



The impact of decomposer size classes and litter quality on litter decomposition in food forests

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Received: 5 June 2025 / Accepted: 14 August 2025 / Published online: 6 September 2025
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Abstract Food forests are perennial, multi-layered food production systems gaining popularity as alternatives to intensive, input-dependent agriculture. With limited use of external inputs, these systems rely on nutrient recycling via litter decomposition for plant nutrient supply. However, little is known about decomposition dynamics during food forest development. We studied how litter of *Alnus glutinosa* (L.) Gaertn. (black alder), *Corylus avellana* (L.) (common hazel) and *Castanea sativa* Mill. (sweet chestnut) (high to low litter quality) was decomposed in food forests planted on grasslands versus neighboring

grasslands. Using litter bags with varying mesh sizes, we assessed the relative contribution of microbes, micro-, meso- and macrofauna on short-term litter mass loss. We also quantified abundance and/or biomass of key decomposer groups. Decomposer communities differed between the land use types, with food forests harboring a higher abundance of oribatid mites, but a lower abundance and biomass of earthworms and lower biomass of arbuscular mycorrhizal fungi than grasslands. We found little differences in litter mass loss between the systems, except for a higher mass loss of high-quality litter in grasslands when the litter was accessible to the entire decomposer community. The lowest-quality (sweet chestnut) litter decomposed slowest and decomposition rates were neither impacted by mesh size nor land use. Overall, high-quality leaf litter generally decomposed faster in grasslands than food forests and the different decomposer communities in young food forests did not favor the breakdown of (recalcitrant) litter. Future research could explore the potential implications of these findings for plant nutrient provisioning in self-sustaining agroecosystems.

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Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10457-025-01299-1>.

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Keywords Food forests · Agroforestry · Decomposition · Litter quality · Decomposer community · Carbon and nutrient cycling

Introduction

Intensive agriculture, characterized by high nutrient inputs and herbicide and pesticide use, has led to global deterioration of soil quality and a decline in soil biodiversity (Bardgett and van der Putten 2014; Tsiafouli et al. 2015). This has resulted in losses of carbon and nutrients from the soil to the environment via greenhouse gas emissions and leaching (Poeplau and Don 2015), thereby contributing to (among others) climate change and eutrophication of aquatic systems (Rockström et al. 2020). Food forests, as an alternative food production system, have the potential to limit these negative environmental impacts of agriculture. These systems that are designed to mimic natural forests are generally managed with limited external inputs of nutrients because it is expected that the presence of plants with high-quality litter and a diversity of microbial symbionts suffices to ensure plant productivity (Crawford 2010; Magnoli and Bever 2023). As a result, plant nutrient supply in food forests is largely dependent on the decomposition of plant litter by the soil community (García-Palacios et al. 2016). However, how litter decomposes in food forest systems is almost fully unknown.

In temperate climates, food forests are often planted on former arable land or managed grasslands and food forest development is expected to follow the trajectory of secondary succession of a (natural) forest, both above- and belowground (Crawford 2010). During food forest development, the inputs of plant litter will change, with an increase in the diversity of litter inputs due to the high planted diversity (Moereels et al. 2024) and decrease in chemical litter quality as tree litters often have more recalcitrant chemical compounds than grasses or forbs (Cornwell et al. 2008; Zhou et al. 2020). Simultaneously, we expect that in food forests, similar to what happens during the succession in many other ecosystems, soil communities will develop towards communities with a more diverse and complex soil food web, with higher fungal biomass and activity and a higher abundance of larger soil organisms prone to soil disturbances (de Groot et al. 2016; Morriën et al. 2017; Zhou et al. 2017). Following the functional breadth hypothesis, we expect that due to the increasing inputs of more complex litter inputs, soil communities in food forests will develop the capacity to degrade a wider range of organic compounds than communities in the grass- or

croplands they were planted on (Keiser et al. 2011, 2014).

Within the decomposer community, fungi, bacteria and archaea act as the primary decomposers because they mineralize organic compounds. Yet, larger detritivores, such as microarthropods, isopods and earthworms, are vital as they break down litter into smaller pieces or convert it into feces and hereby enhance the accessibility of the organic structures to microbes (García-Palacios et al. 2013; Joly et al. 2020). Moreover, soil fauna can also indirectly influence decomposition by altering the microbial habitat and consuming microbes (Cragg and Bardgett 2001). As the abundance of larger soil fauna and fungi may increase during successional development of food forests (de Groot et al. 2016; Zhou et al. 2017), the breakdown of litter can therefore be expected to increase during food forest development as well. Still, how the different size classes of the soil community affect the decomposition of litter types of varying chemical qualities has not yet been studied in food forests.

The aim of our research was to understand how different soil community size classes affect short-term breakdown of tree leaf litter of varying quality in food forests in comparison to grasslands (previous land use). We specifically hypothesized: (1) that litter decomposition rates, measured as litter mass loss, are higher in food forests than grasslands, especially for low quality litter, because decomposer communities have adapted to a broad range of litter qualities, and (2) that this difference in decomposition rate is larger when larger organisms (medium and coarse mesh sizes) have access to litter, as we expect abundances of these organisms to be higher in food forests than grasslands. A better understanding of the role of the soil community in litter decomposition can help the development of agricultural systems less dependent on external inputs, which will help minimizing negative impacts of agriculture on surrounding ecosystems.

Methodology

Study sites

The study was carried out in four paired food forests and grasslands in the Netherlands. The Netherlands has a temperate oceanic climate with mean annual

rainfall of 875 mm and a mean annual temperature of 11.7 °C in 2022 (CBS et al. 2023a, b). Three of the food forest-grassland pairs were established on clay soils (location 1 on river clay and location 2 and 4 on marine clay) and one on sandy soil (location 3). All food forests were established on previous grasslands and between five to eight years old during sampling in 2021 (Fig. 1; example of paired study sites). The size of the food forests ranged between 0.3 and 1.75 hectares. Grassland study sites were permanent, agricultural grasslands with extensive management and limited external inputs, and sampling area was the same size as the food forests. All food forest and grassland sites were divided into six even sized subsites. In those subsites, random coordinates were generated as locations for plots to bury the litter bags and collect soils samples for measurements of abiotic and biotic soil properties, using the *spcosa* package V0.3.11 (Walvoort et al. 2010) in R Statistical software V4.0.0.

Abiotic and biotic soil properties

In each plot, we collected soil samples to study soil abiotic and biotic properties as background variables for understanding differences between the selected food forests and paired grasslands. We measured abiotic soil properties (bulk density, soil moisture, pH, electrical conductivity, soil organic matter, total P, Olsen P, total C and total N) and quantities of some key groups of decomposer organisms, i.e., bacterial and fungal biomass and abundance of springtails, mites and earthworms (see online Appendix A1 for detailed information on soil sampling and analyses).

Litter quality

For the litter bag experiment, approximately 1 kg of standing dead leaf litter from *Alnus glutinosa* (L.) Gaertn. (black alder), *Corylus avellana* L. (common hazel) and *Castanea sativa* Mill. (sweet chestnut) trees was collected on 4 October 2021 in Ede, the Netherlands. These species are common in the Netherlands, both in natural forests and food forests. We collected litter from a standard location, unrelated to our experimental sites, in order to avoid potential home-field advantage effects (Veen et al., 2019). The litter types were chosen to represent a gradient in litter quality (based on C:N ratio and lignin content) (Anderson 1973; Howard and Howard 1974; Chauvet 1987; Sarilidiz 2003; Jílková et al. 2020; Bonanomi et al. 2021).

To verify the expected gradient in litter quality, the quality of the three collected litter species was measured as total carbon (C), nitrogen (N) and lignin content on ground (QIAGEN TissueLyser II) subsamples, consisting of collected leaf litter that was oven-dried at 60 °C. C:N was measured on 10 subsamples with an ElementAnalyser (Flash EA 1112, Thermo Scientific). Lignin content was determined on three (black alder and common hazel) and two (sweet chestnut) subsamples of 250 mg. First, subsamples were extracted with demi water, 99.9% methanol and 99.8% chloroform. Then, subsamples were hydrolyzed using 3 M 37% hydrochloric acid. After additional extraction cycles with again demi water, methanol and chloroform, the residues were analyzed for C and N content and ashed (2 h at 200 °C, 6 h at 550 °C) to calculate lignin content (Poorter and Villar 1997). We statistically compared these aspects



Fig. 1 Images of one of the paired food forest and grassland sites as an example of the study systems

of litter quality between the three litter types. The approach and results of this analysis are given in online Appendix A4.

Litter bag experiment

Collected litter was air-dried for three days before assembling litter bags, of which a subset was oven-dried to determine air-dry to oven-dry conversion rates. We made three types of nylon-mesh litter bags (5×10 cm): (1) fine mesh (100 µm), (2) medium mesh (1 mm), (3) and coarse mesh (1 mm+some 5 mm holes made by using a paper puncher) to allow for the access of (1) microorganisms and microfauna, (2) microorganisms, micro- and mesofauna and (3) microorganisms, micro-, meso- and macrofauna, i.e., the entire decomposer community. The litter bags were filled with 1–3 pre-weighed leaves (mean weight 0.68 g, range from 0.30–1.57 g) each and were closed using a glue gun and stapler. Litter bags were placed in four of the six plots used for measuring abiotic and biotic soil properties (online Appendix A1). In total, 288 (9 litter bags with 3 mesh sizes and 3 litter qualities×4 plots×8 study sites) litter bags were buried in October 2021, at 5 cm depth to prevent photodegradation (Wang et al. 2021).

Litter bags were collected after 58–61 days in the field (in December 2021). Litter bags were opened, plant roots were removed and the remaining material, including litter and attached soil particles, was oven-dried at 70 °C and weighed. Afterwards, litter bag content (litter and soil particles) was ashed at 550 °C for 4.5 h in order to determine mineral soil weight. Initial litter mass was corrected for air-dry to oven-dry ratio, and final litter mass was corrected for mineral soil weight. Then, the proportion of litter mass loss was calculated by dividing final mass over initial mass, subtracting that from 1. Some litter bags were not retrieved, were broken or had negative litter mass loss values and were excluded from the analysis (online Appendix Table A2.1).

Statistical analyses

All data was analyzed using R Statistical Software (V4.4.1) (R Core Team 2024). We used visual inspection of simulated residuals using the *DHARMa* package (V0.4.6) (Hartig 2022) to check for normality and homogeneity of variances. For all models, we did a

post-hoc test using *emmeans* (V1.10.3) (Lenth 2025) to test for pairwise differences between groups with Tukey-adjusted p-values (with alpha at 0.05) and Sidak-adjusted confidence intervals.

To evaluate how abiotic and biotic soil properties differed between food forests and grasslands, we used a linear mixed model with land use as a fixed and location as a random factor (type III SS, Satterthwaite's method) with package *lmerTest* (V3.1.3) (Kuznetsova et al. 2017). Electrical conductivity, total and available P, total C and N and bacterial, AM fungal and non-AM fungal biomass were log-transformed and count data of mites were square-root-transformed prior to analyses. In addition, we visually examined the differences in the soil abiotic and biotic properties between the two land use types and four locations using a Principal Component Analysis (PCA) on the three samples per site (for which all the abiotic and biotic data was collected) with the *stats* (V4.4.1) and *factoextra* (V1.0.7) packages (Kassambara and Mundt 2020). A PERMANOVA using *adonis2* from package *vegan* (V2.6.6.1) with 999 permutations was done to test for the effects of land use and location on these soil properties (Oksanen et al. 2024).

To evaluate the influence of land use, litter type and mesh size on litter mass loss, we used a linear mixed model using *glmmTMB* (V1.1.9) (Brooks et al. 2017), with a three-way interaction type III Wald chi-square test using the *car* package (V3.1.2) (Fox and Weisberg 2018). Land use, litter type, mesh size and all their interactions were used as fixed factors, location as a random factor and litter type as additional dispersion factor to better model the data.

Results

Abiotic and biotic soil properties

Food forests and grasslands differed in both their abiotic and biotic soil properties (online Appendix A3). Food forests had higher soil moisture and soil organic matter content and lower bulk density and electrical conductivity than grasslands (online Appendix Table A3.1). In addition, we found a higher abundance of oribatid mites in food forests than grasslands (on average more than 3 times higher), but a lower abundance and biomass of earthworms (on average more than 2 and 5 times lower respectively) and

lower biomass of arbuscular mycorrhizal (AM) fungi (on average almost 2 times lower) in food forests than grasslands (online Appendix Table A3.1). pH, nutrient concentrations (C, N, P, Olsen-P), bacterial and non-AM fungal biomass and the abundance of spring-tails and mesostigmatic and prostigmatic mites did not differ between grasslands and food forests (online Appendix Table A3.1).

Litter mass loss

Litter mass loss was affected by a three-way interaction between land use, litter quality and mesh size (Table 1) with lower litter mass loss in food forests than grasslands for black alder in coarse mesh size litter bags only ($df=236$, $t\text{-ratio}=4.39$, $p<0.001$) (Fig. 2). For other litter types and mesh sizes, the difference between food forests and grasslands was not statistically significant. When looking at individual litter types, we found that litter mass loss was higher for litter bags with coarse mesh size than fine mesh size for hazel leaves ($df=236$, $t\text{-ratio}=4.91$, $p<0.001$) in grasslands, with a similar trend in food forests ($df=236$, $t\text{-ratio}=3.24$, $p=0.060$) (Fig. 2). For black alder, litter mass loss was also higher for coarse than fine and medium mesh size, but only in grassland sites (coarse vs. fine; $df=236$, $t\text{-ratio}=6.43$, $p<0.001$ and coarse vs. medium; $df=236$, $t\text{-ratio}=4.07$, $p=0.003$) (Fig. 2). For sweet chestnut, litter mass loss was neither impacted by mesh size, nor by land use type. In general, litter mass loss was lower for sweet chestnut than for black alder and common hazel (Fig. 2).

Table 1 Table for the response of litter mass loss to the effects of land use, litter species, mesh sizes and their interactions. The table shows the degrees of freedom (Df), chi-square (χ^2) and P-values based on a type III Wald chi-square test. Significant effects are shown in bold fonts

Parameter	Df	χ^2	P-value
Land use	1	0.29	0.588
Litter species	2	60.30	<0.001
Mesh size	2	3.72	0.155
Land use x litter species	2	0.06	0.969
Land use x mesh size	2	12.01	<0.01
Litter species x mesh size	4	13.34	<0.01
Land use x litter species x mesh size	4	13.03	0.012

Discussion

In this study we investigated how litter quality and the relative contribution of size classes of the decomposer community influenced short-term litter mass loss in food forests and in neighboring grasslands that represented previous land use. We found a three-way interaction between land use, litter quality and mesh size, such that litter mass loss was higher in grasslands than food forests, but only for black alder in coarse mesh size bags that allow access from the entire soil community. For both black alder and hazel, we found that mass loss was higher when the litter was accessible to larger decomposer organisms, but only in grasslands, while for sweet chestnut there was no effect of mesh size or land use on mass loss.

Our first hypothesis was that litter mass loss would be higher in food forests than grasslands, particularly for low-quality litter, because decomposer communities in food forests would have shifted towards communities capable of breaking down a broad range of litter qualities present in the food forest (Keiser et al. 2014; Osburn et al. 2022). In contrast, we found litter mass loss to be higher in grasslands than food forests for the highest-quality litter, i.e., with a low C:N ratio and low lignin content (black alder), while for the lower quality litters there was no difference between land use types. This suggests that the decomposer communities in the grassland sites are functionally different from the food forest sites, but in the opposite direction than we expected. The grassland communities appeared more capable of degrading high-quality black alder litter, at least in the early stages of decomposition, even though they generally do not receive such inputs. This could be because the grassland sites have a high availability of N-rich grass litter providing resources aiding the breakdown of the black alder litter (St. John et al. 2011). For the lower-quality litter, i.e., hazel and sweet chestnut, litter breakdown occurred at similar rates in food forests and grasslands. This implies that both land use types seem to have similar functional breadth despite food forests receiving annual inputs of low-quality tree litter whereas the grasslands generally do not (Osborne et al. 2022). A potential explanation for this unexpected lack of difference is that the food forests were relatively young (5–8 years old). Therefore, even though we did find differences in abiotic and biotic soil properties compared to grassland sites (online Appendix

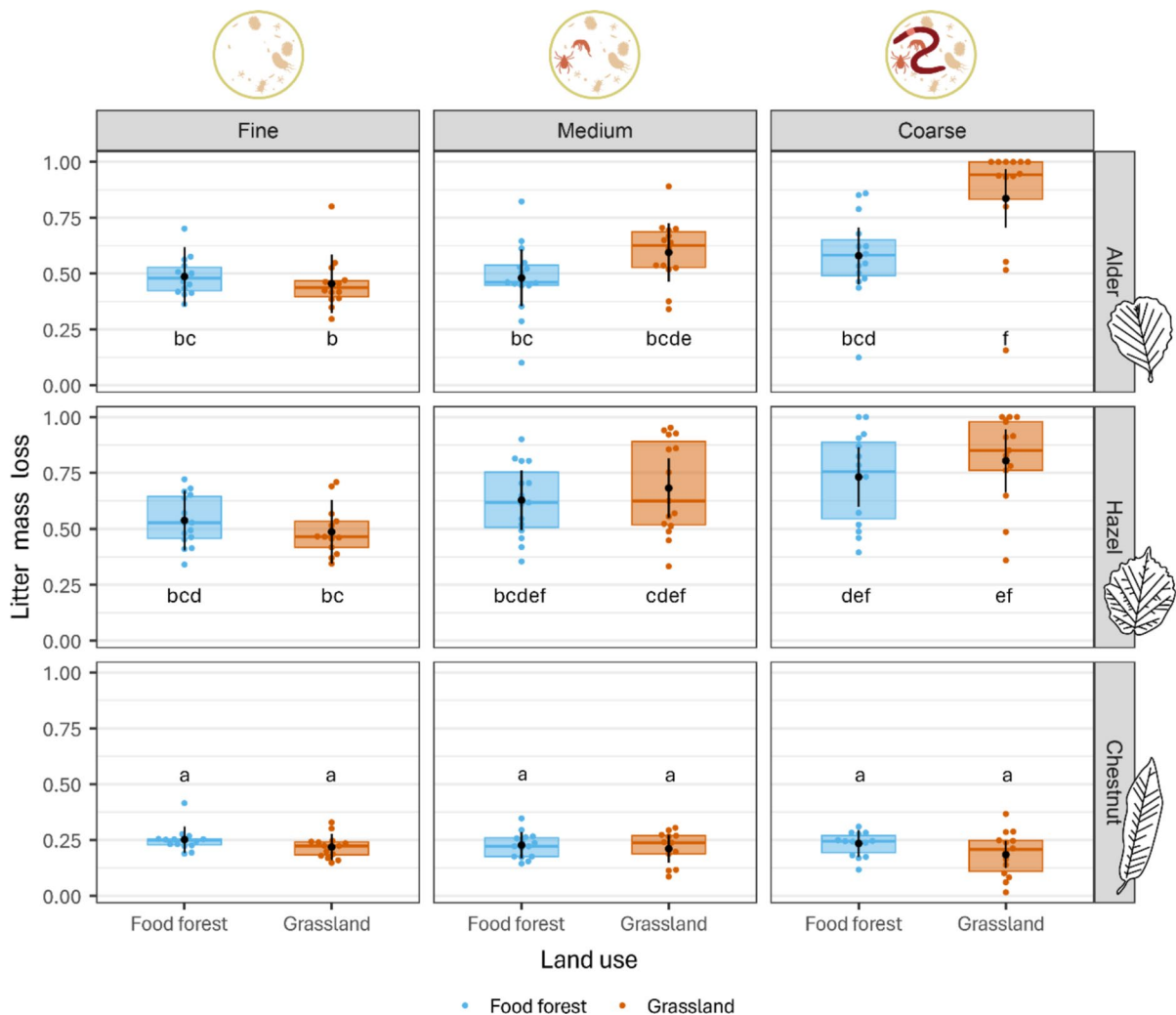


Fig. 2 Boxplots of proportions of litter mass loss grouped per litter species, mesh sizes and land uses. Boxplots represent the median and the interquartile range. Colored dots represent raw data ($n=258$). Black dots and error bars represent (esti-

mated marginal) means and 95% confidence intervals (Sidak-adjusted) per group. Groups not sharing any letter are significantly different by the Tukey-test with 5% level of significance

A3), food forest decomposer communities were perhaps not yet sufficiently adapted to decompose the lower-quality litter more quickly. Indeed, earlier work in other ecosystems has shown that it can take up to decades before decomposer communities are substantially changed after eliminating disturbances (Zaitsev et al. 2006; Kardol et al. 2009; de Groot et al. 2016; Crotty et al. 2023). In our case, we did not (yet) find a higher fungal biomass in food forests than the grasslands that represented their prior land use (online Appendix Table A3.1), while some fungi are known to produce unique enzymes that are needed for the

breakdown of recalcitrant compounds (van der Wal et al. 2013). Further investigation into fungal species present and their decomposition traits (e.g., enzymatic capabilities) could shed more light on the food forest decomposer communities' abilities of breaking down low-quality litter (Leifheit et al. 2024).

Our finding that mass loss of the lowest-quality litter, i.e., sweet chestnut, did not differ between grasslands and food forests might additionally be explained by the way it was presented to the decomposer community. In general, sweet chestnut litter lost less mass than the other litter types, which was expected

because of its high lignin content (28.5% on average) which can limit litter breakdown by N immobilization (Pei et al. 2019). In our study, sweet chestnut litter was presented as a small, homogeneous patch of unattractive litter, easy to avoid for decomposers. Under natural conditions, however, sweet chestnut litter in food forests will be mixed with surrounding litter types as a result of the high diversity of tree species (Moereels et al. 2024), which could aid decomposer organisms to obtain N from surrounding litter types and thereby enhance the decomposition of this low-quality litter (Zhou et al. 2020; Porre et al. 2020). Moreover, for the low-quality litter a longer decomposition experiment might be necessary, because over time the decomposer community could shift from exploitative to more acquisitive resource strategies (Fanin et al. 2020).

Our second hypothesis was that litter breakdown would be enhanced when all size classes of decomposers would be present, particularly for low-quality litter types in food forests. Partly in line with this hypothesis, the mass loss of black alder and common hazel litter was higher for coarse than fine mesh bags, indicating that the presence of a more complete decomposer community stimulated litter breakdown (García-Palacios et al. 2013; Joly et al. 2020). However, in contrast with our expectations, this effect was more pronounced in grasslands than food forests and we did not find this effect for the lowest-quality litter. This may largely be attributable to the activities of earthworms. Earthworms have shown to preferentially feed on high-quality litter (Hedě́nec et al. 2022) and can drastically impact litter mass loss rates (Huang et al. 2020), both directly and indirectly by stimulating bacterial activity (Blouin et al. 2025). The much higher abundance of earthworms in grasslands than food forests (online Appendix Table A3.1) may therefore explain why a higher accessibility of the litter to macrofauna increased litter mass loss more drastically in grasslands than food forests. Still, for common hazel, we did find a trend of a higher mass loss in coarse mesh bags than fine mesh bags in food forests, suggesting that, next to earthworms, other macrofauna, like isopods and millipedes, might stimulate litter breakdown in these systems. The higher abundance of oribatid mites found in the food forests compared to the grasslands did, however, not translate into a higher litter mass loss in medium-sized than fine-sized mesh bags in food forests than grasslands. Probably, the effect of oribatid mites is more indirect via their impact on fungi (Gergőcs and Hufnagel 2016) or it might take

longer for the oribatid mite community to function fully in the food forests (Zaitsev et al. 2006; Kardol et al. 2009). In future research, it will be important to include a wider range of detritivores, such as enchytraeids, isopods and millipedes, to understand which groups are key drivers of litter decomposition in food forests (Joly et al. 2020).

Conclusions

Our results showed that access by a complete decomposer community was favorable for litter breakdown, at least for the two higher-quality litter species, underlining the importance of meso- and macrofauna in the decomposition process. We did not find that litter decomposition was higher in food forests than grasslands, despite changes in soil abiotic and biotic properties, which might be explained by the lack of adaptation of the soil community in the food forest to the more recalcitrant litter types. This could change when food forests age due to further establishment of low-quality litter decomposers. Yet, it could also be that overall decomposition rates remain lower in food forests than for example grasslands, due to the higher presence of lower-quality litters reducing turnover rates (Hedě́nec et al. 2022) and the higher amount of nutrients being locked-up in living biomass (Wardle et al. 2004). Future work could study if and how this might have consequences for the food production goal of the food forest system by directly linking litter decomposition, but also the functioning of mycorrhizal and other symbiotic partners, to nutrient uptake by plants (van't Padje et al. 2021).

Acknowledgements We thank all the owners and managers of the food forest and grassland sites for their cooperation with the field experiment. We would like to extend our gratitude to J.R. van Hal and M.P. Berg for the use of the Tullgren equipment at the Free University of Amsterdam. Moreover, we thank K.M. Wang and N. Koote for their help with counting of the microarthropods. We also thank C. Raaijmakers and F. van Beersum for their assistance in the lab. We are grateful for W.H. van der Putten for reviewing and revising this manuscript.

Author contribution I.Z. and C.V. wrote the funding acquisition and I.Z., G.S. and C.V. were responsible for the conceptualization and methodology of the manuscript. I.Z., G.S. and L.M. collected all the samples and data. I.Z. and G.S. performed the formal analysis and visualized the data. I.Z. wrote the main manuscript text. All authors reviewed the manuscript.

Funding This research was financed by the Dutch Topsector Agri & Food and Horticulture & Starting materials (TKI LWV19184).

Data availability Manuscript data is available through Zenodo (<https://doi.org/10.5281/zenodo.17019218>) and the code is accessible through GitHub, archived at Zenodo (<https://doi.org/10.5281/zenodo.17020388>).

Declarations

Competing interests I.Z. is an unpaid advisory board member of the Dutch Food Forest Association (Stichting Voedselbosbouw Nederland).

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References

- Anderson JM (1973) The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. *Oecologia* 12:275–288. <https://doi.org/10.1007/BF00347567>
- Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. *Nature* 515:505–511. <https://doi.org/10.1038/nature13855>
- Blouin M, Robin A, Amans L et al (2025) A meta-analysis reveals earthworms as mutualists rather than predators of soil microorganisms. *Geoderma* 455:117238. <https://doi.org/10.1016/j.geoderma.2025.117238>
- Bonanomi G, Idbella M, Zotti M et al (2021) Decomposition and temperature sensitivity of fine root and leaf litter of 43 mediterranean species. *Plant Soil* 464:453–465. <https://doi.org/10.1007/s11104-021-04974-1>
- Brooks ME, Kristensen K, Van Benthem KJ et al (2017) glmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378. <https://doi.org/10.32614/RJ-2017-066>
- CBS, PBL, RIVM, WUR (2023a) Jaarlijkse hoeveelheid neerslag in Nederland, 1910–2022 | Compendium voor de Leefomgeving. Accessed 1 Mar 2024 <https://www.clo.nl/indicatoren/nl050809-jaarlijkse-hoeveelheid-neerslag-in-nederland-1910-2022>
- CBS, PBL, RIVM, WUR (2023b) Temperatuur in Nederland en mondiaal, 1907 - 2022 | Compendium voor de Leefomgeving. Accessed 1 Mar 2024 <https://www.clo.nl/indicatoren/nl022615-temperatuur-in-nederland-en-mondiaal-1907-2022>
- Chauvet E (1987) Changes in the chemical composition of alder, poplar and willow leaves during decomposition in a river. *Hydrobiologia* 148:35–44. <https://doi.org/10.1007/BF00018164>
- Cornwell WK, Cornelissen JHC, Amatangelo K et al (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol Lett* 11:1065–1071. <https://doi.org/10.1111/j.1461-0248.2008.01219.x>
- Cragg RG, Bardgett RD (2001) How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. *Soil Biol Biochem* 33:2073–2081. [https://doi.org/10.1016/S0038-0717\(01\)00138-9](https://doi.org/10.1016/S0038-0717(01)00138-9)
- Crawford M (2010) Creating a forest garden. Green Books
- Crotty FV, Demirer UA, Norris SL et al (2023) Evaluating the impact of long-term land use change and age since disturbance on soil faunal diversity. *Forests* 14:1882. <https://doi.org/10.3390/f14091882>
- Fanin N, Alavoine G, Bertrand I (2020) Temporal dynamics of litter quality, soil properties and microbial strategies as main drivers of the priming effect. *Geoderma* 377:114576. <https://doi.org/10.1016/j.geoderma.2020.114576>
- Fox J, Weisberg S (2018) An R companion to applied regression. SAGE Publications, London
- García-Palacios P, Maestre FT, Kattge J, Wall DH (2013) Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecol Lett* 16:1045–1053. <https://doi.org/10.1111/ele.12137>
- García-Palacios P, McKie BG, Handa IT et al (2016) The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. *Funct Ecol* 30:819–829. <https://doi.org/10.1111/1365-2435.12589>
- Gergőcs V, Hufnagel L (2016) The effect of microarthropods on litter decomposition depends on litter quality. *Eur J Soil Biol* 75:24–30. <https://doi.org/10.1016/j.ejsobi.2016.04.008>
- de Groot GA, Jagers op Akkerhuis GAJM, Dimmers WJ et al (2016) Biomass and diversity of soil mite functional groups respond to extensification of land management, potentially affecting soil ecosystem services. *Front Environ Sci* 4:15
- Hartig F (2022) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models
- Heděc P, Jiménez JJ, Moradi J et al (2022) Global distribution of soil fauna functional groups and their estimated litter consumption across biomes. *Sci Rep* 12:17362. <https://doi.org/10.1038/s41598-022-21563-z>
- Howard PJA, Howard DM (1974) Microbial decomposition of tree and shrub leaf litter. 1. Weight loss and chemical composition of decomposing litter. *Oikos* 25:341–352. <https://doi.org/10.2307/3543954>
- Huang W, González G, Zou X (2020) Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: a global meta-analysis. *Appl*

- Soil Ecol 150:103473. <https://doi.org/10.1016/j.apsoil.2019.103473>
- Jílková V, Straková P, Frouz J (2020) Foliage C:N ratio, stage of organic matter decomposition and interaction with soil affect microbial respiration and its response to C and N addition more than C:N changes during decomposition. *Appl Soil Ecol* 152:103568. <https://doi.org/10.1016/j.apsoil.2020.103568>
- Joly F-X, Coq S, Coulis M et al (2020) Detritivore conversion of litter into faeces accelerates organic matter turnover. *Commun Biol* 3:1–9. <https://doi.org/10.1038/s42003-020-01392-4>
- Kardol P, Newton JS, Bezemer TM et al (2009) Contrasting diversity patterns of soil mites and nematodes in secondary succession. *Acta Oecol* 35:603–609. <https://doi.org/10.1016/j.actao.2009.05.006>
- Kassambara A, Mundt F (2020) Factoextra: extract and visualize the results of multivariate data analyses
- Keiser AD, Strickland MS, Fierer N, Bradford MA (2011) The effect of resource history on the functioning of soil microbial communities is maintained across time. *Biogeosciences* 8:1477–1486. <https://doi.org/10.5194/bg-8-1477-2011>
- Keiser AD, Keiser DA, Strickland MS, Bradford MA (2014) Disentangling the mechanisms underlying functional differences among decomposer communities. *J Ecol* 102:603–609. <https://doi.org/10.1111/1365-2745.12220>
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest: package tests in linear mixed effects models. *J Stat Softw* 82:1–26. <https://doi.org/10.18637/jss.v082.i13>
- Leifheit EF, Camenzind T, Lehmann A et al (2024) Fungal traits help to understand the decomposition of simple and complex plant litter. *FEMS Microbiol Ecol* 100:fiac033. <https://doi.org/10.1093/femsec/fiac033>
- Lenth RV (2025) Emmeans: estimated margin2l means, aka least-squares means
- Magnoli SM, Bever JD (2023) Plant productivity response to inter- and intra-symbiont diversity: mechanisms, manifestations and meta-analyses. *Ecol Lett* 26:1614–1628. <https://doi.org/10.1111/ele.14274>
- Moereels L, Bracke J, Mertens J et al (2024) Characteristics of temperate food forestry: a case study in Flanders, Belgium. *Agroforest Syst*. <https://doi.org/10.1007/s10457-024-01052-0>
- Morriën E, Hannula SE, Snoek LB et al (2017) Soil networks become more connected and take up more carbon as nature restoration progresses. *Nat Commun* 8:14349. <https://doi.org/10.1038/ncomms14349>
- Oksanen J, Simpson GL, Blanchet FG et al (2024) Vegan: community ecology package
- Osburn ED, Hoch PJ, Lucas JM et al (2022) Evaluating the roles of microbial functional breadth and home-field advantage in leaf litter decomposition. *Funct Ecol* 36:1258–1267. <https://doi.org/10.1111/1365-2435.14026>
- Pei G, Liu J, Peng B et al (2019) Nitrogen, lignin, C/N as important regulators of gross nitrogen release and immobilization during litter decomposition in a temperate forest ecosystem. *For Ecol Manage* 440:61–69. <https://doi.org/10.1016/j.foreco.2019.03.001>
- Poeplau C, Don A (2015) Carbon sequestration in agricultural soils via cultivation of cover crops – a meta-analysis. *Agric Ecosyst Environ* 200:33–41. <https://doi.org/10.1016/j.agee.2014.10.024>
- Poorter H, Villar R (1997) 2—The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz FA, Grace J (eds) *Plant resource allocation*. Academic Press, San Diego, pp 39–72
- Porre RJ, van der Werf W, De Deyn GB et al (2020) Is litter decomposition enhanced in species mixtures? a meta-analysis. *Soil Biol Biochem* 145:107791. <https://doi.org/10.1016/j.soilbio.2020.107791>
- R Core Team (2024) R: a language and environment for statistical computing
- Rockström J, Edenhofer O, Gaertner J, DeClerck F (2020) Planet-proofing the global food system. *Nat Food* 1:3–5. <https://doi.org/10.1038/s43016-019-0010-4>
- Sarilidiz T (2003) Litter decomposition of *Picea orientalis*, *Pinus sylvestris* and *Castanea sativa* trees grown in Artvin in relation to their initial litter quality variables. *Turk J Agric for* 27:237–243
- St. John MG, Orwin KH, Dickie IA (2011) No ‘home’ versus ‘away’ effects of decomposition found in a grassland–forest reciprocal litter transplant study. *Soil Biol Biochem* 43:1482–1489. <https://doi.org/10.1016/j.soilbio.2011.03.022>
- Tsiafouli MA, Thébault E, Sgardelis SP et al (2015) Intensive agriculture reduces soil biodiversity across Europe. *Glob Change Biol* 21:973–985. <https://doi.org/10.1111/gcb.12752>
- van der Wal A, Geydan TD, Kuyper TW, de Boer W (2013) A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiol Rev* 37:477–494. <https://doi.org/10.1111/1574-6976.12001>
- Veen GF (Ciska), Snoek BL, Bakx-Schotman T, et al (2019) Relationships between fungal community composition in decomposing leaf litter and home-field advantage effects. *Funct Ecol* 33:1524–1535. <https://doi.org/10.1111/1365-2435.13351>
- van't Padje A, Oyarte Galvez L, Klein M et al (2021) Temporal tracking of quantum-dot apatite across in vitro mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. *ISME J* 15:435–449. <https://doi.org/10.1038/s41396-020-00786-w>
- Walvoort DJJ, Brus DJ, de Gruijter JJ (2010) An R package for spatial coverage sampling and random sampling from compact geographical strata by k-means. *Comput Geosci* 36:1261–1267. <https://doi.org/10.1016/j.cageo.2010.04.005>
- Wang Q-W, Pieristè M, Liu C et al (2021) The contribution of photodegradation to litter decomposition in a temperate forest gap and understorey. *New Phytol* 229:2625–2636. <https://doi.org/10.1111/nph.17022>
- Wardle DA, Bardgett RD, Klironomos JN et al (2004) Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633. <https://doi.org/10.1126/science.1094875>
- Zaitsev AS, Wolters V, Waldhardt R, Dauber J (2006) Long-term succession of oribatid mites after conversion of croplands to grasslands. *Appl Soil Ecol* 34:230–239. <https://doi.org/10.1016/j.apsoil.2006.01.005>

- Zhou Z, Wang C, Jiang L, Luo Y (2017) Trends in soil microbial communities during secondary succession. *Soil Biol Biochem* 115:92–99. <https://doi.org/10.1016/j.soilbio.2017.08.014>
- Zhou S, Butenschoen O, Barantal S et al (2020) Decomposition of leaf litter mixtures across biomes: the role of litter identity, diversity and soil fauna. *J Ecol* 108:2283–2297. <https://doi.org/10.1111/1365-2745.13452>

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