⁻¹ (0–23 cm depth) relative to sole-cropping (Pardon et al., 2017). However, the stability of these gains is uncertain, with several studies reporting greater microbial respiration (Lee and Jose, 2003; Mettauer et al., 2022), SOM mineralisation (Ghaley et al., 2014b; Lang et al., 2019), and gaseous emissions (Baah-Acheamfour et al., 2016; Medinski et al., 2015; Peichl et al., 2006; Wotherspoon et al., 2014) under alley-cropping.

A useful framework for assessing SOM persistence distinguishes between particulate organic matter (POM; 53–2000 µm) and mineral-associated organic matter (MAOM; < 53 µm) (Cotrufo et al., 2015). POM consists of partially decomposed material with short residence times (1–50 years), whereas MAOM forms when microbial products or dissolved organic matter bind to mineral surfaces, reducing vulnerability to disturbance and conferring longer

residence times (10–1000 years) (Cotrufo et al., 2019, 2022). Although the upper limit of MAOM accumulation remains uncertain (Georgiou et al., 2025), vast areas of Europe have low to moderate mineral C saturation (Georgiou et al., 2022), suggesting considerable potential to increase long-term C and N storage. Agricultural soils, which show the greatest MAOM undersaturation (Georgiou et al., 2022) and have previously been found to have no upper limit for MAOM accumulation in temperate regions (Begill et al., 2023), offer the largest opportunity. Increasing the concentration of soil C and N stored in MAOM at any one time could therefore achieve lasting soil C sequestration in croplands (Lavalley et al., 2020).

Alley-cropping could promote MAOM formation through both microbial and direct sorption pathways (Lavalley et al., 2020). Compared to sole-cropping, alley-cropping can increase microbial biodiversity, catabolic potential, and substrate-use efficiency (Beule et al., 2022b), as well as faunal biodiversity (Beule et al., 2025), thereby potentially generating more dissolved organic matter (DOM) and microbial necromass for mineral binding (Angst et al., 2024). Localised afforestation in tree rows may also enhance mineral weathering and the availability of sorption sites (Lafleur et al., 2013). Tree rows may further enhance SOM persistence by (i) alleviating the need for microbial N mining (Pardon et al., 2017), (ii) increasing microbial C-use efficiency (Zheng et al., 2024), and (iii) reducing soil disturbance, supporting the formation of stable micro- and macro-aggregates that protect both POM and MAOM (Baah-Acheamfour et al., 2014; Udawatta et al., 2008). Conversely, priming effects associated with litter inputs, tree roots, rhizosphere activity, and elevated N may stimulate decomposition of POM and destabilise MAOM (Jilling et al., 2021b; Pierson et al., 2021; Zheng et al., 2024). As such, alley-cropping has the potential to promote or inhibit MAOM formation and persistence.

Empirical evidence on MAOM responses to alley-cropping in temperate systems remains limited. In an 18-year-old Mediterranean system, C concentration in silt-sized (2–50 μm) MAOM increased in tree rows and crop alleys compared with sole-cropping at 0–10 cm depth, and clay-sized (< 2 μm) MAOM-C was higher in tree rows than in crop alleys (Cardinael et al., 2015). In contrast, several studies report no significant effects of alley-cropping on MAOM (Clivot et al., 2020; Fornara et al., 2018; Wiesmeier et al., 2018). Beyond these inconsistencies, the absence of studies quantifying SOM formation and decomposition processes hampers mechanistic understanding of SOM changes in alley-cropping systems (Ghaley et al., 2014a). Consequently, it remains unclear if and why alley-cropping enhances MAOM formation in temperate regions. Addressing this knowledge gap is crucial, as the stability of newly formed

SOM ultimately determines whether alley-cropping systems can support climate change adaptation and reduce agricultural N losses (Lehmann et al., 2020; Steinfeld et al., 2023).

In this study, a laboratory tracer experiment using dual-labelled *Lolium perenne* shoot material was conducted to investigate the influence of alley-cropping on soil POM and MAOM formation dynamics at five arable farms in England, United Kingdom. *L. perenne* was incubated for 28 days with soils from paired alley-cropping and sole-cropping systems collected at three distances (0 m, 3 m, and 13 m) along linear experimental transects, which in alley-cropping systems represented increasing distances from tree rows. It was hypothesised that there would be:

- 1) Lower recovery of litter-derived $^{13}\text{C}/^{15}\text{N}$ in alley-cropping than in sole-cropping systems, due to predicted increases in microbial respiration, SOM mineralisation, and soil emissions in response to alley-cropping.
- 2) A higher proportion of recovered $^{13}\text{C}/^{15}\text{N}$ in MAOM in alley-cropping compared to sole-cropping systems, due to the potential of alley-cropping tree rows to facilitate the microbial and direct sorption pathways of MAOM formation.
- 3) The highest increases in $^{13}\text{C}/^{15}\text{N}$ recovery in MAOM relative to sole-cropping in and close to the tree rows. This is because the influence of tree rows on soil faunal and microbial communities is often inversely proportional to distance from trees.

5.3 Materials and Methods

5.3.1 Field sites and experimental design

Soil organic matter dynamics were measured in soils taken from paired alley-cropping and sole-cropping fields at five commercial farms in England, United Kingdom. Field sites and a detailed experimental design have previously been fully described in Evans et al. (2025b). Briefly, on each field, three linear transects were established which comprised sampling points at three distances (0, 3, and 13 m). In alley-cropping systems, sampling points were positioned at an increasing distance from tree rows: 1.5 m into tree rows from the edge of the understory vegetation strip (UVS) (0 m, AC0), 1.5 m into crop alleys from the edge of the UVS (3 m, AC3), and the centre of crop alleys (13 m, AC13). The centre of crop alleys was 11.5 m from the edge of the UVS at all farms excluding S2, where it was 7.5 m into crop alleys. Transect distances (SC0, SC3, and SC13) and orientation (W-E) were replicated in sole-cropping systems. All transects were established one metre to the north of a tree, were positioned on the

eastern side of tree rows, and were established a minimum of 30 m from the field edge. Farm and alley-cropping system characteristics are outlined in Table 5.A.1.

5.3.2 *Isotope tracer experiment*

In June 2024, samples were taken from each sampling point ($n = 90$) as intact cores (10 cm diameter x 15 cm depth) using a core sampler, sealed in labelled plastic bags, and transported in coolers to the laboratory. In the laboratory, soil cores were gently mixed by hand to homogenise soil layers, sieved (moist) to 2 mm, and stored at 4 °C in sealed plastic bags for a maximum of 30 days. From these processed samples, 90 subsamples (one 30 g subsample per sample) were taken for incubation with dual-labelled ($^{13}\text{C} = 3.82$ atom%, $^{15}\text{N} = 4.14$ atom%) litter grown in a continuous labelling chamber (i.e., treatment samples). To calculate the natural abundance of $^{13}\text{C}/^{15}\text{N}$ in POM and MAOM in soils at each sampling point, a further 30 subsamples, taken from one transect on each sampled field, were incubated without dual-labelled litter (i.e., experimental blanks). This allowed for more accurate calculation of isotopic excess in SOM fractions post-incubation, as natural abundances of ^{13}C and ^{15}N are expected to differ between POM and MAOM (Poeplau et al., 2017).

Prior to incubation, all samples underwent a five-day pre-incubation. Soil moisture content (MCs) and water-filled pore space (WFPS) were calculated for each sample according to ISO 11465 (International Organization for Standardization, 1993) and Torbert and Wood (1992), respectively. Following this, the 30 g (oven-dried equivalent) subsample was measured into a 250 mL straight-sided HDPE container, adjusted to 50 % WFPS using sterile deionised water, and left to settle in the dark at 20 °C for five days to allow microbial activity to stabilise (Iovieno and Baath, 2008; Zhang et al., 2017). Sample pots were placed inside 1 L screw-top Kilner jars with 100 mL of sterile deionised water in the bottom to maintain humidity and limit changes in soil moisture content (Haddix et al., 2016). Pre-incubation of samples was staggered over three weeks, from 25th June–12th July 2024. Each day of the week (excluding weekends), pre-incubation of nine subsamples began: six treatment samples and three experimental standards. Treatment samples were taken from one set of paired transects (e.g., transect 1 in alley-cropping and sole-cropping systems) at a given farm. Selection of paired transects for pre-incubation were randomised. Due to logistical constraints, pre-incubation of experimental standards from the same farm were initiated over two consecutive days but lasted for the same duration. A detailed incubation plan can be found in Figure 5.S.1.

After pre-incubation, 0.82 g ($\pm 0.01_{SE}$, $n = 90$) of oven-dried dual-labelled *Lolium perenne* shoot material was mixed into the sample for 10 s using a sterile plastic stirrer. The mixture was then incubated in darkness at 20 °C for 28 days, as an incubation period of 28 days was associated with the highest amounts of mineral association in a laboratory investigation of dual-labelled *Andropogon gerardii* litter decomposition (Haddix et al., 2016). Every 7 days, the Kilner jars were aerated for seven hours to prevent the development of anaerobic conditions. During aeration, samples were weighed and sterile deionised water added as necessary to readjust to 50 % WFPS.

After 28 days, samples were weighed and a 10 g subsample taken to verify their moisture content. Following this, the remaining soil was disaggregated via particle size fractionation (PSF). PSF has been shown to outperform aggregate size fractionation when investigating the fate of POM (Moni et al., 2012). Although the additional use of chemical or density-based methods to isolate soil organic C fractions of varying turnover rates is considered most effective (Moni et al., 2012; Poeplau et al., 2018), when isolating only two fractions, PSF is a better option due to its efficiency and ability to be consistently applied to diverse soils (Cotrufo et al., 2019; Poeplau et al., 2018). Importantly, PSF has been shown to isolate fractions similar in size, biogeochemical properties, and turnover rates to particle size density fractionation (Cambardella and Elliott, 1992; Poeplau et al., 2018). Chemical dispersion (i.e., with sodium hexametaphosphate) was avoided due to the impact of sample rinsing on measured SOC contents (Just et al., 2021).

For PSF, samples were placed into 250 mL glass beakers with 150 mL sterile deionised water. A sonication probe was placed 1.5 cm below the surface of the mixture and soil aggregates were dispersed via ultrasonication at an energy input of 450 J mL⁻¹ using an Ultrasonic Disintegrator Soniprep 150 Plus (MSE (UK) Ltd) at an amplitude setting of 10 μ m for 40 mins. This energy input was selected to break down stable microaggregates and a greater proportion of macroaggregates, characteristic of soils with higher clay contents (Just et al., 2021).

Following disaggregation, samples were separated into POM ($> 53 \mu$ m), suspended organic matter (s-OM; $< 53 \mu$ m, $< 1 \text{ g cm}^{-3}$), and MAOM ($< 53 \mu$ m, $> 1 \text{ g cm}^{-3}$) via a process of wet sieving, according to a method adapted from Cambardella and Elliot (1993) and Zimmerman et al. (2007). Here, s-OM was assumed to represent POM decomposition products (fine POM, dissolved organic matter, and microbial biomass) and was primarily included for full tracer accounting. Briefly, samples were rinsed on to a Camlab 53 μ m aperture stainless steel sieve situated in a plastic container filled with sterile deionised. The waterline was positioned

approximately 2 cm higher than the sieve mesh. The sieve was lifted 5 cm out of the water and returned to its original position 30 times over 80 seconds. Occasionally, the sieve was shaken to unclog pores. After the process was complete, the sieve was rinsed with sterile deionised water and moved to a fresh container and the process was repeated a minimum of two times, or until the water remained clear.

The POM fraction (remaining on the sieve) was rinsed into a pre-weighed aluminium tray using sterile deionised water. The suspension obtained from the sieving process was moved into a 2 L jug, covered with aluminium foil, and allowed to sit for five days at 4 °C until the MAOM fraction had settled at the bottom. The supernatant was then carefully poured off into a beaker until only the MAOM fraction and a small volume of liquid remained. A 50 mL aliquot of the supernatant, containing s-OM, was immediately frozen until further processing. The MAOM fraction was then rinsed into a pre-weighed aluminium tray. Both the POM and MAOM fractions were covered in aluminium foil and placed under tungsten bulbs for up to two days to reduce the liquid in the trays before oven-drying (at 40 °C for POM and 105 °C for MAOM). To prepare s-OM fractions for analysis, deforested aliquots were centrifuged at 3,500 rpm for 15 minutes and resulting pellets transferred to 15 mL centrifuge tubes. Centrifugation was repeated on 15 mL centrifuge tubes and most of the excess supernatant, presumed to be predominantly water, was then removed using a plastic transfer pipette. The s-OM fractions were then freeze-dried for 24 hours in a Lablyo benchtop freeze drier. Oven- and freeze-dried soil fractions were ground to < 200 µm using a Retsch Mixer Mill MM 400.

The Stable Isotopes Facility at the UK Centre for Ecology and Hydrology in Lancaster, United Kingdom analysed POM and MAOM fractions for % C/N and $\delta^{13}\text{C}/^{15}\text{N}$ using elemental analysis-isotope ratio mass spectrometry (EA-IRMS). Analysis of s-OM fractions by EA-IRMS was undertaken by the James Hutton Institute, Aberdeen, United Kingdom.

5.3.3 Isotopic calculations

The proportion of litter-derived ^{13}C and ^{15}N recovered in SOM fractions was determined by calculating using Equations 1 and 2. Briefly, the amount (µg) of ^{13}C and ^{15}N applied to samples was calculated using the oven-dried weight, total C and N, and isotopic enrichment (atom% of ^{13}C and ^{15}N) of applied *L. perenne* litter. Litter-derived ^{13}C and ^{15}N (µg) recovered in POM and MAOM fractions calculated using their total C and N and isotopic enrichment, correcting for the natural abundance of ^{13}C and ^{15}N in POM and MAOM of unlabelled experimental controls

(Table 5.A.2). Litter-derived ^{13}C and ^{15}N recovery in SOM fractions was then calculated as a proportion of that applied in *L. perenne* litter.

$$(1) \quad {}^{13}\text{C}_{\text{recovered}} = \left(\frac{\text{TC}_{\text{fraction}} \times (f^{13}\text{C}_{\text{fraction}} - f^{13}\text{C}_{\text{control}})}{\text{TC}_{\text{litter}} \times f^{13}\text{C}_{\text{litter}}} \right) \times 100$$

$$(2) \quad {}^{15}\text{N}_{\text{recovered}} = \left(\frac{\text{TN}_{\text{fraction}} \times (f^{15}\text{N}_{\text{fraction}} - f^{15}\text{N}_{\text{control}})}{\text{TN}_{\text{litter}} \times f^{15}\text{N}_{\text{litter}}} \right) \times 100$$

Where $^{13}\text{C}_{\text{recovered}}$ and $^{15}\text{N}_{\text{recovered}}$ = the proportion (%) of litter-derived ^{13}C and ^{15}N recovered in SOM fractions, $\text{TC}_{\text{fraction}}$ and $\text{TN}_{\text{fraction}}$ = total C and N (μg) measured in SOM fractions (POM or MAOM), $f^{13}\text{C}_{\text{fraction}}$ and $f^{15}\text{N}_{\text{fraction}}$ = the atom% of ^{13}C and ^{15}N measured in SOM fractions, $f^{13}\text{C}_{\text{control}}$ and $f^{15}\text{N}_{\text{control}}$ = the atom% of ^{13}C and ^{15}N measured in experimental control SOM fractions, $\text{TC}_{\text{litter}}$ and $\text{TN}_{\text{litter}}$ = total C and N (μg) of applied *L. perenne* litter, and $f^{13}\text{C}_{\text{litter}}$ and $f^{15}\text{N}_{\text{litter}}$ = the atom% of ^{13}C and ^{15}N of applied litter.

The proportion of C and N in POM, s-OM, and MAOM derived from applied litter was calculated using Equations 3. Values for N were calculated by substituting ^{13}C for ^{15}N .

$$(1) \quad P_{\text{AL}} = \left(\frac{\delta^{13}\text{C}_{\text{op}} - \delta^{13}\text{C}_{\text{mp}}}{\delta^{13}\text{C}_{\text{op}} - \delta^{13}\text{C}_{\text{np}}} \right)$$

Where ‘ P_{AL} ’ = the proportion (%) of the fraction’s C derived from applied litter, ‘ $\delta^{13}\text{C}$ ’ = the isotopic enrichment of ^{13}C , ‘op’ = the original or unlabelled C pool determined from experimental blanks for a given fraction, ‘mp’ = mixed pool or labelled fractions, and ‘np’ = new pool or label material.

5.3.4 Physicochemical analysis

Sixteen soil physicochemical properties were measured at each sampling point: temperature, moisture content (MC_C), bulk density (BD), texture, soil organic matter content (SOM), pH, cation exchange capacity (CEC), and concentrations of total C (TC), total N (TN), and exchangeable Al, Ca, Fe, K, Mg, Mn, and Na (Table 5.A.3). Soil temperature ($^\circ\text{C}$; 10 cm depth) was measured at the time of sample collection in June 2024 using a Fisherbrand Long-Stem Digital Thermometer (Fisher Scientific UK, product code 11799705). MC_C samples were taken at the time of sample collection using a corer (10 cm $\varnothing$ x 15 cm depth) and stored at 4 $^\circ\text{C}$ in sealed labelled plastic bags. Determination of MC_C ($\text{g H}_2\text{O } 100 \text{ g}^{-1}$) occurred within 24 hours on homogenised samples following the method of ISO 11465 (International Organization for Standardization, 1993). Soil bulk density (g cm^{-3}) of the 0–5 cm layer was calculated in November 2023 using the volumetric cylinder method outlined by ISO 11272 (International

Organization for Standardization, 2017). The remaining soil physicochemical properties were measured from soil cores (10 cm $\varnothing$ x 15 cm depth) collected in November 2023, which were thoroughly homogenised and sieved to < 2 mm.

Soil texture was determined by the hand texturing method (Thien, 1979). SOM (g 100 g⁻¹) was calculated via loss-on-ignition overnight at 350 °C (Ayub and Boyd, 1994). Soil pH was determined from a 1:2.5 solution (soil to deionised water) using a Thermo Orion Star A111 pH meter calibrated to pH buffers 4.0, 7.0 and 10.0 (Ministry of Agriculture, Fisheries and Food, 1986). Exchangeable Ca, Mg, K, Na, Al, Fe, and Mn (mg kg⁻¹) were measured in a 0.1 M BaCl₂ extract via inductively coupled plasma-optical emission spectroscopy (ICP-OES) using a Thermo iCAP 7000. According to the method of Hendershot and Duquette (1986), CEC (meq 100 g⁻¹) was calculated using measured element concentrations. However, Fe and Al were excluded from CEC calculations and statistical analysis due to low instrumental accuracy (44 %) and sample concentrations (< 7 % of samples above detection limit), respectively. TC and TN (g kg⁻¹) were determined by elemental analysis using an Elementar Vario EL Cube on soil oven-dried at 40 °C for 48 h and ground to < 200 μ m using a Retsch MM200 ball-mill. Further methodological details, including quality control information (detection limits, accuracy, and precision) for ICP-OES and elemental analysis, can be found in Table 5.A.4.

5.3.5 Statistical analysis

Linear mixed-effects models (LMMs) were used to investigate SOM dynamics in alley-cropping and sole-cropping systems, due to their ability to account for the dependencies and correlations present between observations in nested, hierarchical data (Harrison et al., 2018; Schielzeth and Nakagawa, 2013). The influence of agricultural system (S, alley-cropping or sole-cropping), transect position (TP, 0, 3, or 13 m), and their interaction (S*TP) on litter-derived ¹³C/¹⁵N recovery (Models A–B) and partitioning into POM (Models C–D), s-OM (Models E–F), and MAOM (Models G–H) was investigated.. As high spatial variation was observed in sole-cropping systems, recovery of ¹³C/¹⁵N was also compared between individual transect positions in alley-cropping and the sole-cropping average. Farm and experimental transect were included in models as random effects, as it was assumed that within-group variation would be smaller than between groups. Soil physicochemical properties and farm- and system-level characteristics (e.g., local pedo-climatic conditions, agronomic management) were also included in models to capture variation in ¹³C/¹⁵N recovery, as they are known to influence SOM formation and persistence (Galluzzi et al., 2024; Robertson et al., 2019; Yu et al., 2022). Statistical analyses were undertaken in R version 4.5.2 (R Core Team, 2025) and

modelling was performed using the *lmer* function of the ‘lme4’ package (v. 1.1-35.2, Bates et al., 2015).

A process of backward stepwise selection was used to select fixed effects for final models presented in Table 5.A.5. A full model was created which included (i) agricultural system, transect position, and their interaction (retained in final model), (ii) all measured soil physicochemical properties which, based on scientific literature, could influence litter decomposition or SOM dynamics (Table 5.A.3), (iii) farm- and system-level characteristics (Table 5.A.1), and (iv) nested random effects (farm/transect). This model selection method involved iteratively excluding fixed effects from models which had the greatest negative impact on model fit. Model fit was assessed using the corrected Akaike Information Criterion (AICc), using the ‘MuMIn’ package (v. 1.47.5, Bartoń, 2023), as AICc penalises model overfitting and corrects for a small sample size (Hurvich and Tsai, 1993). Exclusion of fixed effects continued until removal of any variable reduced AICc by < 2 , at which point models with and without a given variable were both deemed to have strong support (Burnham and Anderson, 2002). Exclusion of fixed effects causing autocorrelation was also determined based on AICc. Furthermore, where farm- and system-level variables captured the variation explained by farm, they were included as fixed effects and the random effect removed if this improved model fit. When determining the influence of alley-cropping (S, TP, or S*TP) on $^{13}\text{C}/^{15}\text{N}$ recovery, reduced models were used which excluded soil physicochemical variables which were significantly influenced by S or S*TP. This is because their inclusion was predicted to result in an underestimation of the indirect influence of alley-cropping on SOM dynamics (e.g., via modification of soil properties by tree rows).

Goodness of fit of final models was assessed using diagnostic plots (normality of residuals, normality of random effects, heteroscedasticity, homogeneity of variance, multicollinearity) generated by the *check_model* function of the ‘performance’ package (v. 0.13.0, Lüdtke et al., 2021). Potential model overfitting was assessed by leave-one-group-out cross validation (LOGO-CV) (Roberts et al., 2017; Yates et al., 2023). Models were trained on all but one transects and then tested on the withheld transect. Increases in the average per-fold root mean square error (RMSE) of $< 25\%$ between training and test data were accepted, as some reductions in performance were expected on unseen data without strong evidence for overfitting (Hastie et al., 2009; Yates et al., 2023).

The significance of retained fixed effects as predictors of $^{13}\text{C}/^{15}\text{N}$ recovery was determined via likelihood-ratio tests using the *anova* function of the ‘stats’ package (R Core Team, 2025).

Pairwise comparisons between transect positions across both agricultural systems were made using estimated marginal means generated by the *emmeans* function of the ‘emmeans’ package (v. 1.11.0, Lenth, 2025) with a Benjamini-Hochberg false discovery rate (FDR) correction for multiple comparisons (Benjamini and Hochberg, 1995; Pike, 2011). All tests had a significance of $\alpha = 0.05$. The proportion of the variance explained by fixed effects (R^2_m) and fixed and random effects combined (R^2_c) was determined via the *r2* function of the ‘performance’ package (Lüdtke et al., 2021). Comparisons of label recovery within SOM fractions between ^{13}C and ^{15}N were made using paired t-tests via the *t.test* function of the ‘stats’ package (R Core Team, 2025).

5.4 Results

5.4.1 Recovery of applied ^{13}C and ^{15}N

On average, 27.5 % ($\pm 4.1_{\text{SD}}$) of applied ^{13}C and 59.1 % ($\pm 8.9_{\text{SD}}$) of applied ^{15}N was recovered within SOM fractions. Recovery of applied ^{15}N was estimated to be 31.6 % ($\pm 0.61_{\text{SE}}$) greater than for ^{13}C ($t_{(89.00)} = 51.65$, $p < 0.001$). Agricultural system and transect position significantly influenced the total recovery of ^{13}C and ^{15}N (all SOM fractions combined), whereas their interaction did not (Models A–B) (Table 5.1). Loss of applied ^{13}C increased by 2.71 % ($\pm 1.1_{\text{SE}}$) in alley-cropping relative to sole-cropping ($t_{(40.2)} = 2.52$, $p = 0.016$), whereas no significant change in ^{15}N loss was observed between agricultural systems ($p > 0.05$).

Higher ^{13}C losses were observed only in alley-cropping tree rows (Figure 5.1). At AC0, recovery of applied ^{13}C declined by 4.1 % ($\pm 1.3_{\text{SE}}$) compared to the sole-cropping average ($t_{(63.9)} = 3.16$, $p = 0.014$) and by 3.0 % ($\pm 1.0_{\text{SE}}$) compared to AC3 ($t_{(65.0)} = 2.95$, $p = 0.022$). Similarly, recovery of applied ^{15}N at AC0 was reduced by 8.9 % ($\pm 3.2_{\text{SE}}$) compared to the sole-cropping average ($t_{(54.6)} = 2.77$, $p = 0.023$), as well as by 7.4 % ($\pm 2.2_{\text{SE}}$) compared to AC3 ($t_{(65.3)} = 3.34$, $p = 0.011$) and by 5.9 % ($\pm 2.2_{\text{SE}}$) compared to AC13 ($t_{(64.8)} = 2.66$, $p = 0.037$). Due to the variability in ^{13}C and ^{15}N losses in both agricultural systems, not all sole-cropping transect positions retained more applied $^{13}\text{C}/^{15}\text{N}$ compared to AC0 (Figure 5.1)

Table 5.1. The significance of agricultural system ('S'), transect position ('TP'), and their interaction ('S*TP'), as well as soil physicochemical properties and farm- and system-level variables (fixed effects) as predictors of the recovery of ^{13}C and ^{15}N in SOM ('Total') and in particulate organic matter ('POM') and mineral-associated organic matter ('MAOM'), specifically. Changes in ^{13}C and ^{15}N recovery (est) and standard errors (se) were estimated using linear mixed-effects models. χ^2 and p-values were determined through ANOVA comparisons of models with and without a given fixed effect. '-' indicates that a fixed effect was not included in the model for a given ^{13}C or ^{15}N fraction. Significant predictors are highlighted in bold. Values for 'S', 'TP', and 'S*TP' were estimated from reduced models.

Fixed effect ^{1,2}	est ³	se	Total χ^2	p	est	se	POM χ^2	p	est	se	MAOM χ^2	p
^{13}C												
S	NA	NA	7.14	0.008	NA	NA	2.55	0.111	NA	NA	1.81	0.178
TP	NA	NA	9.95	0.007	NA	NA	0.05	0.978	NA	NA	15.07	< 0.001
S*TP	NA	NA	1.40	0.496	NA	NA	3.30	0.192	NA	NA	3.00	0.223
BD	2.10	2.78	0.57	0.450	2.6	1.8	2.22	0.137	-	-	-	-
Soilscape	NA	NA	8.14	0.043	-	-	-	-	-	-	-	-
CN	0.86	0.32	6.63	0.010	-	-	-	-	0.55	0.28	3.26	0.071
Mn	0.15	0.04	15.26	< 0.001	-	-	-	-	0.12	0.03	14.41	< 0.001
pH	1.73	1.56	1.21	0.27	-	-	-	-	-	-	-	-
Organic	-	-	-	-	1.1	0.62	3.43	0.064	4.5	1.3	10.69	< 0.001
Ca	-	-	-	-	0.09	0.05	3.10	0.079	-0.13	0.07	3.46	0.063
CEC	-	-	-	-	-0.03	0.01	5.03	0.025	0.03	0.02	2.73	0.098
TN	-	-	-	-	-0.12	0.13	0.89	0.346	-	-	-	-
Crop _{div}	-	-	-	-	-	-	-	-	0.57	0.62	0.83	0.364
^{15}N												
S	NA	NA	3.85	0.050	NA	NA	3.59	0.058	NA	NA	1.49	0.222
TP	NA	NA	11.02	0.004	NA	NA	2.45	0.294	NA	NA	15.63	< 0.001
S*TP	NA	NA	2.61	0.272	NA	NA	4.09	0.130	NA	NA	3.59	0.166
CN	1.89	0.76	5.88	0.015	0.33	0.23	2.03	0.154	1.2	0.69	2.67	0.103
Mn	0.33	0.08	15.28	< 0.001	0.04	0.03	2.92	0.087	0.28	0.07	12.89	< 0.001
MC _c	-0.17	0.13	1.62	0.203	-	-	-	-	-	-	-	-
pH	4.41	3.24	1.83	0.176	-	-	-	-	-	-	-	-
Temp	1.12	0.75	2.19	0.139	-	-	-	-	-	-	-	-
Organic	-	-	-	-	2.8	1.0	6.91	0.009	8.8	3.2	6.89	0.009
Ca	-	-	-	-	0.11	0.06	3.14	0.077	-0.27	0.07	2.58	0.108
CEC	-	-	-	-	-0.04	0.02	6.12	0.013	0.06	0.04	1.61	0.205
TN	-	-	-	-	0.29	0.20	2.01	0.157	0.79	0.56	1.94	0.164
BD	-	-	-	-	2.7	2.1	1.74	0.187	-	-	-	-
Crop _{div}	-	-	-	-	1.3	0.59	4.51	0.034	-	-	-	-
Na	-	-	-	-	-	-	-	-	-0.03	0.03	0.95	0.330

¹ Fixed effects: 'S' = agricultural system; 'TP' = transect position; 'BD' = soil bulk density (g cm^{-3}); 'CEC' = soil cation exchange capacity ($\text{meq } 100\text{g}^{-1}$); 'Ca' = soil exchangeable calcium concentration (g kg^{-1}); 'CN' = soil carbon-to-nitrogen ratio; 'crop_{div}' = the number of crops grown between 2021–2024; 'Mn' or 'Na' = soil exchangeable manganese or sodium concentration (mg kg^{-1}); 'organic' = organic management relative to conventional; pH = concentration of H^+ ions (μmol); 'soil type' = Soil type according to the Soilscape Viewer online soil reporting tool (Cranfield Soil and Agrifood Institute, 2025); 'TN' = soil total N content (g kg^{-1}).

² Values for 'S', 'TP', and 'S*TP' were estimated from reduced models, containing only predictors which were not significantly influenced by agricultural system or its interaction with transect position.

³ Estimates indicate the change in $^{13}\text{C}/^{15}\text{N}$ recovery (%) with a one unit increase in the fixed effect.

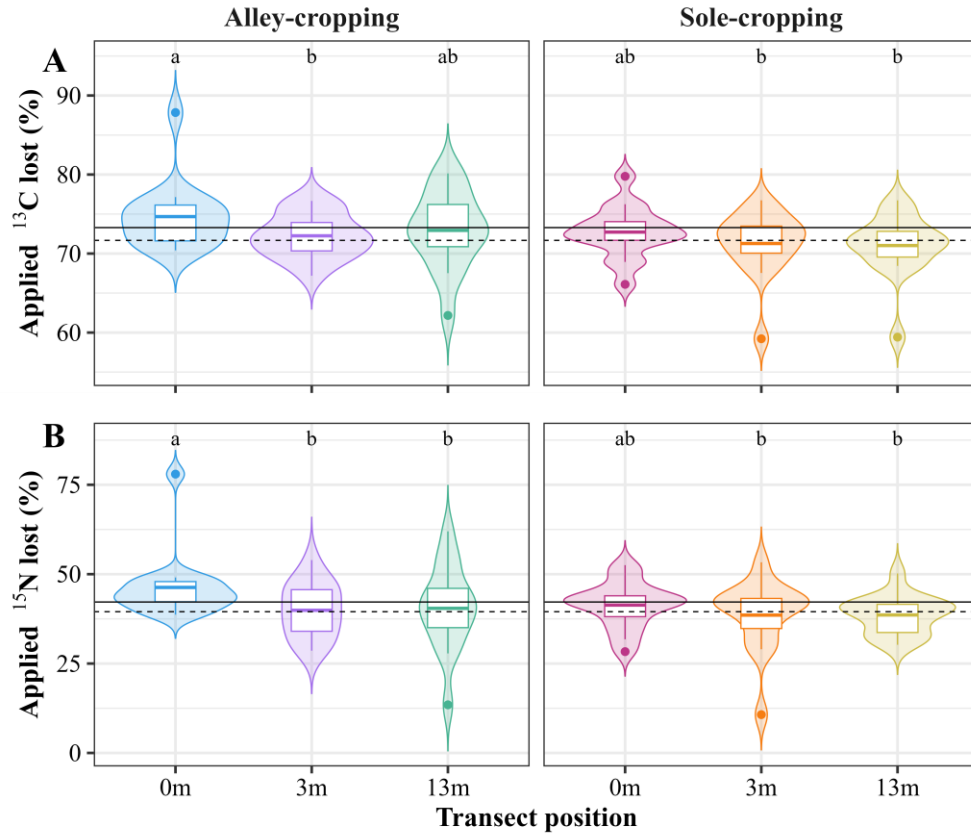


Figure 5.1. Loss of applied (A) ^{13}C and (B) ^{15}N (%) over a 28-day incubation in soils from paired alley-cropping and sole-cropping fields at five arable farms in England, United Kingdom. Transect positions refer to distance (m) along linear transects; in alley-cropping systems, 0 m = 1.5 m into the tree row from the edge of the UVS, 3 m = 1.5 m into the crop alley from the edge of the UVS, and 13 m = 11.5 m into the crop alley from the edge of the UVS (or 7.5 m at S2). Boxplots provide the mean, interquartile range (IQR), and the 25th and 75th percentiles $\pm$ (interquartile range $\times$ 1.5) of $^{13}\text{C}/^{15}\text{N}$ loss. Violin plots display the distribution of the data points for each transect position. Individual points represent outliers. Horizontal lines indicate the average $^{13}\text{C}/^{15}\text{N}$ loss for agricultural systems: solid = alley-cropping, dashed = sole-cropping. No shared letter indicates a significant pairwise difference ($\alpha = 0.05$) between sampling locations across both treatments, as determined by linear mixed-effects modelling and *post hoc* comparisons of estimated marginal means with a false discovery rate correction for multiple comparisons.

5.4.2 Partitioning of applied ^{13}C and ^{15}N

Most of the recovered ^{13}C and ^{15}N was located in MAOM (Figure 5.2): 64.8 % ($\pm 8.9_{\text{SD}}$) of recovered ^{13}C and 72.3 % ($\pm 8.7_{\text{SD}}$) of recovered ^{15}N . However, compared to ^{15}N , significantly more recovered ^{13}C remained in POM ($t_{(89.0)} = 28.09$, $p < 0.001$) and significantly less was transformed into s-OM ($t_{(89.0)} = 13.53$, $p < 0.001$) or MAOM ($t_{(89.0)} = 21.7$, $p < 0.001$), indicating differing decomposition dynamics for litter-derived C and N.

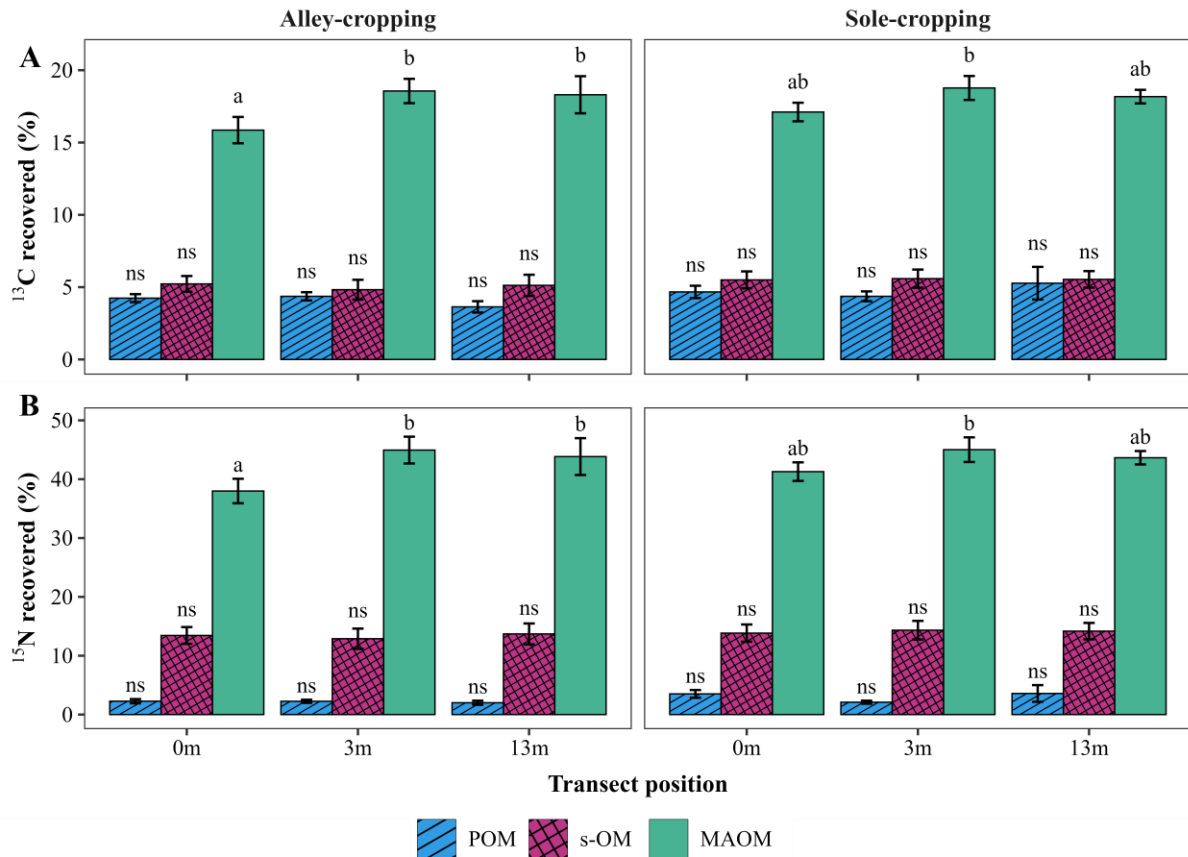


Figure 5.2. $^{13}\text{C}/^{15}\text{N}$ recovered (%) in SOM fractions. Mean proportion (%) of applied (A) ^{13}C and (B) ^{15}N from *L. perenne* shoots recovered in particulate organic matter ('POM'; $> 53\ \mu\text{m}$), suspended organic matter ('Suspended'; $< 53\ \mu\text{m}$ and $< 1\ \text{g cm}^{-3}$), and mineral-associated organic matter ('MAOM'; $< 53\ \mu\text{m}$ and $> 1\ \text{g ml}^{-1}$) after incubation for 28 days in soils from paired alley-cropping and sole-cropping fields at five arable farms in England, United Kingdom. Transect positions refer to distance (m) along linear transects; in alley-cropping systems, 0 m = 1.5 m into the tree row from the edge of the UVS, 3 m = 1.5 m into the crop alley from the edge of the UVS, and 13 m = 11.5 m into the crop alley from the edge of the UVS (or 7.5 m at S2). Error bars provide the standard error of the mean for each fraction and transect position. Letters above error bars highlight significant pairwise differences in $^{13}\text{C}/^{15}\text{N}$ recovery between transect positions across both agricultural systems for a given SOM fraction. No shared letter indicates a significant difference at $\alpha = 0.05$, as determined using linear mixed-effects models and *post hoc* tests with a false discovery rate correction for multiple comparisons.

Agricultural system, transect position, and their interaction had no significant effect on the proportion of applied ^{13}C and ^{15}N recovered from POM or s-OM (Models C–F; $p > 0.05$) (Table 5.1). However, transect position influenced the recovery of applied ^{13}C and ^{15}N in MAOM (Models E–F; $p < 0.001$) (Table 5.1). Recovery of applied ^{13}C and ^{15}N in MAOM were not significantly different between alley-cropping and sole-cropping ($p > 0.05$), but recovery of ^{13}C and ^{15}N in soils from AC0 were reduced by 3.1 % ($\pm 1.2\text{SE}$) ($t_{(63.4)} = 2.49$, $p = 0.031$) and 7.0 % ($\pm 3.0\text{SE}$) ($t_{(60.9)} = 2.32$, $p = 0.048$) compared to the sole-cropping average (Figure 5.2). These declines were driven by differences between AC0 and SC3, specifically, which were 4.1 % ($\pm 1.2\text{SE}$) for ^{13}C ($t_{(79.8)} = 3.28$, $p = 0.012$) and 9.6 % ($\pm 3.0\text{SE}$) for ^{15}N ($t_{(70.3)} = 3.15$, $p = 0.018$) (Figure 5.1).

Recovery of ^{13}C and ^{15}N in MAOM was also lower in soils from AC0 than both AC3 and AC13. Recovery of ^{13}C in MAOM in soils from AC0 was reduced by 3.1 % ($\pm 0.8_{\text{SE}}$) compared to AC3 ($t_{(66.0)} = 3.68$, $p = 0.007$) and by 2.5 % ($\pm 0.8_{\text{SE}}$) compared to AC13 ($t_{(65.7)} = 2.93$, $p = 0.023$). Similarly, ^{15}N recovery in MAOM in soils from AC0 was 7.9 % ($\pm 2.0_{\text{SE}}$) lower than AC3 ($t_{(66.7)} = 3.98$, $p = 0.003$) and 5.9 % ($\pm 2.0_{\text{SE}}$) lower than AC13 ($t_{(66.5)} = 2.96$, $p = 0.021$) (Figure 5.2).

The proportion of C and N in POM, s-OM, and MAOM derived from applied litter was lower in soils from AC0 than arable crop areas, but this was only statistically significant for MAOM-C (Table 2).

Table 5.2. The proportion of carbon ('C') and nitrogen ('N') in particulate ('POM'), suspended ('s-OM'), and mineral-associated ('MAOM') organic matter derived from applied litter in alley-cropping ('AC') and sole-cropping ('SC') systems at three distances (0, 3, and 13 m) along linear transects. No shared letter indicates a significant difference at $\alpha = 0.05$, as determined using linear mixed-effects models and *post hoc* tests with a false discovery rate correction for multiple comparisons.

	AC0	AC3	AC13	SC0	SC3	SC13
C						
POM	17.9 ^{ns} $\pm$ 12.5	19.4 ^{ns} $\pm$ 13.5	18.3 ^{ns} $\pm$ 12.7	21.7 ^{ns} $\pm$ 13.8	21.5 ^{ns} $\pm$ 13.5	22.6 ^{ns} $\pm$ 12.5
s-OM	16.8 ^{ns} $\pm$ 4.9	18.3 ^{ns} $\pm$ 5.8	18.4 ^{ns} $\pm$ 6.0	18.3 ^{ns} $\pm$ 4.8	18.2 ^{ns} $\pm$ 5.2	18.4 ^{ns} $\pm$ 5.3
MAOM	10.8 ^a $\pm$ 4.7	12.4 ^b $\pm$ 5.2	12.7 ^b $\pm$ 5.7	11.8 ^{ab} $\pm$ 5.3	12.4 ^{ab} $\pm$ 5.4	13.2 ^{ab} $\pm$ 6.0
N						
POM	9.0 ^{ns} $\pm$ 5.5	11.7 ^{ns} $\pm$ 8.6	11.8 ^{ns} $\pm$ 7.9	13.9 ^{ns} $\pm$ 9.4	10.7 ^{ns} $\pm$ 6.3	12.8 ^{ns} $\pm$ 7.8
s-OM	22.0 ^{ns} $\pm$ 7.1	24.0 ^{ns} $\pm$ 6.9	24.4 ^{ns} $\pm$ 6.7	23.6 ^{ns} $\pm$ 5.2	23.7 ^{ns} $\pm$ 5.5	23.0 ^{ns} $\pm$ 5.4
MAOM	13.8 ^{ns} $\pm$ 5.7	15.5 ^{ns} $\pm$ 6.1	15.7 ^{ns} $\pm$ 6.3	14.7 ^{ns} $\pm$ 6.0	15.4 ^{ns} $\pm$ 5.9	16.2 ^{ns} $\pm$ 6.3

5.4.3 System and farm-level drivers of ^{13}C and ^{15}N recovery

Higher soil Mn^{2+} concentrations led to greater total recovery of ^{13}C and ^{15}N as well as in MAOM specifically, whereas increases in soil TN reduced the total recovery of ^{13}C (Table 5.1). No soil physicochemical or farm- and system-level characteristics influenced ^{13}C recovery in POM. In contrast, ^{15}N recovery in POM was reduced in soils with higher CEC and increased with temporal crop diversity (Table 5.1; Figure 5.B.1). Total recovery of ^{13}C was influenced by soil type (Table 5.1); ^{13}C recovery was reduced in Soilscape 27, but there were no significant pairwise differences between Soilscares (Figure 5.B.2). Organic management reduced the proportion of litter-derived ^{13}C and ^{15}N recovered in s-OM by 3.5 % ($\pm 0.8_{\text{SE}}$) ($\chi^2_{(1)} = 14.61$, $p < 0.001$) and 8.3 % ($\pm 2.1_{\text{SE}}$) ($\chi^2_{(1)} = 12.94$, $p < 0.001$), respectively. However, it increased the proportion of litter-derived ^{15}N in POM and ^{13}C and ^{15}N in MAOM (Table 5.1).

5.5 Discussion

This study investigated the impact of temperate alley-cropping on litter decomposition and the partitioning of litter-derived C and N into organic matter pools with differing residence times

in soils. In doing so, it provides novel insight into the potential stability of observed SOC and nutrient gains in and near tree rows and the contribution that alley-cropping systems can make to long term SOM stewardship. It was hypothesised that decomposition of *L. perenne* would be greater in alley-cropping than sole-cropping systems, leading to lower recovery of applied $^{13}\text{C}/^{15}\text{N}$ across all SOM fractions (hypothesis 1). However, because tree rows can potentially promote both the microbial and direct sorption pathways of MAOM formation, alley-cropping was also predicted to increase the recovery of applied $^{13}\text{C}/^{15}\text{N}$ in MAOM relative to sole-cropping (hypothesis 2). As the influence of tree rows typically declines with distance into crop alleys, relative differences in $^{13}\text{C}/^{15}\text{N}$ recovery were predicted to be greatest in tree rows and extend partially into crop alleys (hypothesis 3).

5.5.1 Drivers of SOM dynamics in alley-cropping and sole-cropping systems

As predicted, alley-cropping tree rows stimulated greater ^{13}C and ^{15}N losses from applied litter relative to arable crop areas, but they were not the result of higher litter decomposition rates. Both POM, here representing remaining applied litter, and s-OM, representing decomposition products of POM (e.g., fine POM, dissolved organic matter, and microbial biomass), were unaffected by the presence or proximity of tree rows, suggesting that early-stage litter decomposition processes were similar across agricultural systems. This aligns with studies reporting no differences in litter decomposition between tree rows and arable areas (Moran-Rodas et al., 2005; O'Connor et al., 2025; Sutterlütti et al., 2023) but contrasts with reports of enhanced litter decomposition in tree rows (Giray et al., 2025; Wachendorf et al., 2020), including at the farms sampled in this study (Evans et al., 2025a).

Divergent findings regarding litter decomposition rates likely stem from differences in pedoclimatic conditions, management, agroforestry design, and methodology. Notably, unlike Evans et al. (2025a), the present study used *L. perenne* as the litter substrate and decomposition occurred under controlled laboratory conditions. However, consistent with the findings of Evans et al. (2025a), POM persistence declined with increasing soil CEC and, for ^{15}N only, increased with temporal crop diversity between 2021–2024. Evans et al. (2025a) suggested that CEC was acting as a composite soil quality indicator, with higher values reflecting conditions which promote the activity of soil decomposers and detritivores. Conversely, higher temporal crop diversity was assumed to indicate more frequent agronomic activity and changes in vegetation composition which disturbed soil decomposers (Domnariu et al., 2025; Yu et al., 2025) and reduced litter decomposition mediated by microorganisms (Evans et al., 2025a).

In contrast to findings for POM and s-OM, recovery of ^{13}C and ^{15}N in MAOM was significantly lower in tree rows compared to arable crop areas. As leaching was not a possibility, these findings show that tree rows reduced mineral association of applied litter and increased soil gaseous emissions. Continuous, diverse organic inputs from trees can stimulate microbial activity (Jilling et al., 2021; Kuzyakov et al., 2000), alleviate nutrient limitations (Manzoni et al., 2010; Zheng et al., 2024), and support a greater abundance and functional diversity of nutrient-cycling organisms (Beule et al., 2020), resulting in higher basal (Lee and Jose, 2003; Mettauert et al., 2022) and substrate-induced (Beuschel et al., 2019; Guillot et al., 2021; Mungai et al., 2005) respiration and CO_2 and N_2O losses (Baah-Acheamfour et al., 2016; Medinski et al., 2015; Peichl et al., 2006; Wotherspoon et al., 2014). Lower rates of mineral association in tree rows may therefore have been the direct result of higher gaseous emissions and consequently a lower availability of $^{13}\text{C}/^{15}\text{N}$ to form organo-mineral complexes. However, alley-cropping tree rows have also been found to have similar (Guillot et al., 2021) or higher (Beule et al., 2022) microbial substrate-use efficiency compared to arable crop areas, which would favour MAOM formation through the microbial pathway. If this were the case, it may be that lower mineral association in tree rows instead resulted in greater losses of litter-derived $^{13}\text{C}/^{15}\text{N}$, as opposed to the other way around.

MAOM formation depends on available mineral binding sites, which are governed by soil biophysical and local pedo-climatic properties (Bruere et al., 2025). Although Begill et al. (2023) detected no upper limit for MAOM-C in temperate cropland soils, many UK agricultural soils are at risk of MAOM saturation (Bruere et al., 2025). In this study, MAOM-C and -N concentrations were higher in soils from tree rows than from arable areas, suggesting a lower sorption capacity because mineral surfaces were already bound to or coated by existing SOM (Mikutta et al., 2019). Although MAOM is a dynamic C pool (Jilling et al., 2025), presenting opportunities for litter-derived ^{13}C and ^{15}N to replace existing SOM within organo-mineral complexes, there would also have been greater competition for mineral surface binding sites between litter-derived $^{13}\text{C}/^{15}\text{N}$ and existing SOM in tree rows. This was evident from the fact that tree row soils had more SOM and higher TC and TN concentrations than arable crop areas, but a lower proportion of MAOM-C was derived from applied litter. Under such conditions, more decomposition products (i.e., s-OM) would have remained unprotected and vulnerable to further microbial degradation, in this case potentially leading to ^{13}C and ^{15}N losses via gaseous emissions.

Contrary to hypothesis three, tree rows had a negligible effect on litter decomposition and mineral-association dynamics in crop alleys, a finding consistent with previous research which has reported varying changes in SOC within crop alleys (Ivezić et al., 2022). A lack of permanent, diverse vegetation and frequent disturbance in crop alleys meant that soil conditions were more similar to sole-cropping systems than tree rows, an idea supported by the few significant differences in measured soil physicochemical properties between crop alley and sole-cropping transect positions, including SOM content and the MAOM-C and -N concentrations of experimental blanks. As a result, crop alleys were unlikely to be mineral saturated as suspected for tree rows. Furthermore, although not measured in the current research, many alley-cropping studies have reported no change in microbial activity or community structure in crop alleys relative to sole-cropping (Beule et al., 2022, 2025), which due to the central role of microorganisms in MAOM formation (Cotrufo et al., 2015) may explaining their similar MAOM formation rates.

Higher recovery of litter-derived ^{13}C and ^{15}N in MAOM under organic relative to (recently) conventional management appears inconsistent with the idea that sampled soils were near MAOM saturation. Organic systems typically add more residues and organic amendments to soils than conventional systems, increasing SOM and potentially intensifying competition for mineral sorption sites (Koorneef et al., 2025). However, organically managed soils also often support a higher microbial biomass, diversity, and activity (Hartmann et al., 2015; Lori et al., 2017), potentially promoting the microbial pathway of MAOM formation. Improved soil structure and aggregation under organic management (Karami et al., 2012; Tian et al., 2022) may further stabilise newly formed MAOM (Even and Cotrufo, 2024). Critically, even in MAOM-saturated soils, organic fertilisation can increase MAOM-C turnover relative to conventional fertilisation (Mayer et al., 2023), freeing mineral surfaces and allowing applied ^{13}C and ^{15}N to bind. Together, these mechanisms may explain why organically managed soils exhibited higher MAOM formation. However, as only one farm in this study was conventionally managed and transitioned to organic management in September 2023, conclusions about the effects of organic versus conventional management on MAOM formation should be considered preliminary and reflecting legacy effects of conventional management.

Soil exchangeable Mn concentration also positively influenced litter-derived ^{13}C and ^{15}N recovery in MAOM, but only in alley-cropping systems. Previous studies have linked elevated Mn to reduced soil C and N storage (Santos and Herndon, 2023; Stendahl et al., 2017), whereas

combined Mn/N additions have been found to increase residue-derived C recovery in MAOM (Neupane et al., 2023). Soil Mn^{2+} is a precursor to Mn-oxides, which enhance SOM protection by (i) adsorbing to organic compounds through physical and chemical interactions (ii) physically protecting organic compounds via co-precipitation or entrapment, and (iii) increasing recalcitrance through polymerisation (Li et al., 2021). Mn availability can also facilitate fungal decomposition, particularly lignin degradation, enabling hyphal transfer of litter-derived ^{13}C and ^{15}N to microbial biomass or mineral soils as DOC or fungal residues (Santos and Herndon, 2023; Vidal et al., 2021; Klink et al., 2022).

In the current research, higher soil TN in alley-cropping systems, especially tree rows, compared to sole-cropping may have facilitated Mn^{2+} -mediated pathways of mineral association. Alley-cropping systems also typically support more diverse fungal communities (Beule et al., 2022) which may have been stimulated by Mn^{2+} increases to a greater extent than less biodiverse sole-cropping communities. Alternatively, through oxidative and reductive processes, Mn-oxides may have destabilised existing MAOM, increasing the availability of binding sites for litter-derived C/N (Li et al., 2021; Zhang et al., 2025). This would have been beneficial in alley-cropping systems, where there was suspected mineral saturation, but may have been detrimental in sole-cropping where saturation was presumed to be less of an issue. However, as Mn-oxides specifically were not measured in the current study, further research is needed to confirm the key role soil Mn plays in mineral association dynamics.

5.5.2 Opportunities and limitations

Findings from the current research indicate that established tree rows may have limited capacity to increase MAOM formation in arable soils, likely because higher SOM contents have resulted in mineral surfaces which are already saturated. Instead, established tree rows can increase C and N losses from organic inputs to soils, a trade-off which must be considered when assessing the full C budget of alley-cropping systems and their potential contributions to climate change adaptation. However, this trade-off does not diminish alley-cropping's potential for enhanced soil C sequestration over multiple timescales compared to sole-cropping (Cardinael et al., 2018; Oelbermann et al., 2006; Wotherspoon et al., 2014). Even if their capacity is constrained, well-managed tree rows can sustain larger POM and MAOM pools over long timeframes than sole-cropping, functioning as important C and N stores (Angst et al., 2023). This was evident in the current research from the higher POM and MAOM mass, C and N concentrations observed in tree row experimental blanks compared to arable crop areas. The relevance of POM in particular for long-term C storage is expected to increase over time, due to the higher projected

sensitivity of MAOM to climate change (Lugato et al., 2021). Consequently, alley-cropping can contribute substantially to climate change adaptation and N management in croplands, even in soils approaching mineral saturation. However, to understand the broader implications of these results, it is also necessary to consider how laboratory conditions may have constrained their relevance to field SOM dynamics.

SOM dynamics observed under laboratory conditions are unlikely to fully reflect those occurring in the field. Here, sample preparation and controlled laboratory conditions disrupted soil structure, disturbed soil biota, removed above-ground litter and live roots, and standardised soil water-filled pore space and temperature. As such, the findings represent the potential influence of alley-cropping on SOM dynamics in the absence of indirect effects which are expected to influence SOM cycling, such as soil structural improvements (Dor et al., 2025; Even and Cotrufo, 2024), altered soil microclimates (Haddix et al., 2020), higher vegetation diversity (Angst et al., 2025; Canisares et al., 2023), and reduced soil disturbance regimes in the presence of tree rows. Moreover, contained incubations precluded investigation of SOM transfer to, and MAOM formation within, subsoils. Subsoils can be substantial C and N stores (Almaraz et al., 2025; Jones et al., 2026) and can exhibit higher MAOM formation rates than topsoils due to lower SOM content, reduced biological activity, and greater availability of mineral surfaces (Button et al., 2022). As tree rows often have deep root systems (Cardinael et al., 2015) and more biodiverse fungal communities capable of transferring SOM to deeper soil layers (Beule et al., 2022a; Giray et al., 2024; Vaupel et al., 2023), the greatest benefits of alley-cropping on SOM stabilisation may be observed in subsoils.

5.6 Conclusions

Temperate alley-cropping systems are promoted as multifunctional land uses which can address both agricultural nutrient pollution and climate change through increased SOM accumulation and storage. However, research investigating the formation and persistence of SOM fractions with contrasting residence times in alley-cropping systems remains limited, impeding understanding of their capacity for long-term, stable C and N storage.

In this study, alley-cropping had no effect on *Lolium perenne* decomposition and POM persistence. However, MAOM formation, or the recovery of litter-derived ^{13}C and ^{15}N in MAOM, was reduced in tree rows soils compared to soils from crop alleys and sole-cropping systems. Lower MAOM formation may be the result of greater $^{13}\text{C}/^{15}\text{N}$ losses as gaseous emissions and/or higher MAOM-C and -N saturation and competition with existing SOM in

tree row soils. Changes in measured soil physicochemical properties in tree rows did not provide any insight into the mechanistic drivers of mineral association dynamics. In contrast, organic management and higher soil Mn^{2+} concentrations increased MAOM formation.

It can be concluded that in established alley-cropping systems, tree rows may have a limited capacity to increase MAOM stocks, instead experiencing greater C and N losses from litter inputs relative to arable crop areas. Alley-cropping may still increase C and N storage in SOM compared to sole-cropping where organic inputs to soils exceed losses, but stabilisation of additional organic matter inputs from trees within MAOM is not guaranteed. Further research is needed to substantiate these findings under field conditions and on more farms, as well as to investigate the role of ions such as Mn^{2+} in C and N cycling.

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5.8 Appendix A | Additional methodological details and results

Contents

5.8.1. Farm and alley-cropping system characteristics

Table 5.A.1

5.8.2. C and N and isotope data for experimental standards

Table 5.A.2

5.8.3. Soil physicochemical properties in alley-cropping and sole-cropping systems

Table 5.A.3

5.8.4. Quality control information for soil nutrient concentrations

Table 5.A.4

5.8.5. Model details

Table 5.A.5

5.8.1 Farm and alley-cropping system characteristics

Table 5.A.1: Characteristics of alley-cropping ('AC') and sole-cropping ('SC') systems at five farms in England, United Kingdom. This table has been adapted from Evans et al. (2025b); crop rotations in bold have been changed to reflect the crops grown at the time of the litter bag experiment.

	C1	C2	N1	S1	S2
County	Cambridgeshire	Cambridgeshire	Nottinghamshire	Suffolk	Suffolk
Crop rotation ¹ (2021–2024)	ww-ao-ly- ly	ao-ao-ao- ao	lg-ww-sw- sc	AC: sc-wb-ly- ly SC: ly-ly-sw- wb	AC: sw-lg-ly- ly SC: lg-ly-ly- ly
Soil type ²	9	27	8	18	18
Soil texture ³	Silty clay	Sandy clay loam	Sandy clay	Clay/sandy clay	Clay/sandy clay
Year AC established	2015	2008	2015	2014	2000
Tree row orientation ⁴	N-S	N-S	N-S	N-S	N-S
Tree diversity ⁵	25 species	1 species	5 species	6 species	3 species
Tree density (ha ⁻¹)	58	85	75	138	64
Tree row width (m)	4	3	4	6 (double row)	5
Intra-row (m)	4	3	3	3	6
Alley width (m)	24	24	24	24	15

¹ Four most recent crops in the rotation provided. Crops: 'ao' = autumn oats, 'lg' = legumes, 'ly' = fertility-building ley, 'sc' = secondary cereal (e.g., spelt or rye grass), 'sw' = spring wheat, 'ww' = winter wheat, 'wb' = wheat + beans. Bold letters indicate the crop grown at the time of the litter bag experiment.

² Soil type according to the Soilsclapes Viewer online soil reporting tool hosted by Cranfield University (Cranfield Soil and Agrifood Institute, 2025): '8' = "slightly acid loamy and clayey soils with impeded drainage", '9' = "lime-rich loamy and clayey soils with impeded drainage", '18' = "slowly permeable seasonally wet slightly acid but base-rich loamy and clayey soils", and '27' = "fen peat soils".

³ Soil texture determined by feel (Thien, 1979).

⁴ Orientations: 'N' = North, 'S' = South.

⁵ Tree species information can be found in Table 3.A.1 in Evans et al. (2025b).

5.8.2 C/N and isotope data for experimental blanks

Table 5.A.2: Mean ($\pm$ standard deviation) mass (g), C and N concentrations (mg g^{-1}), and natural abundance of ^{13}C and ^{15}N of particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions of 30 experimental blank samples¹ taken from paired alley-cropping ('AC') and sole-cropping ('SC') systems at three distances (m) along linear experimental transects ('0m', '3m', and '13m'). No shared superscript letter indicates a statistically significant ($p < 0.05$) difference between transect positions across both agricultural systems, as determined by linear mixed models and Tukey post-hoc comparisons.

			AC			SC		
			0m	3m	13m	0m	3m	13m
POM	Mass	(g)	9.3 ^{ns} ± 3.8	9.0 ^{ns} ± 3.9	9.0 ^{ns} ± 3.8	8.6 ^{ns} ± 3.6	8.8 ^{ns} ± 3.8	8.5 ^{ns} ± 3.9
	C	(mg g^{-1})	66.0 ^{ns} ± 119.2	55.8 ^{ns} ± 101.0	50.1 ^{ns} ± 89.0	54.1 ^{ns} ± 107.0	55.0 ^{ns} ± 109.9	52.70 ^{ns} ± 103.6
	^{13}C	(%)	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00
	N	(mg g^{-1})	4.0 ^{ns} ± 7.9	3.5 ^{ns} ± 6.9	3.1 ^{ns} ± 6.0	3.5 ^{ns} ± 7.1	3.6 ^{ns} ± 7.2	3.5 ^{ns} ± 7.0
	^{15}N	(%)	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.01	0.37 ± 0.01	0.37 ± 0.01
S-OM	Mass	(g)	3.5 ± 1.7	3.3 ± 2.0	3.5 ± 2.1	3.6 ± 1.7	3.6 ± 1.7	4.1 ± 1.7
	C	(mg g^{-1})	58.9 ± 26.4	59.2 ± 28.1	55.4 ± 27.4	50.8 ± 24.9	50.6 ± 26.1	41.7 ± 18.1
	^{13}C	(%)	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00
	N	(mg g^{-1})	6.1 ± 2.6	5.2 ± 1.9	4.9 ± 1.5	5.5 ± 2.3	5.4 ± 2.3	4.5 ± 1.7
	^{15}N	(%)	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00
MAOM	Mass	(g)	11.2 ^{ns} ± 2.0	11.7 ^{ns} ± 2.2	11.3 ^{ns} ± 2.0	10.2 ^{ns} ± 2.8	10.4 ^{ns} ± 2.6	10.8 ^{ns} ± 2.7
	C	(mg g^{-1})	82.2 ^a ± 57.9	65.5 ^{ab} ± 40.9	61.6 ^b ± 43.8	72.5 ^{ab} ± 52.7	70.1 ^{ab} ± 59.7	59.4 ^b ± 48.3
	^{13}C	(%)	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00	1.08 ± 0.00
	N	(mg g^{-1})	7.2 ^a ± 4.1	6.1 ^{ab} ± 3.2	5.4 ^b ± 3.1	6.4 ^{ab} ± 3.4	6.1 ^{ab} ± 3.9	5.2 ^b ± 3.3
	^{15}N	(%)	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00	0.37 ± 0.00

¹ Experimental blanks were treated in the same way as labelled samples prior to fractionation.

5.8.3 Soil physicochemical properties in alley-cropping and sole-cropping systems

Table 5.A.3: Soil physicochemical properties¹ of paired alley-cropping and sole-cropping systems at five farms in England, United Kingdom. Values provide the mean $\pm$ standard deviation calculated from 90 sampling points. The influence of agricultural system ('S'; alley-cropping or sole-cropping), transect position ('TP'; 0m, 3m, or 13m), and their interaction ('S*TP') are indicated by the following: ns = not significant, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. No shared superscript letter indicates a statistically significant pairwise difference between transect positions across agricultural systems, as determined by linear mixed-effects models and Tukey *post hoc* comparisons of estimated marginal means. This table has been adapted from Evans et al. (2025b).

	Alley-cropping			Sole-cropping			Fixed effects		
	0m	3m	13m	0m	3m	13m	S	TP	S*TP
Reduced²									
CN	13.19 ^{ns} ± 1.51	13.16 ^{ns} ± 1.71	13.03 ^{ns} ± 1.48	12.61 ^{ns} ± 1.91	12.59 ^{ns} ± 1.83	12.65 ^{ns} ± 1.98	ns	ns	ns
CEC (meq 100g ⁻¹)	13.11 ^{ns} ± 7.32	13.51 ^{ns} ± 8.21	13.68 ^{ns} ± 8.87	13.55 ^{ns} ± 7.13	23.49 ^{ns} ± 27.10	23.55 ^{ns} ± 38.83	ns	ns	ns
Ca (mg kg ⁻¹)	6559.4 ^{ns} ± 4074.5	6455.6 ^{ns} ± 4472.4	6681.3 ^{ns} ± 4861.3	6435.7 ^{ns} ± 4236.7	9217.7 ^{ns} ± 11659	6287.4 ^{ns} ± 3987.9	ns	ns	ns
Mg (mg kg ⁻¹)	447.86 ^{ns} ± 327.26	554.02 ^{ns} ± 1024.4	680.85 ^{ns} ± 820.43	758.50 ^{ns} ± 1018.5	948.74 ^{ns} ± 1322.9	714.07 ^{ns} ± 941.12	ns	ns	ns
Mn (mg kg ⁻¹)	13.50 ^{ns} ± 19.27	10.18 ^{ns} ± 12.00	14.20 ^{ns} ± 20.15	7.68 ^{ns} ± 6.17	7.92 ^{ns} ± 6.59	9.39 ^{ns} ± 7.67	ns	ns	ns
Full²									
K (mg kg ⁻¹)	650.4 ^a ± 969.9	344.7 ^{ab} ± 188.1	354.0 ^{ab} ± 197.0	250.6 ^b ± 56.38	261.8 ^b ± 82.04	330.9 ^b ± 310.8	*	ns	*
Na (mg kg ⁻¹)	59.61 ^{ns} ± 64.14	64.61 ^{ns} ± 67.95	62.19 ^{ns} ± 65.24	77.80 ^{ns} ± 59.48	77.69 ^{ns} ± 62.99	77.00 ^{ns} ± 58.72	*	ns	ns
pH	7.00 ^{ns} ± 0.76	7.15 ^{ns} ± 0.71	7.24 ^{ns} ± 0.61	7.03 ^{ns} ± 0.58	7.01 ^{ns} ± 0.56	6.96 ^{ns} ± 0.65	ns	ns	*
TC (g kg ⁻¹)	59.38 ^a ± 54.76	51.17 ^b ± 51.39	51.49 ^b ± 50.54	50.89 ^b ± 54.36	50.42 ^b ± 54.20	49.49 ^b ± 52.72	**	***	***
TN (g kg ⁻¹)	4.38 ^a ± 3.62	3.76 ^b ± 3.46	3.78 ^b ± 3.31	3.70 ^b ± 5.51	3.68 ^b ± 4.94	3.26 ^b ± 5.00	ns	***	***
SOM (g 100g ⁻¹)	11.01 ^a ± 10.57	9.34 ^b ± 9.70	9.38 ^b ± 9.65	9.62 ^b ± 9.92	9.62 ^b ± 9.92	9.74 ^b ± 10.18	ns	***	***
MCs (g 100g ⁻¹)	32.56 ^a ± 11.76	30.46 ^{ab} ± 9.44	27.62 ^b ± 10.50	28.72 ^{ab} ± 11.76	29.49 ^{ab} ± 11.69	28.35 ^{ab} ± 11.44	ns	*	*
BD (g cm ⁻³)	0.89 ^a ± 0.21	1.04 ^b ± 0.25	1.05 ^b ± 0.25	1.00 ^{ab} ± 0.22	1.00 ^{ab} ± 0.21	1.04 ^b ± 0.24	ns	**	*
Temp (°C)	11.52 ^a ± 1.50	11.74 ^b ± 1.55	11.74 ^b ± 1.56	11.77 ^{ab} ± 1.90	11.79 ^{ab} ± 1.97	11.86 ^{ab} ± 2.02	ns	***	ns

¹ Abbreviations: 'BD' = bulk density, 'CEC' = cation exchange capacity, 'MCs' = moisture content at the start of the laboratory incubation, 'SOM' = organic matter content, 'Temp' = soil temperature at 10 cm depth at time of sample collection, 'TC' = total C, 'TN' = total N, and 'CN' = the ratio of TC to TN.

² Reduced models contained only soil physicochemical properties which were not significantly influenced by agricultural system or its interaction with transect position ('Reduced'), whereas full models contained all properties not excluded during stepwise selection ('Full' and 'Reduced').

5.8.5 Quality control data for soil nutrient concentrations

Table 5.A.4: Quality control information for soil carbon and nutrient concentrations. Values provided represent the mean (and range) across analytical runs, except for precision, which provides the median (and range). Table taken from Evans et al. (2025b).

Element ¹	Accuracy ² (%)	DL ³ (mg kg ⁻¹)	Precision ⁴ (%)
Al (mg kg ⁻¹)	114.0 (110.9-116.7)	7.4 (6.1-8.3)	25.2 (20.5-95.9)
Ca (mg kg ⁻¹)	106.3 (104.8-107.5)	154.9 (9.4-443.1)	0.84 (0.79-1.5)
Fe (mg kg ⁻¹)	43.8 (36.9-55.2)	4.5 (3.3-4.1)	32.9 (12.2-41.5)
K (mg kg ⁻¹)	122.1 (117.8-126.8)	79.9 (13.7-153.4)	7.5 (6.2-12.5)
Mg (mg kg ⁻¹)	109.6 (109.3-109.9)	4.2 (0.24-11.5)	0.7 (0.5-1.4)
Mn (mg kg ⁻¹)	111.0 (109.7-112.0)	1.1 (0.68-1.3)	2.1 (1.2-7.6)
Na (mg kg ⁻¹)	116.3 (113.5-118.2)	56.6 (0-126.8)	7.1 (6.2-13.4)
TC (g kg ⁻¹)	104.6 (100.9-110.6)	17.4 (17.4-21.2)	2.85 (0.4-6.0)
TN (g kg ⁻¹)	98.4 (93.2-105.1)	1.5 (1.0-1.7)	4.7 (0.0-8.7)

¹ Element concentrations were determined via ICP-OES, except for TC and TN which were calculated via elemental analysis.

² For ICP-OES, instrumental accuracy was determined through analysis of Merck ICP multi-element standard solution IV at a concentration of 0.25 mg L⁻¹. Accuracy for TC and TN was determined via analysis of 20 mg of a soil reference standard material (0.13 % N, 1.55 % C).

³ Detection limits were determined by ten repeat analyses of a calibration blank (or nine for TC and TN) (Walsh, 1997). Concentrations are provided in mg kg⁻¹ excluding TC and TN which are in g kg⁻¹.

⁴ Precision was determined through duplicate analysis of 10 % of samples on each analytical run (Gill and Ramsey, 1997). Values presented are the median precision (and range).

5.8.6 Model details

Table 5.A.5: Structure of linear mixed-effects models used to investigate the proportion (%) of applied litter $^{13}\text{C}/^{15}\text{N}$ recovered in particulate organic matter ('POM'), mineral-associated organic matter ('MAOM'), and both SOM fractions combined ('Total') in 90 soil samples (0–15 cm layer) taken from paired alley-cropping and sole-cropping systems at five farms ($n = 5$) in England, United Kingdom.

Name	Response variable	Random effects ¹	Fixed effects ^{2,3}	R ² value ⁴	χ^2 , p-value ⁵
A	Total ^{13}C	Transect	S * TP + Soilscape + CN + Mn + pH + BD	R ² _c = 0.60, R ² _m = 0.36	$\chi^2 = 37.32$ p < 0.001
B	Total ^{15}N	Transect	S * TP + CN + Mn + MC_c + pH + Temp	R ² _c = 0.61, R ² _m = 0.28	$\chi^2 = 32.20$ p < 0.001
C	POM- ^{13}C	Transect	S * TP + Manage + Ca + CEC + BD + TN	R ² _c = 0.32, R ² _m = 0.21	$\chi^2 = 18.58$ p = 0.046
D	POM- ^{15}N	Transect	S * TP + Manage + Ca + CEC + CN + Crop_{div} + Mn + BD + TN	R ² _c = 0.53, R ² _m = 0.24	$\chi^2 = 22.39$ p = 0.050
E	s-OM- ^{13}C	Transect	S * TP + Manage	R ² _c = 0.85, R ² _m = 0.36	$\chi^2 = 16.58$ p = 0.011
F	s-OM- ^{15}N	Transect	S * TP + Manage	R ² _c = 0.86, R ² _m = 0.33	$\chi^2 = 14.55$ p = 0.024
G	MAOM- ^{13}C	Transect	S * TP + Manage + Ca + CEC + CN + Crop_{div} + Mn	R ² _c = 0.63, R ² _m = 0.31	$\chi^2 = 35.91$ p < 0.001
H	MAOM- ^{15}N	Transect	S * TP + Manage + Ca + CEC + CN + Mn + TN + Na	R ² _c = 0.66, R ² _m = 0.30	$\chi^2 = 36.21$ p < 0.001
I	POM- $^{13}\text{C}_A$	Transect	S * TP + Soilscape + CEC + CN + BD	R ² _c = 0.83, R ² _m = 0.79	$\chi^2 = 64.93$ p < 0.001
J	POM- $^{15}\text{N}_A$	Transect	S * TP + BD + SOM + Temp	R ² _c = 0.65, R ² _m = 0.59	$\chi^2 = 50.79$ p < 0.001
K	s-OM- $^{13}\text{C}_A$	Transect	S * TP + Soilscape + CEC + Mn + BD + MC_c + Na	R ² _c = 0.96, R ² _m = 0.92	$\chi^2 = 114.4$ p < 0.001
L	s-OM- $^{15}\text{N}_A$	Transect	S * TP + Manage + Mn + BD + K + Na + TN	R ² _c = 0.91, R ² _m = 0.65	$\chi^2 = 52.18$ p < 0.001
M	MAOM- $^{13}\text{C}_A$	Transect	S * TP + Soilscape + Ca + CEC + Mg + Mn + BD + MC_c	R ² _c = 0.92, R ² _m = 0.89	$\chi^2 = 112.4$ p < 0.001
N	MAOM- $^{15}\text{N}_A$	Transect	S * TP + Crop_{div} + Manage + CN + Na + Temp + TN	R ² _c = 0.92, R ² _m = 0.89	$\chi^2 = 110.1$ p < 0.001

¹ Random effect: transect, a 30-level factor indicating the experimental transect.

² Fixed effects are as follows: S = agricultural system, a two-level factor indicating the farming system (alley-cropping or sole-cropping); TP = transect position, a three-level factor indicating distance (m) along the experimental transect (0 m, 3 m, or 13 m); BD = bulk density (g cm^{-3}); Ca = exchangeable calcium concentration (g kg^{-1}); CEC = cation exchange capacity ($\text{meq } 100\text{g}^{-1}$); CN = ratio of total C to total N in soils; crop_{div} = number of crops grown in the period 2021–2024; manage = a two-level factor indicating the agricultural management history (conventional or organic); Mn = exchangeable manganese concentration (mg kg^{-1}); Na = exchangeable sodium concentration (mg kg^{-1}); pH = concentration of H⁺ ions (μmol); TN = total nitrogen content (g kg^{-1}).

³ Models were also used to compare alley-cropping transect positions with the sole-cropping average.

'Agricultural system * transect position' was replaced by 'position_{SCavg}', a four-level factor including three transect positions in alley-cropping and the average across transect positions for each transect in sole-cropping.

⁴ R^2_c = conditional, variation explained by both fixed and random effects; R^2_m = marginal, variation explained by fixed effects, only.

⁵ χ^2 and p-values for final models generated by comparison (ANOVA) with null models containing only random effects; model fit was significantly worse for models C and D.

5.9 Appendix B | Additional results

Contents

- 5.9.1. Relationship between ^{13}C and ^{15}N recovery and soil physicochemical variables
 - Soil CEC, Mn^{2+} , and temporal crop diversity, Figure 5.B.1*
 - Soilscape, Figure 5.B.2*

5.9.1 Relationship between ^{13}C and ^{15}N recovery and soil physicochemical variables

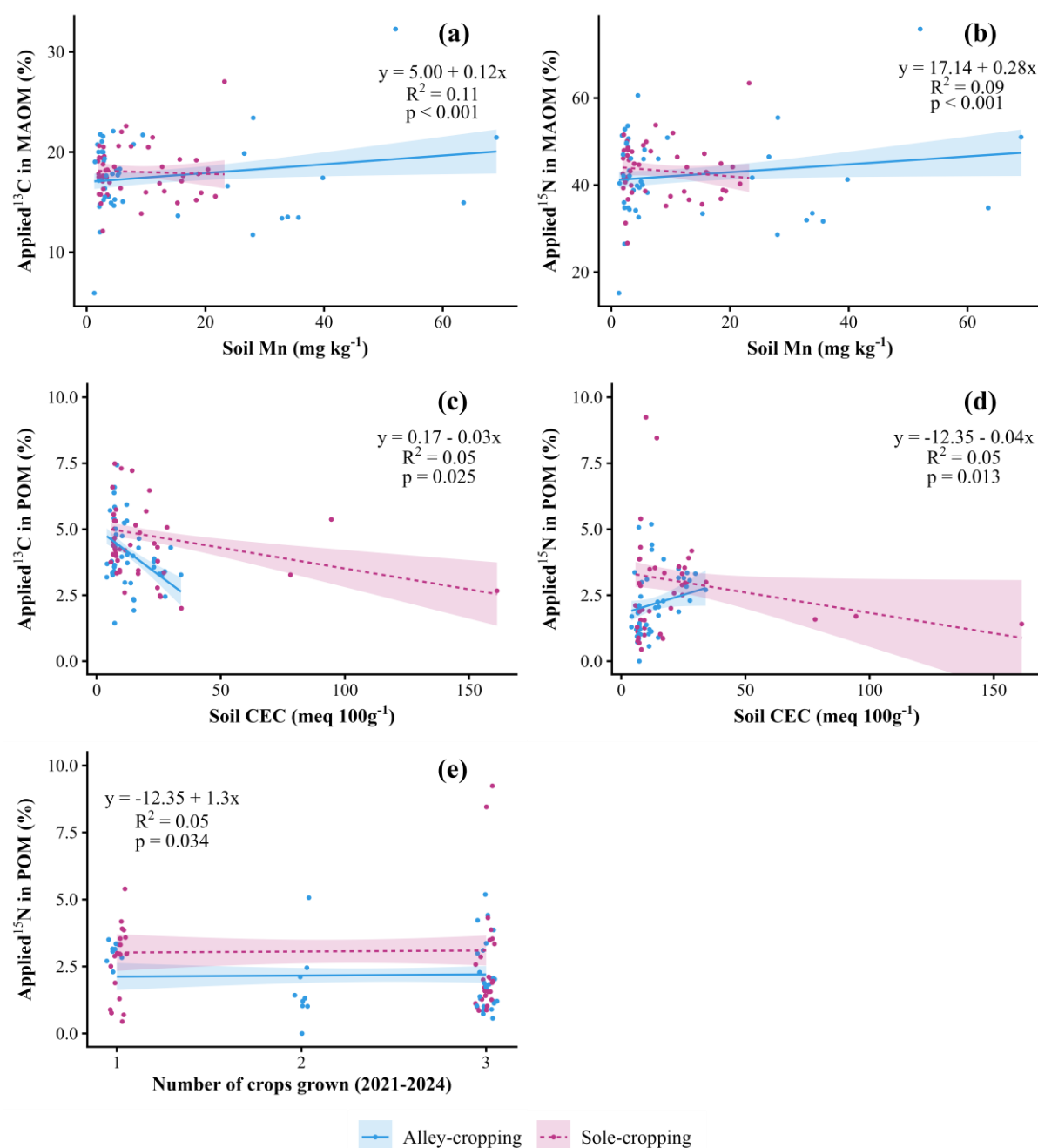


Figure 5.B.1. The relationship between ^{13}C and ^{15}N recovery in SOM fractions and soil physicochemical variables. The proportion (%) of applied ^{13}C and ^{15}N recovered in POM, MAOM or in total as a function of soil Mn^{2+} concentration (mg kg^{-1}) (a–b), CEC ($\text{meq } 100\text{g}^{-1}$) (c–d), and temporal crop diversity (e). Points represent observed values from alley-cropping and sole-cropping systems. Regression lines were estimated using linear mixed-effects models (LMMs) and generated in-plot using the *predict* function of the ‘car’ package (Fox and Weisberg, 2018). with random effects set to zero. Solid blue lines = alley-cropping, dashed red lines = sole-cropping. Shaded areas provide the 95 % confidence interval of the mean. R^2 and p-values were calculated as the change in marginal R^2 and the significance of the change in model fit between LMMs with and without a given fixed effect, respectively.

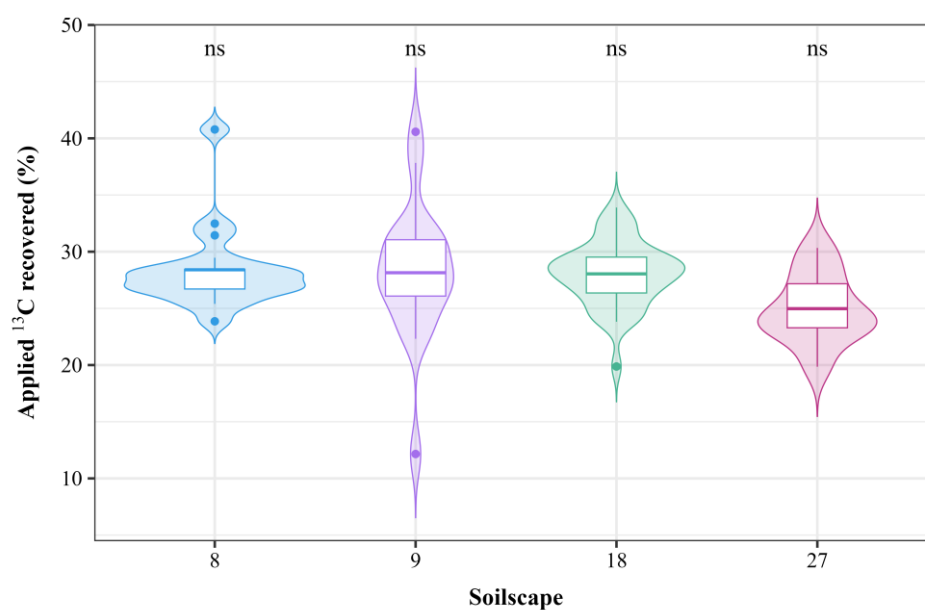


Figure 5.B.2. Applied ¹³C recovered (%) in all SOM fractions combined according to soil type. Soil types were classified into Soilscales according to Cranfield Soil and Agrifood Institute (2025): 8 = “slightly acid loamy and clayey soils with impeded drainage”, 9 = “lime-rich loamy and clayey soils with impeded drainage”, 18 = “slowly permeable, seasonally wet, slightly acid but base-rich loamy and clayey soils”, and 27 = “fen peat soils”. No shared letter indicates a significant pairwise difference at $\alpha = 0.05$, determined from *post hoc* tests of the final linear mixed-effects model with a false discovery rate correction for multiple comparisons.

5.10 Supplementary material A | Additional methodological details

Contents

5.10.1. Incubation plan for isotope tracer experiment

Figure 5.S.1

5.10.1 Isotope tracer experiment incubation plan

Week	Day	Date	S1 09:00	S2 09:50	S3 10:40	S4 11:30	S5 12:20	S6 13:30	S7 14:20	S8 15:10	S9 16:00
1	Tue	25-Jun	C1.SC.1.1	C1.SC.1.2	C1.SC.1.3	C1.AF.1.1	C1.AF.1.2	C1.AF.1.3	N1.AF.1.1	N1.AF.1.2	N1.AF.1.3
	Wed	26-Jun	S1.AF.2.1	S1.AF.2.2	S1.AF.2.3	S1.SC.2.1	S1.SC.2.2	S1.SC.2.3	N1.SC.1.1	N1.SC.1.2	N1.SC.1.3
	Thur	27-Jun	N1.AF.1.1	N1.AF.1.2	N1.AF.1.3	N1.SC.1.1	N1.SC.1.2	N1.SC.1.3	S2.SC.1.1	S2.SC.1.2	S2.SC.1.3
	Fri	28-Jun	S2.SC.1.1	S2.SC.1.2	S2.SC.1.3	S2.AF.1.1	S2.AF.1.2	S2.AF.1.3	S2.AF.1.1	S2.AF.1.2	S2.AF.1.3
2	Mon	01-Jul	C2.AF.3.1	C2.AF.3.2	C2.AF.3.3	C2.SC.3.1	C2.SC.3.2	C2.SC.3.3	C1.SC.1.1	C1.SC.1.2	C1.SC.1.3
	Tue	02-Jul	C2.AF.1.1	C2.AF.1.2	C2.AF.1.3	C2.SC.1.1	C2.SC.1.2	C2.SC.1.3	C1.AF.1.1	C1.AF.1.2	C1.AF.1.3
	Wed	03-Jul	S1.SC.1.1	S1.SC.1.2	S1.SC.1.3	S1.AF.1.1	S1.AF.1.2	S1.AF.1.3	C2.AF.1.1	C2.AF.1.2	C2.AF.1.3
	Thur	04-Jul	S2.AF.3.1	S2.AF.3.2	S2.AF.3.3	S2.SC.3.1	S2.SC.3.2	S2.SC.3.3	C2.SC.1.1	C2.SC.1.2	C2.SC.1.3
	Fri	05-Jul	C1.AF.3.1	C1.AF.3.2	C1.AF.3.3	C1.SC.3.1	C1.SC.3.2	C1.SC.3.3			
3	Mon	08-Jul	N1.SC.3.1	N1.SC.3.2	N1.SC.3.3	N1.AF.3.1	N1.AF.3.2	N1.AF.3.3	S1.SC.1.1	S1.SC.1.2	S1.SC.1.3
	Tue	09-Jul	S1.AF.3.1	S1.AF.3.2	S1.AF.3.3	S1.SC.3.1	S1.SC.3.2	S1.SC.3.3	S1.AF.1.1	S1.AF.1.2	S1.AF.1.3
	Wed	10-Jul	C1.AF.2.1	C1.AF.2.2	C1.AF.2.3	C1.SC.2.1	C1.SC.2.2	C1.SC.2.3	N1.AF.2.1	N1.AF.2.2	N1.AF.2.3
	Thur	11-Jul	N1.SC.2.1	N1.SC.2.2	N1.SC.2.3	S2.AF.2.1	S2.AF.2.2	S2.AF.2.3	S2.SC.2.1	S2.SC.2.2	S2.SC.2.3
	Fri	12-Jul	C2.SC.2.1	C2.SC.2.2	C2.SC.2.3	C2.AF.2.1	C2.AF.2.2	C2.AF.2.3			

Figure 5.S.1. Incubation plan for the isotope tracer experiment outlining the date (day-month) and time (hh:mm) that pre-incubations for each sample began. Sample codes provide information on the farm (N1, C1, C2, S1, or S2), agricultural system ('AF' or 'SC'), transect (1–3), and transect position (1–3) of a given sample. 'AF' = alley-cropping, 'SC' = sole-cropping. Colours indicate which farm the sample was taken from: N1 = yellow, C1 = blue, C2 = pink, S1 = orange, S2 = green. Grey indicates the sample is an experimental standard (no dual-labelled litter added).

5.11 Supplementary material B | Relationship between litter decomposition and POM persistence

5.11.1 Background

Section 5.5.2 discussed the potential confounding influence of controlled laboratory conditions on observed SOM dynamics. To further explore this idea, POM persistence, which acts as a proxy for *Lolium perenne* litter decomposition in Chapter 5, was compared with field-based litter decomposition measured in Chapter 4.

5.11.2 Materials and methods

Spearman correlations were calculated between litter decomposition of soil microorganisms and fauna (Chapter 4) and recovery of ^{13}C and ^{15}N in POM (Chapter 5) using the *cor.test* function of the ‘stats’ package in R (R Core Team, 2025).

5.11.3 Results and interpretation

No correlations were identified between field-based litter decomposition and laboratory-based POM persistence ($p > 0.05$; Figure 5.A.1). This may indicate that controlled laboratory conditions couldn’t replicate field litter decomposition dynamics, or simply reflect differences in litter substrate, sampling timings, and incubation durations.

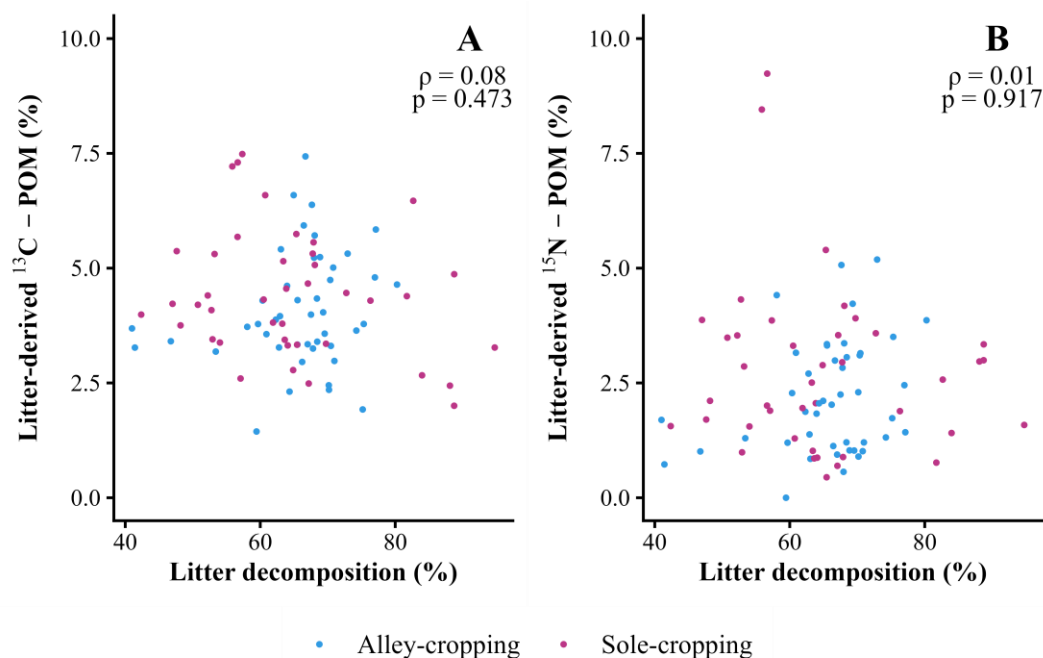


Figure 5.S.2. The relationship between litter decomposition and particulate organic matter persistence. Litter-derived (A) ^{13}C and (B) ^{15}N recovered in particulate organic matter (‘POM’) (%) (Chapter 5) is plotted against litter decomposition (%) (Chapter 5). Points represent observed values in alley-cropping (blue) and sole-cropping (red) systems. Spearman’s rank correlation test ρ and p -values are provided.

6 General discussion

6.1 Introduction

The overarching aim of this thesis was to understand how alley-cropping agroforestry influences soil biodiversity and functioning in temperate croplands. In recent years, temperate alley-cropping systems have received substantial research interest in recognition that they are multifunctional and can simultaneously address issues of climate change, biodiversity loss, and nutrient pollution in agricultural landscapes, whilst supporting financial diversification and rural development. This interest has resulted in major advances in our understanding of how alley-cropping tree rows influence crop productivity (Majaura et al., 2024; Panozzo et al., 2026), soil biodiversity (Beule et al., 2025; Kletty et al., 2023) soil-based ecosystem services (Quinkenstein et al., 2009; Torralba et al., 2016;), and soil properties (Ivezic et al., 2022; Jacobs et al., 2022). However, there remain large gaps in our knowledge regarding the influence of temperate alley-cropping on (i) soil nutrient cycling functions, (ii) soil faunal biodiversity, and (iii) the interaction between the two. To address these knowledge gaps, and thus the aims of this thesis, laboratory and field experiments were carried out to answer the following key research questions:

- 1) Does alley-cropping influence soil meso- and macro-faunal biodiversity?
- 2) Does alley-cropping influence litter decomposition?
- 3) Does alley-cropping influence the decomposition activity of soil meso- and macro-fauna?
- 4) Does alley-cropping influence the persistence and stabilisation of litter-derived organic matter?

This thesis makes several contributions to the field of temperate alley-cropping research: it has (i) examined for the first time how tree rows influence the biodiversity of soil meso- and macro-faunal communities, as opposed to a limited number of taxa; (ii) assessed the validity of applying a low taxonomic resolution indicator based on soil arthropods (i.e., the QBS-ar Index) to assess soil faunal communities within temperate alley-cropping systems; and (iii) quantified the impact of alley-cropping on two key nutrient-cycling processes: litter decomposition and the formation of mineral-associated organic matter. Unlike much existing literature from temperate alley-cropping systems, which often lacks suitable comparisons and controls (Beule et al., 2025; Kletty et al., 2023), the presented experiments compare soil biodiversity and functioning between alley-cropping tree rows, crop alleys, and appropriate sole-cropping

reference systems. Consequently, the presented results provide information on what changes to soil biodiversity, soil physicochemical properties, and nutrient cycling functions can be expected if sole-cropping systems are converted to alley-cropping systems and explores whether these changes are restricted to the tree rows or extend into the crop alley.

The contribution made by each experimental chapter, as well as supplementary analyses, to address the outlined research questions is summarised below. This chapter then goes on to suggest future work related to soil biodiversity and nutrient cycling in temperate alley-cropping systems before bringing together the key findings from each chapter in final conclusions.

6.2 Main findings

6.2.1 Does alley-cropping influence soil meso- and macro-faunal biodiversity?

The significant threat posed to soil fauna, and presumably their associated functions, by intensive agriculture has motivated a number of studies investigating the potential for alley-cropping agroforestry to preserve and enhance soil faunal biodiversity (Beule et al., 2025; Marsden et al., 2020). However, a focus on limited subsets of primarily epigeous and macro-faunal taxa (De Clerck et al., 2025; Kletty et al., 2023; Marsden et al., 2020) has failed to generate clear evidence of alley-cropping's effects on soil faunal communities with which to inform agroforestry policy and management. Extrapolating macrofaunal patterns to other size groups is poorly supported (Wu and Wang, 2019), necessitating further study of neglected groups to better understand how soil faunal communities respond to alley-cropping. Chapter 3 therefore aimed to make a much-needed contribution to this limited evidence base by assessing whether alley-cropping benefits soil meso- and macro-faunal communities, and particularly disturbance-sensitive and uncommon taxa.

Alley-cropping increased soil meso- and macro-faunal abundance, richness, and biological quality relative to sole-cropping. Significant increases in taxonomic richness and SBQ extended 1.5 m into crop alleys (Figures 3.2A–B and 3.3A), while changes in abundance and community composition were restricted to tree rows (Figures 3.2D and 3.3B). Despite the often-variable response of different faunal taxa to alley-cropping (Kletty et al., 2023), tree rows had a broadly positive effect in the current research, with compositional shifts driven by increases in the abundances and incidences of taxa with diverse life-history strategies, functional roles, and levels of disturbance-sensitivity. These findings demonstrate that tree rows can at least partially offset the detrimental effects of intensive management on faunal biodiversity (Tsiafouli et al., 2015; Turbé et al., 2011), both in tree rows and arable crop areas

close to tree rows. These areas of crop alleys can act as islands of biodiversity in otherwise harsh arable landscapes and support landscape-scale biodiversity by enhancing habitat heterogeneity (Santos et al., 2022) and the connectivity of semi-natural features and green infrastructure for mobile taxa (Jurečka et al., 2025). As such, arable alley-cropping systems could make substantial contributions to targets for wildlife-rich habitat creation outlined in England's Environmental Improvement Plan 2025 (Department for Environment, Food & Rural Affairs, 2025a).

Given the importance of soil fauna to key soil functions—including nutrient cycling, carbon transformations, soil structure formation and maintenance, and pest regulation—higher biodiversity in and near tree rows may enhance agroecosystem multifunctionality (Delgado-Baquerizo et al., 2020; dos Santos Nascimento et al., 2025; Schittko et al., 2022). The importance of tree rows for soil functionality can be expected to increase with continued climate change, as both the threats to soil fauna and faunal contributions to ecosystem service delivery become more pronounced (Leal Filho et al., 2023; Phillips et al., 2024; Yang et al., 2021). This is especially true in countries such as the United Kingdom, which may be more vulnerable to declines in ecosystem service delivery associated with biodiversity declines due to its moderate-low estimated soil α diversity (Guerra et al., 2022; Marchal et al., 2026). However, as noted by Marsden et al. (2020), it is often the case that soil faunal studies in agroforestry systems are justified based on the functional importance of soil fauna, without any effort dedicated to measuring soil functions or quantifying biodiversity-function relationship within these systems. Consequently, the remaining two experimental chapters of this thesis were dedicated to investigating how alley-cropping influences key soil functions involved in carbon and nutrient cycling: litter decomposition and organic matter stabilisation.

6.2.2 Does alley-cropping influence litter decomposition and the activity of soil meso- and macro-fauna?

Globally, soil biodiversity research far outweighs that of soil functioning (Guerra et al., 2020), a trend which is also evident in agroforestry research (Marsden et al., 2020). However, interest in litter decomposition dynamics within temperate alley-cropping systems has grown in recent years (Giray et al., 2025; Moran-Rodas et al., 2025; O'Connor et al., 2025; Sutterlütty et al., 2023; Wachendorf et al., 2020), reflecting the need for a greater understanding of the mechanisms driving observed changes in SOM and fertility with which to inform system design and management.

In the second field experiment (Chapter 4), a litter bag assay with a faunal exclusion component investigated the influence of alley-cropping on litter decomposition and the relative contributions of microorganisms versus soil meso- and macro-fauna to litter decomposition. Litter decomposition was significantly higher in alley-cropping compared to sole-cropping systems, both in tree rows and at 1.5 m into crop alleys. Contrary to previous research from temperate alley-cropping systems which reported a negligible impact of tree rows on litter decomposition (Moran-Rodas et al., 2025; Mungai and Motavalli, 2006; O'Connor et al., 2025, Oelbermann et al., 2006; Sutterlütli et al., 2023) or increases in litter decomposition only in tree rows (Giray et al., 2025; Wachendorf et al., 2020), this finding demonstrates that alley-cropping can enhance an important soil function involved in nutrient cycling and carbon transformations in tree rows and adjacent areas of crop alleys. As a result, the efficacy of agronomic practices aimed at enhancing soil carbon sequestration and fertility, such as residue incorporation (Taghizadeh-Toosi et al., 2026), may increase in alley-cropping systems.

Access of soil meso- and macro-fauna to litter bags significantly increased litter decomposition but faunal contributions to litter decomposition were not influenced by alley-cropping. Faunal biodiversity metrics were also not significant predictors of litter decomposition (Table 4A.1), together indicating that it was the activity of soil microorganisms driving changes observed in tree rows and adjacent areas of crop alleys. This is perhaps surprising given that, in Chapter 3, soil meso- and macro-faunal biodiversity were significantly correlated with litter decomposition rates (Figure 4A.1) and, more broadly, faunal biodiversity is known to enhance litter decomposition (de Graaff et al., 2015; Handa et al., 2014). This finding highlights the importance of taxonomic identity and trophic interactions, as opposed to biodiversity *per se*, for soil functioning.

Although Mettauer et al. (2022) previously reported that tree rows had no effect on faunal feeding activity, as measured by bait lamina, the present study is the first to measure the relative contributions of soil fauna versus microorganisms to litter decomposition in alley-cropping systems. Consequently, the current research makes an important contribution to our understanding of the primary pathways through which alley-cropping influences litter decomposition: in this case, microbial activity. Although microbial communities were not characterised at experimental farms due to budgetary constraints, a well-developed body of research has shown that tree rows generate favourable conditions for soil microbial communities, leading to higher biodiversity and activity (Beule et al., 2022b, 2025). This is

known to reduce the relative contribution of soil fauna to litter decomposition (Frouz, 2018; Peguero et al., 2019).

Even a modest increase in litter decomposition of 4.1 % could enhance SOM formation, with positive implications for carbon sequestration and soil fertility. Indeed, the UK's Net Zero Growth Plan (Department for Energy Security and Net Zero, 2023) aims to have agroforestry systems on 10 % of arable land by 2050 for the purpose of carbon sequestration, with litter decomposition forming an important pathway for SOM accumulation in topsoils (Cardinael et al., 2018). Higher litter decomposition rates could be particularly beneficial when combined with agronomic approaches which rely on the decomposition of retained residues and organic matter inputs to manage soil fertility, such as regenerative agriculture (Elevitch et al., 2018). As such, alley-cropping can form part of holistic strategies for sustainable soil management in arable systems, supporting the UK government's goal to have 60 % of England's agricultural soils under sustainable management by 2030 (Department for Environment, Food & Rural Affairs, 2025a). However, whether elevated decomposition rates ultimately support long-term SOM accumulation depends on the decomposition pathway taken. Higher rates of microorganism-mediated litter decomposition could enhance SOM stocks by facilitating the microbial pathway of mineral-association (Cotrufo et al., 2022) or alternatively could lead to higher carbon and nutrient losses via respiration and denitrification (Beule et al., 2022). It is therefore vital to understand the long-term fate of litter-derived carbon and nutrients to effectively inform agroforestry policy and system management.

6.2.3 Does alley-cropping influence the persistence and stabilisation of litter-derived organic matter?

Despite substantial interest in litter decomposition and SOM dynamics within alley-cropping systems, literature which (i) investigates the long-term fate of litter-derived carbon and nutrients (Giray et al., 2025; Wachendorf et al., 2020), or (ii) quantifies the partitioning of SOM into fractions with different persistence times in soils, is limited (Cardinael et al., 2015; Fornara et al., 2018; Wiesmeier et al., 2018). However, it is necessary to consider the stability of newly accumulated SOM, and how management practices will affect its persistence, to accurately assess the climate change adaptation potential of alley-cropping systems and the long-term stability of fertility gains. This was investigated in Chapter 5, which, under controlled laboratory conditions, measured the partitioning of litter-derived carbon and nitrogen into three SOM pools with varying residence times in soils: particulate organic matter (POM), suspended organic matter (s-OM), and mineral-associated organic matter (MAOM).

In this experiment, and contrary to the findings of Chapter 4, alley-cropping had no effect on litter decomposition rates. However, losses of litter-derived carbon and nitrogen from soils, presumably as gaseous emissions, were higher, and rates of mineral-association lower, in tree rows compared to arable crop areas. These findings contrast with those reporting greater carbon and nitrogen accumulation in soils of tree rows relative to arable crop area even when losses are also higher (Giray et al., 2025; Wachendorf et al., 2020). In the current research, higher competition for mineral surface binding sites from existing SOM in tree row soils combined with potential mineral saturation in the sampled agricultural soils (Breure et al., 2025) are a likely explanation for this. These findings suggest that there is a limit to the amount of MAOM which can be stored in established tree row soils at any one time and further substantiate that alley-cropping can drive higher gaseous emission from SOM and incorporated litter where mineral association is reduced (Baah-Acheamfour et al., 2016; Medinski et al., 2015; Peichl et al., 2006; Wotherspoon et al., 2014).

Although alley-cropping did not increase MAOM *formation* from fresh litter in this experiment, this does not necessarily imply reduced MAOM *storage* relative to sole-cropping. Higher initial MAOM-C and -N concentrations in tree rows relative to arable production areas demonstrates that tree rows have a greater capacity for MAOM storage, but the potential for additional MAOM formation is finite and likely limited to younger alley-cropping systems which are not yet enriched with SOM. Consequently, policies aiming to use agroforestry as a tool to increase soil carbon stocks will benefit from prioritising the establishment of new alley-cropping systems using a targeted approach which considers both existing SOM contents and MAOM saturation levels. Furthermore, strategies to increase SOM accumulation within established alley-cropping systems will be more effective if prioritising the protection of POM, which often has a greater potential for accumulation and is also a direct precursor to MAOM (Angst et al., 2023). This would require a greater focus on reduced disturbance, residue retention, and microclimatic stabilisation compared to strategies aiming to increase MAOM (Li et al., 2024a; Samson et al., 2020).

6.2.4 *Through what mechanisms do tree rows influence soil biodiversity and functioning?*

Literature investigating soil biodiversity and functioning within alley-cropping systems, while effective at demonstrating the benefits and trade-offs of tree rows, is often lacking a mechanistic explanation for their effects (Beule et al., 2022). In response to this, the present research begins to disentangle possible mechanistic pathways by including soil physicochemical properties which are both changed and unchanged by the presence of tree

rows in final models. In doing so, this thesis provides novel insight into plant-soil-biodiversity interactions within alley-cropping systems.

Across chapters 3–5, several soil physicochemical properties were identified as significant predictors of soil biodiversity and functioning, but few explained the observed effects of alley-cropping. This may indicate that differences between tree rows are primarily driven by differences in disturbance regimes, vegetation composition, and organic inputs from trees, as previously posited (Beule et al., 2025; Boinot et al., 2019; Pardon et al., 2019). As is the case in many alley-cropping systems, tree rows experienced minimal physical or chemical disturbance, whereas crop alleys were subject to tillage and fertiliser applications to the same extent as sole-cropping fields. While crop alley edges may receive some above- and below-ground inputs from trees, arable crop areas lacked continuous and diverse vegetation, and subsequently a developed litter layer, which could support epigeous and litter-dwelling fauna.

The relationships between soil meso- and macro-faunal biodiversity and soil disturbance regimes and vegetation composition are potentially reflected in the positive relationships between soil faunal biodiversity (abundance and SBQ) and soil K^+ and TN concentrations (Table 3.2), which were both elevated in tree rows compared to arable production areas (Table 3.B.1). Being essential plant nutrients, their relationships with faunal biodiversity were assumed to reflect the positive effects of improved soil structure, resource and habitat availability associated with diverse and continuous UVS (Liu et al., 2023c, 2024b; Mueller et al., 2024; Schwalb et al., 2024). Similarly, that declines in soil pH led to higher rates of faunal-mediated litter decomposition specifically may demonstrate the effect of litter inputs, permanent vegetation, and disturbance regimes, all of which influence soil pH (Fu et al., 2015) on detritivore communities.

These findings underscore the importance of soil chemistry for faunal biodiversity and SOM formation. However, a challenge associated with assessing the impact of soil physicochemical properties on soil biodiversity and functioning through an observational rather than manipulative approach is the presence of bidirectional or cyclical relationships. For example, faunal processing of litter can stimulate rapid leaching in the early stages of decomposition (Frouz, 2018), leading the release of acidifying cations. It may therefore be that higher faunal-mediated litter decomposition in fact directly reduces soil pH, not the other way around. Similarly, litter decomposition, a process mediated by soil fauna, is a major source of soil K^+ and N, potentially reversing the relationship observed between faunal biodiversity and these

nutrients. Although faunal biodiversity had no relationship with litter decomposition rates in the current research, it is possible that these relationships would have emerged if within-litter bag faunal biodiversity had been measured, rather than the biodiversity of ambient soils (Peng et al., 2023). While this discussion is purely speculative, with data lacking to adequately investigate these relationships, it highlights the need to approach these findings with caution and substantiate them in controlled experiments.

6.2.5 Farm-level variation in soil biodiversity and functioning

Farm or the interaction between farm and agricultural system were significant drivers of soil faunal abundance, litter decomposition and MAOM formation, often explaining a large proportion of their observed variation (Table 6.1). These findings indicate that not only did soil properties and processes differ between farms, but so too did their responses to alley-cropping. Farm-level differences in soil faunal biodiversity (Table 3.2) and litter decomposition (Table 4.1) were best explained by a combination of soil type and temporal crop diversity, whereas differences in POM persistence and MAOM formation were associated with agronomic management style (conventional vs. organic) (Table 5.1).

Table 6.1: The influence of farm ('F') and the interaction between farm and agricultural system ('F*S') on measured soil biodiversity, litter decomposition, and SOM dynamics (response variables). Test statistics ('F' or ' χ^2 ')¹ and p-values were determined by ANOVA. R² values indicate the proportion of variation in response variables explained by 'F' or 'F*S' (e.g., 0.29 = 29 %). Degrees of freedom = 90 for all variables excluding 'total litter decomposition', for which df = 180. Analyses were undertaken on reduced models presented in Chapters 3–5 (C3–5), with 'F*S' introduced and farm- and system-level variables removed.

Response variable ¹	² F / χ^2	F p-value	R ²	F / χ^2	F*S p-value	R ²
Biodiversity (C3)						
Abundance	13.06	< 0.001	0.29	2.59	0.001	0.16
Richness	2.33	0.061	0.037	1.51	0.097	0.067
QBS-ar score	1.94	0.108	0.025	1.08	0.389	0.010
Litter decomposition (C4)						
Total	44.91	< 0.001	0.44	2.39	0.002	0.06
Microorganisms	41.36	< 0.001	0.66	1.29	0.220	0.02
Fauna	7.38	0.117	0.08	24.44	0.224	0.13
SOM dynamics (C5)						
¹³ C recovery	7.98	0.092	0.085	38.49	0.008	0.20
¹⁵ N recovery	3.89	0.421	0.00	37.15	0.011	0.13
¹³ C recovery in POM	6.83	0.145	0.084	26.37	0.154	0.12
¹⁵ N recovery in POM	15.18	0.004	0.22	30.81	0.058	0.075
¹³ C recovery in MAOM	9.85	0.043	0.097	34.37	0.024	0.13
¹⁵ N recovery in MAOM	9.91	0.042	0.089	33.88	0.027	0.11

¹ See Chapters 3, 4, and 5 for descriptions of response variables.

² F or Wald chi-squared tests, depending on whether the input models contained random effects.

Soil type is a well-established determinant of soil biodiversity and functioning because it integrates physical, chemical, biological, and hydrological properties of soils shaped by local

pedo-climatic conditions (Chassain et al., 2021; Lavelle et al., 2022; Peng et al., 2022b). For example, differences in SOM content, temperature, moisture content, bulk density, and nutrient concentrations between soil types driven by localised pedo-climatic contexts and land-use histories likely explain some of the observed differences in soil biodiversity and function in the current research. Furthermore, soil types with impeded drainage and periodic waterlogging (i.e., Soilscape 8) reduced faunal biodiversity and litter decomposition, potentially due to associated impacts on soil structure and oxygen availability (Carlesso et al., 2019; Li et al., 2002; Liu et al., 2023a; Xu et al., 2021).

Higher temporal crop diversity (the number of major crops grown between 2021–2024) was associated with reduced faunal biodiversity and litter decomposition, presumably reflecting more frequent soil disturbance (Domnariu et al., 2025; Yu et al., 2025; Struijk et al., 2026). However, increases in faunal abundance with temporal crop diversity may reflect positive effects of disturbance where it alleviates drainage or compaction, or may instead be driven by proliferation of disturbance-tolerant, highly-abundant taxa.

Organic management increased ^{13}C and ^{15}N recovery in MAOM relative to recently conventional management, potentially by promoting microbial biodiversity and thus the microbial pathway of MAOM formation (Hartmann et al., 2015; Lori et al., 2017), increasing MAOM turnover (Mayer et al., 2023), or improving soil structure and aggregation (Karami et al., 2012; Tian et al., 2022) for better protection of newly formed MAOM (Even and Cotrufo, 2024). However, because only one farm in this study had a recent history of conventional management (prior to conversion to organic management in September 2023), this finding, which should be interpreted as preliminary, better reflects the legacy effects of conventional management.

The strong influence of farm-level properties on faunal biodiversity and nutrient cycling functions reflects the diversity of environmental and management settings in which alley-cropping is implemented. They also reinforce the importance of (i) land managers evaluating whether alley-cropping will support them in meeting their objectives within their farm's unique environmental context prior to establishment, and (ii) the development of tools which provide evidence-informed guidance on where establishment of alley-cropping systems can deliver soil benefits, now and in the future.

6.3 Research limitations

The findings presented in Chapters 3–5 provide novel insights into the influence of alley-cropping and soil physicochemical properties on soil meso- and macro-faunal biodiversity, litter decomposition, and SOM dynamics within temperate arable systems. However, interpretation and generalisation of these findings require consideration of the limitations of the presented research. Limitations relating to the experimental design and methodology applied in this thesis are discussed below.

6.3.1 *Experimental design*

6.3.1.1 *Sample size & replication*

Across this thesis, the small scale of experiments represents a key limitation. The number of samples included (90) is modest for investigations of soil biodiversity and functioning in agroecosystems (Minarsch et al., 2024; Welsch et al., 2019), despite being comparable to previous multi-site alley-cropping studies (Cardinael et al., 2017; Pardon et al., 2019; Wachendorf et al., 2020). Both soils and alley-cropping systems exhibit substantial spatial and temporal heterogeneity, generating variability that requires large sampling effort to capture reliably. This variability was evident for soil biodiversity (3.2–3) and litter decomposition (Figure 4.2). Small sample sizes and limited replication (e.g., five true replicates in the current research) may have therefore increased uncertainty in regression estimates, reducing statistical power and increasing the likelihood of type II errors (i.e., false negatives) (Gelman and Hill, 2006; Stamps and Linit, 1999). For this reason, a false discovery rate correction was applied to pairwise comparisons (Benjamini and Hochberg, 1995; Pike, 2011).

Small sample sizes also present statistical challenges for mixed-effects modelling. Combined with limited replication across hierarchical levels, models with small sample sizes risk (i) overparameterisation and unreliable variance estimates (Kéry & Royle, 2015), and (ii) unreliable estimation of random effects (Bolker et al., 2009; Harrison et al., 2018; Gomes, 2022) and limited generalisability of group-level inferences (Gelman & Hill, 2006; Schielzeth & Nakagawa, 2013). While five levels has been deemed adequate to begin estimating random effect variance (Bolker et al., 2009; Gomes, 2022; Harrison et al., 2018), > 10 levels is recommended to robustly estimate between-group variances (i.e., between farms or transects in the current research) and avoid underestimation of fixed effect standard errors (Schielzeth and Nakagawa, 2013; Gelman and Hill, 2006) and type I errors (Harrison et al., 2018). Furthermore, only random intercepts were fitted due to sample size constraints, although

random slopes would have been informative regarding farm-specific responses to alley-cropping.

Steps were taken to ensure that final models had an appropriate level of complexity for the available data. Model fits were compared with and without random effects, tested for overfitting using LOGO-CV, and, where appropriate, random effects were substituted for fixed effects which could explain the same variation (e.g., a combination of soil type, temporal crop diversity, and/or agronomic management style replaced ‘farm’ in all models) to reduce model complexity. However, a larger sample size and/or level of replication would have increased the confidence of model estimates and the power to identify significant differences between transect positions in alley-cropping and sole-cropping systems. Expanded sampling would also have enabled more advanced analyses to explore the indirect pathways through which alley-cropping exerts influence (e.g., Luo et al., 2024), such as via changes to soil physicochemical properties, and facilitated investigation of farm-scale moderators of soil biodiversity and nutrient cycling functions.

6.3.1.2 Temporal replication

Adequate replication also needs to extend across time. Soil communities are dynamic, responding to soil management cycles (Shao et al., 2022), seasonal dynamics (including those of alley-cropping trees) and, for some taxa, developmental cycles. Consequently, the responses of soil biota (D’Hervilly et al., 2022; Marsden et al., 2020; Mungai et al., 2005; Veldkamp et al., 2023) and associated soil processes (Battie-Laclau et al., 2020; Beaudette et al., 2010; Wolz et al., 2018a) to alley-cropping will also vary over time alongside changes in (i) their dependence on tree rows for habitat and resources, and (ii) the influence of tree rows on soil microclimates and resource availability (D’Hervilly et al., 2022, 2024). Capturing these dynamics therefore requires sufficient temporal replication.

Temporal dynamics were not examined in Chapters 3–5 due to multiple practical limitations. First, sampling across all seasons, preferably over multiple years would have been needed to sufficiently capture temporal trends in alley-cropping’s effects. Processing the required number of samples whilst maintaining the same experimental design, deemed the most appropriate for addressing the outlined research questions and hypotheses, would not have been feasible with the available resources and within the timeframe of the project. Second, taking intact cores from heavy clay soils in summer and winter would have required the use of equipment, specifically an automatic soil corer, which was not available. The findings presented in Chapters 3–5 therefore represent only a temporal snapshot. Soil meso- and macro-faunal

biodiversity and nutrient cycling functions are likely to exhibit differing responses to alley-cropping throughout and between years, and these temporal dynamics require further investigation.

6.3.2 Suitability of methods

6.3.2.1 Taxonomic resolution

In Chapter 3, soil meso- and macro-fauna were identified to taxonomic orders, a common level of precision in soil faunal biodiversity research due to limitations in taxonomic expertise, time, and funding (Gongalsky, 2021). Even though higher-resolution identifications were likely better positioned to capture β diversity patterns and the significance of treatment effects (Birkhofer et al., 2017; Timms et al., 2013), a coarse taxonomic resolution proved sufficient to detect differences in faunal biodiversity between tree rows and arable crop areas, as well as between the edge of crop alleys and sole-cropping systems. As such, it appears that comparisons of coarse taxonomic information could capture the effects of subtler environmental gradients (i.e., soil microclimates and physicochemical properties) introduced by tree rows in crop alleys on soil faunal biodiversity. Despite this, because soils are commonly dominated by the same mega-diverse faunal taxa (Coyle et al., 2017; George et al., 2017), a finer taxonomic resolution may have revealed clearer and more detailed shifts in α - and β -diversity in response to alley-cropping, particularly in crop alleys (Timms et al., 2013; Zhang et al., 2025)

Finer resolution information may also have facilitated investigations of soil biodiversity-function relationships in the studied agroecosystems. Using the litter decomposition experiment presented in Chapter 4 as an example, no significant relationships were identified between soil meso- and macro-faunal biodiversity and litter decomposition (Chapter 6, Section 6.2.2). However, Burtis et al. (2024) reported that soil fauna extracted from the leaf litter residue in temperate forest ecosystems were predominantly Acari and Collembola, which would have been present at most, if not all, sampling points in the current research. More precise biodiversity estimates for these major faunal taxa, through finer-resolution identifications, could have revealed relationships with litter decomposition which were not evident when considering coarse-resolution estimates based on faunal communities. Finer resolution (e.g., species- or genus-level) information on soil fauna would also have allowed for their categorisation into functional groups, the analysis of which is increasingly recognised for its ability to identify changes in the composition of multi-trophic, highly interactive soil networks and associated ecosystem processes (Marsden et al., 2020; Tsiafouli et al., 2015).

6.3.2.2 *Survey methods*

Hand-sorting and Berlese-Tullgren funnels are widely used to assess soil meso- and macro-faunal communities. However, these techniques are less suitable for highly mobile and/or predominantly surface-dwelling soil fauna, which are better characterised using repeated pitfall sampling and emergence traps (Boinot et al., 2020; Matevski et al., 2024; Pardon et al., 2019). Moreover, below-ground pitfall traps have been shown to recover a higher abundance and diversity of springtails and larger meso-faunal taxa than Berlese-Tullgren funnels (Fioratti Junod et al., 2023). Thus, a combination of complementary methods to assess soil fauna which included surface pitfall traps, Berlese-Tullgren funnels, and potentially emergence and below-ground pitfall traps, would have generated a more complete picture of soil faunal communities in alley-cropping and sole-cropping systems in the current research.

In Chapter 4, the field litter decomposition experiment ran for 16 weeks. Although 16 weeks is within the range reported for comparable studies (Chassain et al., 2021; Xie, 2020), it falls at the shorter end. Medium- to long-term litter experiments (i.e., > one year) with multiple retrieval points capture a larger portion of the decomposition continuum, particularly for recalcitrant substrates with lower decomposition rates. This is particularly important when assessing the contribution of soil fauna to litter decomposition, which increases with time (Njoroge et al., 2022) as conditions for microbial decomposition become less favourable (Frouz, 2018; Peguero et al., 2019). The relatively modest faunal contribution to litter decomposition observed in Chapter 4 may therefore reflect the short incubation period (Xie, 2020).

As discussed in Section 6.3.1, a longer incubation period would also have better encompassed seasonal climatic variability. In the current research, litter bags were buried in early November to align with both deciduous tree litterfall and soil preparation for planting of winter cereals, with observed litter decomposition dynamics thus more reflective of those for alley-cropping litter or retained crop residues. However, the 16-week duration allowed comparisons of litter decomposition dynamics primarily in winter and to a lesser extent autumn and spring, but not summer. This constrains interpretation of seasonal differences in decomposition processes and the extent to which tree rows may buffer climatic limitations such as low temperature or moisture deficits.

6.3.2.3 *Laboratory-based experiments*

Finally, the limitations of laboratory investigations of soil processes, and the relevance of findings from these investigations to field conditions, have been discussed in Chapter 4

(Section 5.4.1). In Chapter 5, alley-cropping had no discernible effect on litter-derived ^{13}C and ^{15}N recovery in POM (Figure 5.1), contradicting findings from Chapter 4 that alley-cropping stimulated litter decomposition. A key distinction between the experiments conducted in Chapters 4 and 5 is methodological: the isotope tracer experiment in Chapter 5 was conducted under controlled laboratory conditions, which likely disrupted soil biotic communities, excluded soil fauna which contribute to SOM transformation processes (Soong and Nielsen, 2016), and altered soil physicochemical properties such as structure, moisture content and temperature which are known to regulate decomposition activities (Carlesso et al., 2019; Tan et al., 2021). For example, mixing labelled litter into samples appeared to disrupt the structure of those with a more clay-dominant texture, breaking down soil macroaggregates and possibly altering decomposition processes. Thus, results of the field-based litter decomposition experiment in Chapter 4 are likely to better represent litter decomposition dynamics in situ.

6.4 Future research

The experimental work presented in this thesis has generated a number of recommendations for future research in temperate alley-cropping systems.

Section 3.1 highlights the importance of characterising whole soil faunal communities when evaluating the effects of alley-cropping on soil biodiversity. This principle extends to the broader soil biota. Although soil microbes and, to a lesser extent, macro-fauna have received considerable attention in temperate alley-cropping research (Beule et al., 2022b; Kletty et al., 2023), many important taxa have been neglected, including soil meso- and micro-fauna, archaea, and protists (Beule et al., 2025; Kletty et al., 2023; Marsden et al., 2020). Furthermore, due to practical constraints, very few studies characterise the full soil food web rather than a limited suite of taxa or size classes. Addressing these gaps should be a priority for future research if we are to understand how alley-cropping shapes soils trophic networks and associated functions. Integrating classical morphological methods with molecular approaches within the same experimental framework would enable more complete characterisation of below-ground communities. As discussed in Section 6.3.2, fine-resolution identifications would also improve understanding of taxonomic and functional diversity, functional redundancy, and soil food-web resilience in alley-cropping systems (Bardgett & van der Putten, 2014; Thiele-Bruhn et al., 2020; Griffiths and Philippot, 2013), thereby advancing interpretation of biodiversity-function relationships (Fierer et al., 2021; de Vries et al., 2013).

Interactions between alley-cropping tree rows, soil biota, and functions are often assumed rather than empirically quantified in alley-cropping studies (Marsden et al., 2020), and this thesis is no exception. While the effects of alley-cropping on litter decomposition and SOM dynamics were interpreted with reference to expected shifts in soil communities, the contribution of soil biota to measured soil functions was only quantified in Chapter 4. This reflects the inherent difficulty of quantifying soil fauna effects on nutrient cycling, which are often indirect, as well as the time and financial constraints associated with measuring both soil biodiversity and associated functions. That said, where possible, coordinated sampling of soil biota and functions in time and space would greatly improve our understanding of soil biodiversity-function relationships (Guerra et al., 2020; Marsden et al., 2020), as would the use of field-based isotopic and manipulative approaches capable of isolating the contributions of soil biota to functions of interest.

Sections 5.4.1 and 6.2.3 emphasise the need for further field-based research investigating MAOM formation dynamics within temperate alley-cropping systems to validate the findings generated under controlled conditions in Chapter 5. More broadly, coupling stable isotope techniques with field-based experiments should become more routine when investigating soil processes which are difficult to observe *in situ*. Although associated with higher costs (Ghaley et al., 2014a), isotopic approaches provide mechanistic insight into C and N cycling that cannot be achieved with traditional methods alone. As demonstrated in Chapters 4 and 5, a conventional litter bag approach proved sufficient to quantify litter decomposition rates, but isotope tracing was required to assess the fate of decomposition products and the influence of alley-cropping across a larger portion of the overall decomposition process (Wachendorf et al., 2020). Stable-isotope approaches, whether enriched or natural abundance, could also be applied to investigate a wider suite of soil C and nutrient-cycling functions and their relationships with soil biota (Klink et al., 2022). For instance, this thesis focussed on litter decomposition and SOM stabilisation in topsoils, but future research of C and nutrient cycling dynamics in alley-cropping systems would benefit from targeted studies of less-explored processes such as root exudation, SOM mineralisation, and aggregate formation at multiple soil depths.

Finally, this thesis sought to address several methodological limitations identified in previous alley-cropping literature. Across all experiments (i) appropriate sole-cropping controls were included, (ii) soil variables were measured in tree rows and multiple positions in crop alleys, and (iii) statistical approaches suitable for nested, hierarchical data typical of alley-cropping

studies were employed. Alongside these recommendations, future alley-cropping studies should aim to (iv) select a sufficient sample size and level of replication to address their research questions, based upon evidence (i.e., results of a power analysis) where possible, and (v) include sufficient temporal replication to capture seasonal and inter-annual variability, especially given increasing climate variability and extreme events.

6.5 *Conclusions*

Alley-cropping tree rows increased soil meso- and macro-faunal abundance, richness, and biological quality relative to sole-cropping. Shifts in faunal composition revealed that tree rows provided vital habitat for taxa reliant on litter layers, above-ground vegetation, and low-disturbance conditions. Although biodiversity gains did not extend to the centre of crop alleys, significant increases in taxonomic richness and biological quality were observed at 1.5 m into the crop alley, presumably due to spill-over from tree rows, but not in the crop alley centre.

Alley-cropping increased litter decomposition increased by 4.1 % relative to sole-cropping systems. Increases were not uniform across alley-cropping fields; compared to sole-cropping, litter decomposition was significantly increased in tree rows and at 1.5 m into the crop alley, but not in the crop alley centre. Soil meso- and macro-fauna increased litter decomposition by 4.8 % but, despite observed increases in faunal diversity and detritivore abundance in alley-cropping tree rows, faunal decomposition activity was unaffected by alley-cropping. Increases in soil CEC promoted litter decomposition, possibly by ensuring a consistent supply of nutrients to decomposer communities.

Alley-cropping had little to no effect on POM persistence and MAOM formation relative to sole-cropping under controlled laboratory conditions. However, recovery of litter-derived ^{13}C and ^{15}N was significantly reduced in alley-cropping tree rows compared to 1.5 m into the crop alley and the 13 m transect position in sole-cropping, suggesting greater losses SOM losses by microbial respiration. Soil C:N ratio and exchangeable Mn concentration positively influenced POM persistence and MAOM formation, potentially by suppressing microbial decomposition or increasing the availability of mineral binding sites for litter-derived organic matter in the form of Mn-oxides, respectively.

Overall, these results suggest that relative to sole-cropping, alley-cropping can increase soil meso- and macro-faunal biodiversity, with tree rows acting as important habitat islands across otherwise harsh and homogenous arable fields. The beneficial effects of alley-cropping on soil biodiversity increased biotically mediated C and nutrient cycling functions, such as litter

decomposition. However, greater litter decomposition in alley-cropping systems did not increased litter-derived organic matter stabilisation within MAOM, instead resulting in more C and N losses from tree rows. This may be because higher SOM in mature tree rows reduced mineral surface availability for MAOM formation. Together, these findings indicate that SOM increases in temperate alley-cropping systems are likely the result of more organic inputs to soils, rather than increases in SOM formation rates or stability. Further research is needed to confirm the generalisability of these findings to other alley-cropping systems and, considering SOM dynamics, under field conditions, as well as explore in more detail the role of soil chemistry in decomposition dynamics within temperate alley-cropping systems.

6.6 References

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