



Decomposition constraints in acidified oak forests impacted by N deposition: a litterbag study on microarthropods

Marie-Charlott Petersdorf^{a,*}, Joren Bruggink^a, Maaïke J. Weijters^b, Wilbert L.P. Janssen^a, Wilco C.E.P. Verberk^a, Henk Siepel^{a,c}

^a Department of Ecology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Heyendaalseweg 135, 6525 AJ, Nijmegen, the Netherlands

^b Onderzoekcentrum B-WARE, Mercator III, Toernooiveld 1 (2e verdieping), 6525 ED, Nijmegen, the Netherlands

^c Wildlife Ecology & Conservation, Wageningen University, Droevendaalsesteeg 3a, 6708 PB, Wageningen, the Netherlands

ARTICLE INFO

Dataset link: [Datasets and code: Decomposition constraints in acidified oak forests impacted by N deposition: a litterbag study on microarthropods \(Original data\)](#)

Keywords:

Microarthropods
Decomposition
Litterbags
Feeding guilds
Nitrogen deposition

ABSTRACT

Nitrogen deposition causes soil acidification, which has been shown to slow down decomposition of organic matter in old oak forest stands. To restore this critical ecosystem function, we need to understand the current diversity and functional roles of decomposer organisms. We conducted a 21-month litterbag study in a *Quercus robur* forest in the Netherlands, using 6 different leaf treatments. These included leaves from *Populus tremula* as an easy degradable leaf type or *Quercus robur* leaves. Furthermore, leaves from each species originated from 3 different seasons (spring, summer, autumn). We extracted microarthropods from the litterbags, identified them to species level, and assigned feeding guilds to understand different stages of species establishment of microarthropods during decomposition. We found differences in decomposition rates between treatments, with spring leaves from *Populus tremula* decomposing the quickest and autumn leaves from *Quercus robur* decomposing the slowest. Feeding guild composition also differed significantly between leaf treatments; easily decomposable *Populus* leaves harboured more herbivorous grazers, while more recalcitrant *Quercus* leaves supported greater species diversity and abundance of fungivores, especially in autumn leaves, which had the overall highest microarthropod abundances. These patterns indicate that microarthropod community composition is consistent with different leaf chemistry.

1. Introduction

Nitrogen (N) deposition has been shown to disrupt ecosystem functions. In the Netherlands, 80 % of all Natura 2000 habitats are in poor ecological condition due to the effects of nitrogen deposition (Galloway et al., 2003; Janssen et al., 2020). One important reason for this situation is that N causes acidification and accumulates in ecosystems (Bobbink et al., 2010). This acidification also dissolves active iron and aluminium ions that can bind elements such as phosphorus (P) in inorganic compounds. The relative lack of these nutrients combined with the accumulated N causes nutrient imbalances in the soil (Nijssen et al., 2017; Siepel et al., 2019; Tian and Niu, 2015). In particular, the N/P ratio increases negatively affecting producers and consumers (Sturner and Elser, 2017; Vogels et al., 2024, 2023, 2020).

The Veluwe in the Netherlands is one such highly sensitive forest ecosystem, situated on nutrient-poor sandy soil (de Vries et al., 2019). It represents the largest contiguous area of the protected Natura 2000

network in the Netherlands. The region features various biotopes, with the oldest parts of the forest composed predominantly of different oak species (*Quercus robur*, *Quercus petraea*). The topsoil pH has decreased over the last decades from 4.5 to pH 3, with a base saturation of only 10 % of the pre-deposition level and a strongly increased Al/Ca ratio in the first 10 cm soil (Weijters et al., 2020). Recent research identifies nitrogen deposition and its effects as the main drivers behind the increasing mortality of oak trees, with the complex ecological consequences playing out on many different levels (Bobbink, 2021; Tresch et al., 2025). One key mechanism is the decrease in decomposition rates due to acidification, leading to the accumulation of leaf litter. As a result, essential nutrients remain trapped in the undecomposed organic layer, preventing their reintegration into the food web (Braun et al., 2020). To ensure long-term ecosystem recovery, it is essential to look beyond soil chemistry alone and consider the biological components of the system, particularly the decomposer community. What is the effect of accumulated N and the increased N/P ratio on the potential of restoration of the

* Corresponding author.

E-mail address: marie-charlott.petersdorf@ru.nl (M.-C. Petersdorf).

<https://doi.org/10.1016/j.apsoil.2025.106734>

Received 8 July 2025; Received in revised form 14 December 2025; Accepted 15 December 2025

Available online 20 December 2025

0929-1393/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

decomposer community, mainly dominated by microarthropods?

Microarthropods are a diverse group of small soil-dwelling organisms that play a key role in decomposition and nutrient cycling. These small arthropods are between 0.1 mm and 2 mm and reach high densities in the first 5 cm of the topsoil layer. They contain (sub-) orders from Acari (Oribatida including Astigmatina, Endeostigmata, Mesostigmata, Prostigmata), Hexapoda (Collembola, Protura, and Diplura) as well as some Pseudoscorpions, Pauropods, and Symphylans (Hopkin, 1997; Koch and Hahn, 1831; Weigmann, 2006). Microarthropods contribute actively to the process of leaf litter decomposition both by feeding directly on the organic plant material itself and by stimulating growth of soil microflora (Nielsen, 2019). To increase our understanding of the ecological role of this group, we use the feeding guild classification of Siepel and de Ruiter-Dijkman (1993) for microarthropods based on measured gut enzyme activities, which delineates between species that fed on plants (herbivorous), fungi (fungivorous) or a combination (herbo-fungivorous). In addition, species are classified as grazers when they can digest both cell walls and cell content and as browsers if they are only able to digest cell contents only (e.g. by piercing). Some microarthropods are known to feed on other soil animals (omnivores, general predators). Importantly, fungivorous grazers are able to stimulate decomposition (Siepel, 1994), presumably by recycling nutrients and hence stimulating the growth of soil microflora.

We want to understand the role of different feeding guilds of microarthropods in the process of leaf litter decomposition in an oak forest affected by continuous nitrogen loading. We are interested in chemical composition of leaf treatments as a driver for microarthropod occurrence and contribution to decomposition. For that, we used 6 different leaf treatments. These included leaves from *Populus tremula* as an easy degradable leaf type or *Quercus robur* leaves as being more recalcitrant. Furthermore, leaves from each species originated from 3 different seasons (spring, summer, autumn), resulting in differences in nutrient compositions across leaf treatments. We expect to find differences between the leaf treatments in terms of rate of decomposition and in species composition of microarthropods both between tree species and season, because both processes, decomposition rate and microarthropod occurrence are driven by nutrient availability. We also expect to find differences in species composition over time, as nutrient availability changes with ongoing process of decomposition. Important decomposition stimulating species, such as fungivorous grazers, are expected to increase later in time and to be more dominant in *Quercus* compared to *Populus*.

2. Methodology

2.1. Field site

The experiments were carried out in a private forest stand of Nieuw Dennenlust, a small estate on the Veluwe south of Beekbergen (52°08'52.0"N 5°57'43.4"E). The forest is not accessible to the general public and does not host wild boar. Therefore, the experiment could be carried out without any disturbance of the litterbags. The dominant tree at the experimental plot is *Quercus robur*, and the current forest stand is at least 120 years old. The soil type is a spodic dystrudept (Soil Survey Staff, 1999), or dystric cambisol (IUSS Working Group WRB, 2022) developed in moderately coarse sandy parent material containing about 15 % loam in the deeper soil. Experiments were carried out from November 2022 to August 2024.

Following the weather data of the royal Dutch institute for meteorology, an average yearly temperature of 11.6 °C with 729 mm rainfall was measured for 2022. It was recorded to be a harsh winter and very warm summer with the highest temperature in August. The year 2023 experienced, on average, 11.8 °C and 1060 mm rainfall as the warmest and wettest weather year since measurements. The final year, 2024, recorded an average temperature of 11.8 °C and 986 mm total rainfall ("KNMI - Jaar 2022, 2023"; "KNMI - Jaar 2023," n.d.-b; "KNMI - Jaar

2024," n.d.-c).

2.2. Litterbag set-up

All leaves for this litterbag experiment were collected at the height of 1.5 m – 2 m directly from the tree. We randomly chose several *Quercus robur* and *Populus tremula* trees in the vicinity of the experimental area (52°08'57.0" N 5°57'29.8" E for the oak leaves and 52°10'03.1" N 6°00'41.1" E for the poplar leaves) and sampled their leaves at different seasons of the year: one day in spring, summer and autumn in 2021. Then, all leaves were pooled together among trees per season, oven dried at 70 °C for 24 h in paper bags and put into the litterbags (see litterbag preparation). The same litter material was used in earlier feeding trial experiments with *Platynothrus peltifer*, see Petersdorf et al. (2024).

In the results section in the plots, the treatment types are referred to as their full description: *Quercus robur* spring/summer/autumn and *Populus tremula* spring/summer/autumn. The original abbreviations for the treatments are exclusively used in the statistical analysis. They have been adapted from the project plan, and samples taken before this project: P = *Populus tremula* or Q = *Quercus robur* as the first letter in the treatment code, and V = spring, Z = summer or N = autumn as the second. Table 1 gives the main leaf chemistry data from Petersdorf et al., 2024. For the written text, abbreviations for the trees are used as Q. *robur* (*Quercus robur*) and P. *tremula* (*Populus tremula*).

All litterbags were hand-crafted from a non-decomposable polyamide plastic net material, normally used to protect garden plants from insects. This material has a mesh size of approximately 2 mm to exclude all other arthropods from the decomposition experiments. Each litterbag received a coloured plastic label with one colour per treatment, with its individual sample identifier as a combination of treatment abbreviation and -number 1–60. Litterbags were filled with 5 g (±0.5 g) of dry litter material and closed. In total, 360 litterbags were put into the soil. Though only 240 litterbags were collected for the experiment, an excess of litterbags was used to ensure random sampling at all sampling dates and to account for lost samples in the forest. Any remaining litterbags still buried in the ground after the experiments were finalized were collected and discarded.

Litterbags were set on November 1, 2022 in the first 5 cm of the topsoil with one row of litterbags per treatment. In a marked area, all litterbags of one treatment were put into the soil in random order in a straight line, with approximately 15 cm between litterbags. Lines of litterbags have been placed next to each other, with approximately 50 cm distance to each line. The area was marked visibly to be found again for later sample collection.

Sampling took place 1, 3, 6, 9, 12, 15, 18, and 21 months after placement, where 5 replicates per treatment were sampled.

2.3. Leaf chemistry

Leaves of the six leaf treatment for the litterbags were measured for earlier experiments for Petersdorf et al. (2024), values have been rounded for one decimal place.

Table 1

Measured chemical contents of leaf litter treatments with 2 measurements for phenolics and one measurement for N and P.

Treatment	N [PPM]	P [PPM]	Phenolics [PPM]	SD phenolics
P. <i>tremula</i> spring	283	6.1	4719.7	4.951488
P. <i>tremula</i> summer	222	5.5	3549.7	9.32205
P. <i>tremula</i> autumn	90	5.2	8625.7	34.29311
Q. <i>robur</i> spring	279	5.1	11,466.7	37.13616
Q. <i>robur</i> summer	318	3.2	8689.4	68.84266
Q. <i>robur</i> autumn	156	4.5	14,274.9	25.1244

2.4. Microarthropod extraction and sample procession

Litterbags were placed in a Tullgren funnel set-up at Wageningen University and Research to extract microarthropods following a standard protocol (Siepel and Bund, 1988). After one week of extraction, microarthropods were collected in 70 % ethanol in a plastic vessel and were, together with dried litterbags, brought to Radboud University for further investigation.

Microarthropods were transferred to object cavity slides in lactic acid (20 %) for clarification and species identification. Virtually all microarthropods were identified to the species level (including juveniles). For species with high numbers of juveniles in the litterbags, adults and juveniles were recorded separately. Identification keys used were e.g. Weigmann (2006) for Oribatida, (Karg, 1993) for Gamasina, (Karg, 1989) for Uropodina, and several family and generic keys for Prostigmata, Endeostigmata, and Astigmatina. Nomenclature is according to the checklists of (Siepel et al., 2009) for Oribatida, (Siepel et al., 2016) for Astigmatina, (Siepel et al., 2018) for Mesostigmata, and (Siepel, 2022) for Endeostigmata. For the other groups, <https://www.gbif.org/species/> was used. After microarthropod extraction, litterbags were oven-dried for at least 24 h at 70 °C. After drying, all litterbags were weighed on a micro scale with three decimal places (measured to 0.001 g) to calculate weight loss.

2.5. Data handling microarthropods

Juveniles identified to species were combined with adults, while few unidentified juveniles (e.g., Mesostigmata juv.) were excluded. To address seasonal variations of microarthropod abundances due to weather, proportional species abundances per litterbag were analysed instead of total abundances. For all species in this litterbag study, a feeding guild based on (Siepel and de Ruiter-Dijkman, 1993) was used.

All species that were summed up in 9 feeding guilds; herbivorous

grazer (hg), herbivorous browser (hb), fungivorous grazer (fg), fungivorous browser (fb), opportunistic herbo-fungivore (ohf), herbo-fungivorous grazer (hfg), omnivore (o), general predator (gp) and bacterivores (b). Since the bacterivores just contain the single species *Histioglyphus sapromyzae*, it is referred to as the species name in the result section.

We weighted the litter put into each litterbag and weighted the bag as a whole (litter + bag material). When we calculated the weight loss over time, we used the individual weights per bag (weighted before experiment) and calculated the percentage weight loss per bag to avoid bias due to 10 % difference in litter weight among all litterbags. In Fig. 1, we used remaining mass in percentages, where 100 % are calculated from litterbags pre-experiment weight that were then collected in month 1.

All statistical analysis, data procession, and creation of plots were done in R Studio version 4.5.1 (R Core Team, 2021). To explain decomposition rate, a linear model with log10 transformed remaining mass in percentages (+1) and log10 Month is used, since mass loss was strong in the first few months and slowed down over time. We used month as a numeric variable as months after deployment of litterbags and season2 as the calendar months in the year (Dec, Feb, May, Aug, Nov) as a categorical variable. This model proved to be a good fit (see Supplemental material for tests and R code). For statistical models, leaves from the autumn season were used as a default since the experiment took place in a *Q. robur* stand that received leaves from the autumn season as natural litter fall.

Microarthropod counts varied greatly between replicates, among treatments, and through time. Pearson's correlation coefficient showed that total abundances of microarthropods were positively correlated with more mass remaining in the litterbags because more litter can also support more microarthropods. We checked General additive models (GAM) using counts to also allow for non-linear trends, where models considering the total amount of microarthropods showed a worse fit

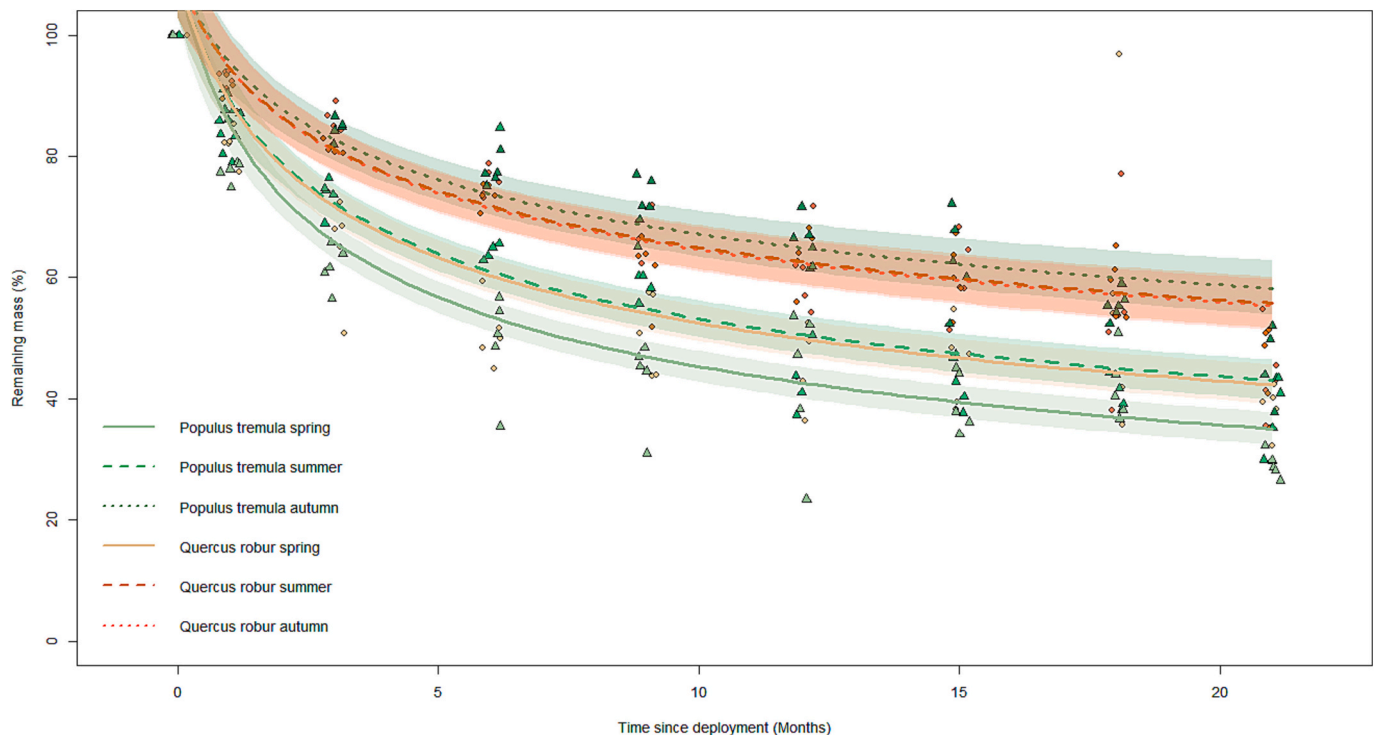


Fig. 1. Decomposition rate of Litterbags as percentage of remaining mass. Remaining weight of litterbags (g) over time since deployment in the soil (Months), fitted with a log-regression model for remaining weight and time, including confidence intervals. The x-axis represents time in months, where month 0 is calculated from the exact same litterbags collected in month 1. All weight differences for litterbags have been calculated per individual litterbag, each data point of all the 5 replicates per treatment per time point are displayed. Circles are litterbags with *Populus tremula* leaves, triangles are litterbags with *Quercus robur* leaves. Each leaf treatment is displayed in its own color as a fitting curve. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with diluted data patterns. GAMs without considering the total amount were sensitive to the fluctuations in total counts. We transformed our total counts of individual species into proportions between 0 and 1 per sample and then summed all individuals up that belonged to a feeding guild as mentioned above. We chose this approach because we are not interested in explaining the variation in counts that is caused by several reasons we did not control for, but instead in researching the species and feeding guild composition. The GAM provided a good fit for non-linear trends over the time for the different feeding guild groups. We did not transform proportions of feeding guilds, which leads to an interdependence between feeding guild proportions per sample, since one proportion is dependent on the other. However, we just tested one feeding guild at a time per model to avoid this negative correlation.

For the GAM, we treated treatment (leaf species-season combination) and season as fixed effects, since these represent specific, controlled experimental conditions. We checked normality and heteroscedasticity by examining the qq-plots beforehand. The GAMs themselves were evaluated by the `gam.check` function. There were no random effects included in the GAMs. We used quasibinomial family with a log-link function. Time as month was modelled with a smooth effect ($k = 8$) which showed to be the best fit for this data. Separate Wilcoxon rank-sum tests were conducted for each time point with *fdr* correction.

The packages *dplyr*, *tidyr*, and *purrr* have been used to prepare data for the analysis (Wickham et al., 2023, 2025; Wickham and Henry, 2025), the packages *ggplot2*, *viridis* and *patchwork* have been used to create figures (Garnier et al., 2024; Pedersen, 2024; Wickham, 2016). For statistical analysis, the packages *lmer*, *MASS* and *mgcv* for GAM models were used (Kuznetsova et al., 2017; Venables and Ripley, 2002; Wood, 2011). To illustrate regression models, the package *visreg* was used (Breheny and Burchett, 2017).

3. Results

Over the course of the experiment, decomposition progressed steadily over time (linear model: $F_{10,236} = 96.0$, $p < 0.001$; $R^2 = 0.80$, adjusted $R^2 = 0.79$). Temporal effects were strong ($\beta = -0.30 \pm 0.06$, $p < 0.001$), indicating consistent weight loss in litterbags. Leaf origin significantly shaped decomposition rates: leaves collected in spring decomposed faster than those from other seasons ($\beta = -0.087 \pm 0.013$, $p < 0.001$), with especially pronounced effects for *P. tremula*. *Populus* leaves from both spring ($\beta = -0.077 \pm 0.019$, $p < 0.001$) and summer ($\beta = -0.100 \pm 0.019$, $p < 0.001$) decomposed significantly faster compared to *Q. robur* leaves from autumn, which decomposed slowest (Fig. 1). Calendar month of deployment (February, May, August, November) did not significantly affect decomposition rates (Supplementary Tables S1–S4). In total, 51,804 individuals were collected from litterbags, comprising 163 species.

Herbivorous grazers displayed a significant non-linear temporal pattern throughout the experiment (GAM: $edf = 5.87$, $F_{6,589} = 8.808$, $p < 0.001$; adjusted $R^2 = 0.277$, deviance explained = 32.1 %). Among treatments, *Populus* leaves collected in spring hosted the highest proportions of herbivorous grazers ($\beta = 0.36 \pm 0.15$, $p = 0.02$) (Fig. 2), in comparison to *Q. robur* leaves from autumn as the default value in the model (Supplementary Tables S5 and S6).

Fungivorous browsers increased significantly over time, reaching their highest proportions during later stages of the experiment.

This temporal pattern was best explained by a generalized additive model with a smooth term for month (GAM: $edf = 2.033$, $F = 18.22$, $P < 0.001$), indicating a significant nonlinear trend (Supplementary Tables S7–S9) (Fig. 3).

Fungivorous microarthropod species richness (guilds *fb*, *fg*, *hfg*, *ohf*) was significantly higher in *Quercus* than in *Populus* litter during several sampling periods. Wilcoxon rank-sum tests performed per month revealed significant differences in month 12 ($W = 52.5$, $p = 0.0263$),

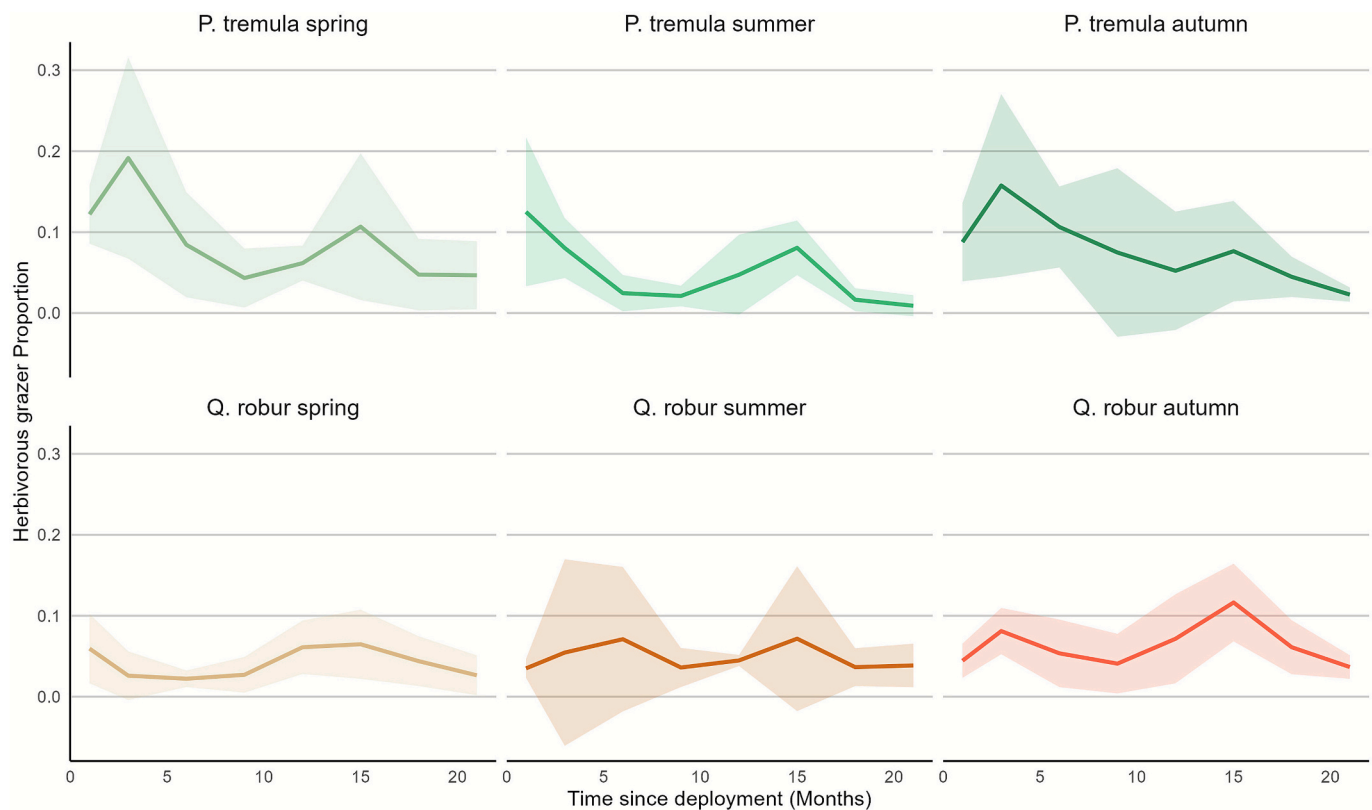


Fig. 2. Proportion of Herbivorous grazer over time per treatment. Proportion of herbivorous grazers over all replicates per treatment per time point of sampling is plotted over time in months. The confidence intervals are calculated across all replicates per treatment per time point.

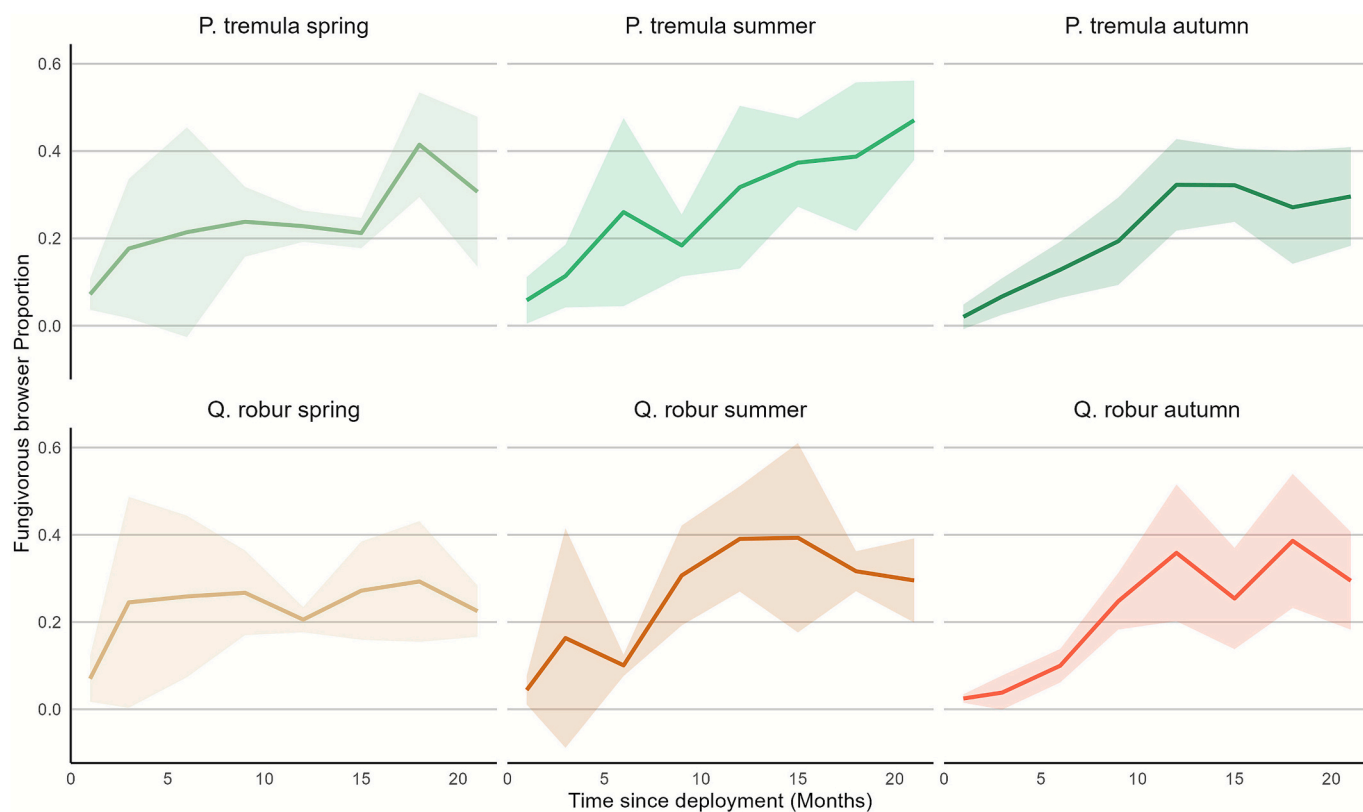


Fig. 3. Proportion of Fungivorous browser over time per treatment. Proportion of fungivorous browser over all replicates per treatment per time point of sampling is plotted over time in months. The confidence intervals calculated across all replicates per treatment per time point.

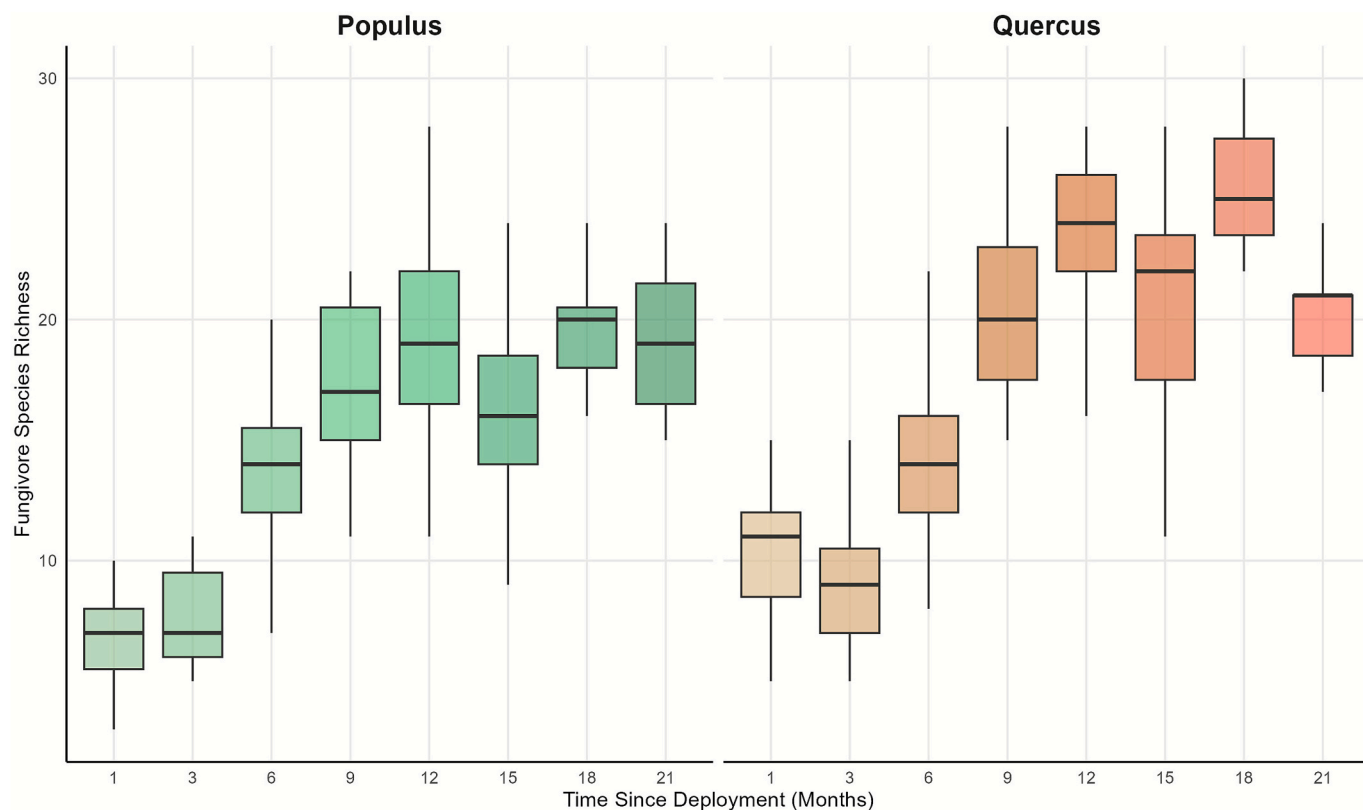


Fig. 4. Species richness of fungivorous microarthropods. Species richness of all fungivorous microarthropods (contains individuals from the feeding guilds fb, fg, ohf, and hfg) over time across all treatments, plotted for leaf species of tree. The species richness is calculated as number of species present (with an abundance higher than 0) per treatment per sampling point.

month 15 ($W = 52, p = 0.0263$), and month 18 ($W = 49.5, p = 0.0263$), indicating consistently higher fungivore richness in *Quercus* samples over time (Fig. 4) (Supplementary Table S10).

Eupodes truncatus (Prostigmata, Eupodidae), a small nematode preferring omnivore, exemplifies the initial high abundance followed by a decline over time for all treatments (Fig. 5, A).

The abundance of *Hypochothonius rufulus* (Oribatida, Hypochothoniidae), feeding on exuviae of Collembola, follows the Collembola abundance, as it increases when Collembola abundance decreases - a pattern seen in all treatments (Fig. 5, B).

4. Discussion

We found clear differences in rates of decomposition between leaf treatments. *Populus* leaves decomposed faster than those from *Q. robur*. *Populus* trees do occur in the Veluwe, but not in our experimental plot. The decomposer community of micro arthropods in this specific location are used to oak tree leaf litter. In fact, decomposition was slowest for autumn *Quercus* leaves, i.e. the natural litter in this ecosystem. In the literature, the so-called “home-field advantage effect” states that home litter decays the fastest within their own home range of trees (Ayres et al., 2009). Our results seemingly contrast this idea, but previous studies researching this effect suggest that, while home-field advantage may play a role, decomposition is also driven by leaf chemistry (Freschet et al., 2012; Veen et al., 2015). *P. tremula* leaves had higher amounts of phosphorus, high amounts of nitrogen and the lowest amount of phenolics compared to leaves from *Q. robur* collected in the same season. Not only could these initial chemical values pre-decomposition explain differences in decomposition rate, but they have also been shown to explain fecundity in feeding trials with the herbivore *Platynothrus peltifer* (Petersdorf et al., 2024) where the same leaf material was used. Thus,

the different chemical composition of leaves affected their nutritional quality and subsequent rate of decomposition.

We used the different treatments to create a gradient of different chemical compositions that was as natural as possible, although we are aware that green leaves collected directly from trees and subsequently left to dry will differ in leaf chemistry from the senescent leaves that make up the leaf litter (Rosenfield et al., 2020). Nevertheless, the gradient in chemical composition allowed us to test the functional role of microarthropod decomposers. Our study took place in an oak forest stand that is impacted by the effects of continuous nitrogen deposition. Since we wanted to isolate the effect of microarthropods on decomposition, we excluded all other fauna with the mesh size of 2 mm for litterbags. Other litterbag studies have either examined microarthropod groups that are mainly predatory and do not directly contribute to leaf litter decomposition (Urbanowski et al., 2021), or found species composition of mites adapting to their habitat (Lindo and Winchester, 2009; Mitchell et al., 2016). Some studies confirmed a species turnover through time in litterbags (Anderson, 1975), with a study from Gergócs et al. (2015) showing how litter quality impacts species composition of mites. This is the first study that examined individuals of microarthropods to the species level and assigned them to feeding guilds, thus allowing us to evaluate their role during the different stages of litter decomposition. Past studies to determine stages of decomposition mainly focused on microbial contribution (Berg, 2014), even though microarthropods are known to have major contributions to leaf litter decomposition (Kampichler and Bruckner, 2009).

Herbivorous grazers in the litterbag experiment strongly preferred *Populus* leaves, being less abundant in litterbags with leaves from *Q. robur*. This pattern is consistent with the feeding trials performed by Petersdorf et al. (2024), which demonstrated that a higher fecundity in the herbivorous grazer *Platynothrus peltifer* when fed *Populus* leaves. This

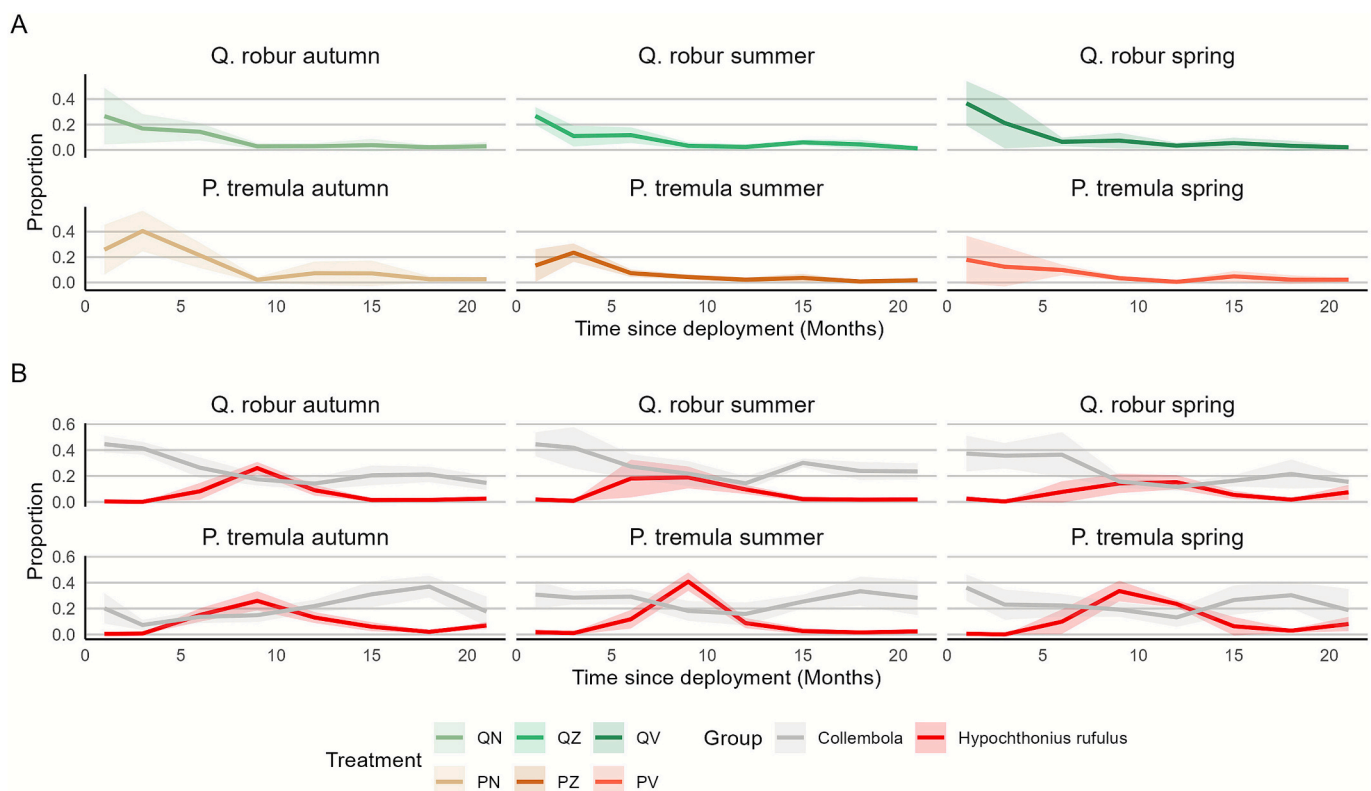


Fig. 5. Proportional abundance for two specific examples of microarthropods in the litterbag experiment: (A) Proportional abundance of *Eupodes truncatus* per leaf treatment plotted over time in months. The confidence intervals are calculated over all 5 replicates per treatment per time point. (B) Proportional abundance of *Hypochothonius rufulus* (in red) and all Collembola species (in grey) for all treatments plotted over time in months. Abundances for both plots include confidence intervals, which are calculated over the 5 replicates per treatment per time point. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pattern suggests that herbivorous grazers may be influenced by leaf chemistry, and that they are potentially deterred by the presence of phenolics. Phenolics are stored in the vacuoles of plant cells (Perry et al., 2008) and they are released when plant tissue gets damaged (Divekar et al., 2022). Herbivorous grazers that feed on the whole plant cell will also unavoidably feed on the vacuoles with the phenols. This likely explains why the highest proportion of herbivorous grazers was observed in leaf treatments with the lowest phenols (*Populus* spring) while the lowest proportion was observed in leaf treatments with the highest phenols (*Q. robur* spring).

Herbivorous grazers play a key role in the early stages of decomposition, establishing themselves as the first microarthropods to break down freshly fallen leaf material. They appeared in high abundance for all *Populus* treatments in the first few months of the experiment. This feeding guild can feed on both plant cell walls (using cellulase) and cell contents (no differentiating enzymes) explaining why these are first on the scene and showing that they will facilitate decomposition. Most of the herbivorous grazers also appeared to have a life-history tactic with slower developmental rates, or are adapted to fairly constant environments (thelytokous reproduction) (Siepel, 1994). This is an indication that it is not their quick life cycle that causes them to arrive as one of the first groups but are crucial to process fresh leaf material before further decomposition by microarthropods can take place.

In the second phase of decomposition, all the easily degradable parts of organic matter have been eaten, and other organisms such as soil fungi become more dominant to degrade what is left by the early arrivals. The growing presence of soil fungi in the litterbags can be inferred from the increase of fungivorous browsers, which have their highest relative abundance across all leaf treatments in the last few months of the experiment. This is because fungivorous browsers, can only digest the cell contents of living fungal cells (Siepel and de Ruiter-Dijkman, 1993). Since slow-growing soil fungi, such as some saprotrophic and most mycorrhizal fungi, take time to colonize the litterbags, this explains why the browsers are only seen in the second phase of decomposition. In contrast to the browsers, fungivorous grazers, did not coincide with fungal colonisation. Instead, the grazers have a high overall presence. These can consume entire fungal cells, including membranes and contents. Thus, grazers are not exclusively dependent on actively growing fungi; they also feed on dead hyphae (Siepel and de Ruiter-Dijkman, 1993). Their high overall abundance likely reflects that these soils typically receive leaves from *Q. robur* that fall to the ground in autumn (therefore, comparable to our *Q. robur* autumn treatment). The decomposition of *Q. robur* leaves from autumn seems strongly dependent on fungi, since fungivore microarthropods make up almost 50 % of all microarthropods through the course of experiments (Fig. 3). We can conclude that fungivorous grazers may be omnipresent year-round and likely happen to walk into the litterbags, without being directly attracted by a newly available food source in the litterbags. Their food source is available through the whole year. For the process of recycling, the fungivorous grazers are especially important, as they can also feed on fungal cell walls. In doing so, they contribute to breaking down structurally resistant fungal biomass, unlocking nutrients that would otherwise remain inaccessible. This function is analogous to the role of sponges in coral reef ecosystems, where sponges recycle dissolved organic matter and retain energy within the reef food web (de Goeij et al., 2013). Similarly, fungivorous grazers support a soil-based microbial loop by mobilizing nutrients trapped in fungal structures, thereby enhancing fungal turnover and sustaining decomposition processes. Their role in recycling energy and facilitating nutrient flow in soils is likely underestimated and merits greater attention in models of soil ecosystem functioning.

While analysing the dataset, we came across two specific examples of microarthropods.

They exhibit a specific lifestyle, enabling them to occupy specific niches during different stages of decomposition and influence nutrient cycling within the litterbag system: *Hypochothonius rufulus* and *Eupodes*

truncatus. *Eupodes truncatus* is known to feed on bacterivorous nematodes (Siepel et al., 2023; Walter, 1987). Bacteria, which are themselves the exclusive food source of the nematodes, are the first organisms in the process of leaf decomposition due to their quick growth rates and their ubiquitous presence in the soil. This mite is an example of a species quickly exploiting an ephemeral resource (Georgieva et al., 2005).

Hypochothonius rufulus food sources were a riddle for a while until Siepel and de Ruiter-Dijkman (1993) confirmed it as an omnivore, while other papers reported it feeds on fungus (Maraun et al., 1998; Schneider and Maraun, 2005).

Its main food source is, in fact, the exuviae (cast-off skin) of arthropods, mainly Collembola species, as these continue moulting during their lives, whereby it does not seem to have any preference for a specific Collembola species. In Fig. 5, it can be seen in grey how Collembola increases in relative abundance, followed by *Hypochothonius rufulus* in red which can increase after its providers moult in the litterbags while growing. Notably, *Hypochothonius rufulus* was shown to be unimpacted by high temperature. This graph also shows this species had its peak abundance during the summer months of our litterbag experiment (months 6–9) (Madge, 1964). Both microarthropod species serve as a good example in pinpointing species establishment not only as a collective phenomenon of overall feeding guilds (that sum up several species) but also in following the different windows of nutrient availabilities from the perspective of microarthropods.

In conclusion, decomposition rates suggest that autumn leaves from *Q. robur* contain such a complex chemical composition to break down that the slow decomposition rate displayed could be the quickest possible under given circumstances, since leaves from *Populus* do decompose quicker in an oak forest stand. We did not test home-field-advantage directly, but can conclude that, in our case, the decomposition rates of the different treatments are reflected in the microarthropod species composition. In particular, microarthropod communities assemble according to the chemical composition of the leaf litter, with *Quercus* leaves displaying the highest species richness and overall abundance of microarthropods. Further, fungivorous microarthropods specialised in feeding on fungi are found significantly higher for treatments containing *Q. robur* leaves. Phosphorus, as a crucial element for all life forms, exhibits a positive influence on decomposition rate overall and showed to be important, at least for herbivorous grazers. With ongoing nitrogen deposition, stoichiometric imbalances will result in a scarcity of phosphorus relative to nitrogen. A promising direction for future research is how phosphorus scarcity in turn decreases decomposer performance, and nutrient turnover rates. Via this cascade of effects, phosphorus scarcity could reinforce the slow decomposition rates observed in *Quercus* litter, creating long-term consequences for forest nutrient cycling and overall ecosystem stability.

CRedit authorship contribution statement

Marie-Charlott Petersdorf: Writing – review & editing, Writing – original draft, Visualization, Project administration, Formal analysis, Conceptualization. **Joren Bruggink:** Writing – review & editing, Investigation. **Maaike J. Weijters:** Investigation, Conceptualization. **Wilbert L.P. Janssen:** Investigation. **Wilco C.E.P. Verberk:** Writing – review & editing, Visualization, Supervision, Formal analysis. **Henk Siepel:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation.

Funding

This work was kindly supported by the Province of Gelderland (Bodemcondities Landelijk gebied (2020-003370), Perceel 2 (2020-013583)).

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgements

Special thanks to Wim Dimmers who gave us access to the Tullgren-funnel facilities at Wageningen University for extracting microarthropods. We also thank Dr. Elke Wenting for logistic support, and proofreading this manuscript. We also thank all staff from B-Ware that supported us in the analysis of our samples.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2025.106734>.

Data availability

New version of repository with corrected data has been published (see list of attachments)

Datasets and code: Decomposition constraints in acidified oak forests impacted by N deposition: a litterbag study on microarthropods (Original data) (Zenodo)

References

- Anderson, J.M., 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *J. Anim. Ecol.* 44, 475–495.
- Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009. Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biol. Biochem.* 41, 606–610.
- Berg, B., 2014. Decomposition patterns for foliar litter—a theory for influencing factors. *Soil Biol. Biochem.* 78, 222–232.
- Bobbink, R., 2021. Effecten van stikstofdepositie nu en in 2030: een analyse.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Corderby, S., Davidson, E., Dentener, F., Emmett, B., Erismann, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59. <https://doi.org/10.1890/08-1140.1>.
- Braun, S., Schindler, C., Rihm, B., 2020. Foliar nutrient concentrations of European beech in Switzerland: relations with nitrogen deposition, ozone, climate and soil chemistry. *Front. For. Glob. Change* 3, 33. <https://doi.org/10.3389/ffgc.2020.00033>.
- Breheny, P., Burchett, W., 2017. Visualization of regression models using visreg. *R J.* 9, 56–71.
- de Goeij, J.M., van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J.J., de Goeij, A.F.P.M., Admiraal, W., 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342, 108–110. <https://doi.org/10.1126/science.1241981>.
- de Vries, W., Weijters, M., de Jong, A., van Delft, B., Bloem, J., van den Burg, A., van Duinen, G.-J., Verbaarschot, E., Bobbink, R., 2019. Verzuuring van loofbossen op droge zandgronden en herstelbaarheid door steenmeeltoediening. VBNE, Vereniging van Bos-en Natuurterreineigenaren.
- Divekar, P.A., Narayana, S., Divekar, B.A., Kumar, R., Gadratagi, B.G., Ray, A., Singh, Achuit Kumar, Rani, V., Singh, V., Singh, Akhilesh Kumar, Kumar, A., Singh, R.P., Meena, R.S., Behera, T.K., 2022. Plant secondary metabolites as defense tools against herbivores for sustainable crop protection. *Int. J. Mol. Sci.* 23, 2690. <https://doi.org/10.3390/ijms23052690>.
- Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *J. Ecol.* 100, 619–630. <https://doi.org/10.1111/j.1365-2745.2011.01943.x>.
- Galloway, J.N., Aber, J.D., Erismann, J.W., Seitzinger, S.P., Howarth, R.W., Cowling, E.B., Cosby, B.J., 2003. The nitrogen cascade. *Bioscience* 53, 341–356.
- Garnier, Simon, Ross, Noam, Rudis, Robert, Camargo, Pedro A., Sciaini, Marco, Scherer, Cédric, 2024. viridis(Lite) - Colorblind-friendly Color Maps for R (Manual). <https://doi.org/10.5281/zenodo.4679423>.
- Georgieva, S., Christensen, S., Stevnbak, K., 2005. Nematode succession and microfauna-microorganism interactions during root residue decomposition. *Soil Biol. Biochem.* 37, 1763–1774.
- Gergöcs, V., Rétháti, G., Hufnagel, L., 2015. Litter quality indirectly influences community composition, reproductive mode and trophic structure of oribatid mite communities: a microcosm experiment. *Exp. Appl. Acarol.* 67, 335–356. <https://doi.org/10.1007/s10493-015-9959-3>.
- Hopkin, S.P., 1997. *Biology of the Springtails (Insecta: Collembola)*. OUP Oxford.
- IUSS Working Group WRB, 2022. World Reference Base for Soil Resources: International Soil Classification System for Naming Soils and Creating Legends for Soil Maps, 4th ed. International Union of Soil Sciences (IUSS), Vienna, Austria.
- Janssen, J.A.M., Bijlsma, R.J., Arts, G.H.P., Baptist, M.J., Hennekens, S.M., de Knecht, B., van der Meij, T., Schaminée, J.H.J., van Strien, A.J., Wijnhoven, S., 2020. Habitatrichtlijnrapportage 2019: Annex D Habitattypen. Wettelijke Onderz. Nat. Milieu Wagening. Environ. Res. Wagening.
- Kampichler, C., Bruckner, A., 2009. The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biol. Rev.* 84, 375–389. <https://doi.org/10.1111/j.1469-185X.2009.00078.x>.
- Karg, W., 1989. *Acari (Acarina), Milben, Unterordnung Parasitiformes (Anactinochaeta)*. Uropodina Kramer, Schildkrötenmilben.
- Karg, W., 1993. *Acari (Acarina), Milben Parasitiformes (Anactinochaeta), Cohors Gamasina Leach, Raubmilben: mit 4 Tabellen*. Fischer.
- KNMI - Jaar 2022, 2023. URL (WWW Document, 2023). <https://www.knmi.nl/nederl-and-nu/klimatologie/maand-en-seizoensoverzichten/2022/jaar>. (Accessed 14 May 2025).
- KNMI - Jaar 2023, 2024. URL (WWW Document, 2024). <https://www.knmi.nl/nederl-and-nu/klimatologie/maand-en-seizoensoverzichten/2023/jaar>. (Accessed 14 May 2025).
- KNMI - Jaar 2024, 2025. URL (WWW Document, 2025). <https://www.knmi.nl/nederl-and-nu/klimatologie/maand-en-seizoensoverzichten/2024/jaar>. (Accessed 14 May 2025).
- Koch, C.L., Hahn, C.W., 1831. Die Arachniden : Getreu nach der Natur abgebildet und beschrieben. In der C. H. Zeh'schen Buchhandlung, Nürnberg. <https://doi.org/10.5962/bhl.title.43744>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lindo, Z., Winchester, N.N., 2009. Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. *Oecologia* 160, 817–825. <https://doi.org/10.1007/s00442-009-1348-3>.
- Madge, D.S., 1964. The water-relations of Belba geniculosa Oudms. and other species of Oribatid mites. *Acarologia* 6, 199–228.
- Maraun, M., Migge, S., Schaefer, M., Scheu, S., 1998. Selection of microfungi food by six oribatid mite species (Oribatida, Acari) from two different beech forests. *Pedobiologia* 42, 232–240.
- Mitchell, R.J., Urpeth, H.M., Britton, A.J., Black, H., Taylor, A.R., 2016. Relative importance of local- and large-scale drivers of alpine soil microarthropod communities. *Oecologia* 182, 913–924. <https://doi.org/10.1007/s00442-016-3688-0>.
- Nielsen, U.N., 2019. *Soil Fauna Assemblages*. Cambridge University Press.
- Nijssen, M.E., WallisDeVries, M.F., Siepel, H., 2017. Pathways for the effects of increased nitrogen deposition on fauna. *Biol. Conserv.* 212, 423–431.
- Pedersen, T.L., 2024. patchwork: The Composer of Plots (Manual).
- Perry, D.A., Oren, R., Hart, S.C., 2008. *Forest Ecosystems*. Johns Hopkins University Press.
- Petersdorf, M.-C., Bruggink, J., de Nijs, E.A., Siepel, H., 2024. Reproductive response of Platyothrus peltifer (CL Koch, 1839) to continuous nitrogen deposition. *Diversity* 16, 340.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Rosenfield, M.V., Keller, J.K., Clausen, C., Cyphers, K., Funk, J.L., 2020. Leaf traits can be used to predict rates of litter decomposition. *Oikos* 129, 1589–1596. <https://doi.org/10.1111/oik.06470>.
- Schneider, K., Maraun, M., 2005. Feeding preferences among dark pigmented fungal taxa ("Dematiaceae") indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). *Pedobiologia* 49, 61–67.
- Siepel, H. and Bund, C.V.D., 1988. The influence of management practices on the microarthropod community of grassland.
- Siepel, H., 1994. Life-history tactics of soil microarthropods. *Biol. Fertil. Soils* 18, 263–278.
- Siepel, H., Cremers, H.J.W.M., Vierbergen, G., 2016. Provisional checklist of the astigmatic mites of the Netherlands (Acari: Oribatida: Astigmatina). *Nederlandse Faunistische Mededelingen* 47, 49–87.
- Siepel, H., Cremers, H.J.W.M., Dimmers, W.J., Loomans, A.J.M., Vierbergen, G., 2018. Checklist of the mesostigmatic mites of the Netherlands (Acari: Mesostigmata). *Nederlandse Faunistische Mededelingen* 51, 115–188.
- Siepel, H., de Ruiter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on their carboxylase activities. *Soil Biol. Biochem.* 25, 1491–1497.
- Siepel, H., Zaitsev, A., Berg, M.P., 2009. Checklist of the oribatid mites of the Netherlands (Acari: Oribatida). *Nederlandse faunistische mededelingen* 30, 83–112.
- Siepel, H., Bobbink, R., van de Riet, B.P., van den Burg, A.B., Jongejans, E., 2019. Long-term effects of liming on soil physico-chemical properties and micro-arthropod communities in Scotch pine forest. *Biol. Fertil. Soils* 55, 675–683.
- Siepel, H., 2022. Checklist of the endostigmatic mites of the Netherlands (Acari: Sarcotiformes: Endeostigmata). *Nederlandse Faunistische Mededelingen* 59, 57–64.
- Siepel, H., Baas, W., Jongejans, E., den Ouden, J., Veen, C., 2023. Effecten van strooisel van de Amerikaanse vogelkers op het bodemleven. *Vakbl. Nat. Bos Landsch.* 196, 14–17.
- Soil Survey Staff, 1999. *Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys*. In: *Agriculture Handbook No. 436*, 2nd ed. United States Department of Agriculture, Natural Resources Conservation Service, Washington, D.C.

- Sterner, R.W., Elser, J.J., 2017. Ecological stoichiometry. In: *Ecological Stoichiometry*. Princeton university press.
- Tian, D., Niu, S., 2015. A global analysis of soil acidification caused by nitrogen addition. *Environ. Res. Lett.* 10, 024019.
- Tresch, S., de Witte, L.C., Hopf, S.-E., Schindler, C., Rihm, B., Braun, S., 2025. Drought and N deposition impact roots and ectomycorrhizal colonisation of European beech down to deep soil layers. *Appl. Soil Ecol.* 210, 106055.
- Urbanowski, C.K., Horodecki, P., Kamczyc, J., Skorupski, M., Jagodziński, A.M., 2021. Does litter decomposition affect mite communities (Acari, Mesostigmata)? A five-year litterbag experiment with 14 tree species in mixed forest stands growing on a post-industrial area. *Geoderma* 391, 114963.
- Veen, G.F., Freschet, G.T., Ordonez, A., Wardle, D.A., 2015. Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos* 124, 187–195. <https://doi.org/10.1111/oik.01374>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, 4th ed. Springer, New York.
- Vogels, J., Weijters, M., Bobbink, R., Bijlsma, R., Lamers, L.P.M., Verberk, W.C.E.P., Siepel, H., 2020. Barriers to restoration: soil acidity and phosphorus limitation constrain recovery of heathland plant communities after sod cutting. *Appl. Veg. Sci.* 23, 94–106. <https://doi.org/10.1111/avsc.12471>.
- Vogels, J., Van De Waal, D.B., WallisDeVries, M.F., Van Den Burg, A.B., Nijssen, M., Bobbink, R., Berg, M.P., Olde Venterink, H., Siepel, H., 2023. Towards a mechanistic understanding of the impacts of nitrogen deposition on producer–consumer interactions. *Biol. Rev.* 98, 1712–1731. <https://doi.org/10.1111/brev.12972>.
- Vogels, J., Verberk, W.C.E.P., Kuper, J.T., Weijters, M.J., Verbaarschot, E., Lamers, L.P.M., Siepel, H., 2024. Nitrogen deposition and heathland management cause multi-element stoichiometric mismatches, reducing insect fitness. *Funct. Ecol.* 38, 2537–2552. <https://doi.org/10.1111/1365-2435.14671>.
- Walter, D.E., 1987. Trophic behavior of "mycophagous" microarthropods. *Ecology* 68, 226–229.
- Weigmann, G., 2006. Hornmilben (Oribatida): Acari, Actinochaetida. Goecke & Evers Keltern, Keltern.
- Weijters, M., Siepel, H., Bobbink, R., 2020. Selectie en uitzetten steenmeeltrials voor herstel van Oude Eikenbossen op arme zandgronden (H9190) (No. RP-19.167.20.56). Onderzoekcentrum B-WARE, Nijmegen.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Wickham, H., Henry, L., 2025. *purrr: Functional Programming Tools (Manual)*.
- Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., 2023. *dplyr: A Grammar of Data Manipulation (Manual)*.
- Wickham, H., Vaughan, D., Girlich, M., 2025. *tidyr: Tidy Messy Data (Manual)*.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73, 3–36.